Mirza Hasanuzzaman *Editor*

Plant Ecophysiology and Adaptation under Climate Change: Mechanisms and Perspectives I

General Consequences and Plant Responses

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This book is dedicated to
Prof. Dr. Md. Fazlul Karim *(left)*
and
Prof. Dr. Md. Rafiquel Islam *(right)*
of Sher-e-Bangla Agricultural University,
Dhaka
who inspired me in the journey of teaching.

Preface

Impact of climate change is expected to be broadly negative, including reduced water availability, salinity, flood, and infestation of pests and diseases. Due to the significant climate change over the centuries, the incidence of various abiotic stresses such as salinity, drought, extreme temperature, atmospheric pollutions, and metal toxicities regularly affect plant life and productivity. Many crops perform only at 30% of their genetic potential under adverse environmental conditions. The predictable loss of crop production is as much as 70% in an average and might be 100% in extreme cases. The resulted economic loss caused by environmental stress is a great concern in agriculture.

To sustain productivity against the environmental stresses, the crucial importance is to know and understand the plants-specific responses to the different environmental factors. Plant ecophysiology is the science of interaction of plants with the environment, and the vital underlying acclimation and adaptation processes. The off-putting effects of abiotic stresses result in alteration in plant metabolism and physiology, which challenge survival, productivity, reproductive biology, and reproducibility. These adverse effects result from structural and functional alteration of cellular components of plant. Structural alterations of cellular organelles due to environmental stresses cause alteration in physiological processes, such as water entrance and transportation, nutrient uptake, chloroplast functioning, photosynthetic efficiency, mitochondrial activity, vacuolar structure and function, and the altered structure of nucleus cause genetic modification. The physiology and adaptive mechanisms of plants are greatly varied in different species and genotypes. The ability of various plant groups to tolerate the extremes posed by natural conditions and/or chemically rich environments involves morphological and physiological adaptation as well as changes in ecological behavior to sustain in relatively protected niches within an extreme environment.

To survive under environmental extremity, plants respond at the molecular, cellular, and physiological level, which involves a complex network supporting perception and transmission of stress signals, which subsequently initiate a plethora of responses. Against different kinds of stress-induced responses, there are two broad outcomes: programmed cell death (PCD) or stress acclimation. The PCD is considered a lethal effect whereas acclimation often leads to adaptation to certain adverse environmental stresses, which sustain plant survival and productivity. A deeper understanding of the mechanisms underpinning plant stress adaptation may offer novel opportunities to develop crop plants with an enhanced ability to tolerate environmental fluctuations, which are the focal points of concern of plant ecophysiological study. In modern concept, the survival mechanism and potential of plants are not left behind as a natural process. Rather how the adaptation process can be enhanced is a great concern of scientists of the related fields. In present perspectives, scientists are manipulating the surrounding environment of target plants so that the plant can be less affected by natural environmental stresses. Use of a broad range of exogenous phytoprotectants including plant nutrients, trace elements, phytohormones, and signaling molecules, probiotic microorganisms to improve adaptation processes of plants are being explored day by day. Scientists are going through the genetic manipulation and biotechnological processes to sustain plant productivity under the adverse environmental conditions. Much progress has been gained in the last few decades in the area of plant ecophysiology research and on their adaptive mechanisms. Although there are numerous publications in journal and proceedings, there is a scarcity of a comprehensive book dealing with both ecophysiology and adaptive mechanisms of plants under climate change.

This is the first volume of the two-volume book, *Plant Ecophysiology and Adaptation under Climate Change: Mechanisms and Perspectives* that provides current state-of-the-science knowledge of plant ecophysiology, with particular emphasis on adaptation to a changing environment. This volume will provide the reader with a wide spectrum of information, including vital references. This is done through 29 chapters written by hundreds of experts in the field of Botany, Plant physiology, Ecology, Crop science, and Environmental sciences, ultimately aiming to become a useful information tool for plant biologists, crop scientists, ecologists, plant breeders as well as a guide for students in the field of Plant Science, Agriculture and Environmental Sciences.

I like to give special thanks to the authors for their outstanding and timely work in producing such fine chapters. Our profound thanks also go to Mr. Sayed Mohammad Mohsin, Dr. M.H.M. Borhannuddin Bhuyan, Ms. Khurshida Parvin, Dr. Kamrun Nahar, Khussboo Rahman, Khadeja Sultana Sathi, and Mr. Abdul Awal Chowdhury Masud, for their critical review and valuable support in formatting and incorporating all editorial changes in the manuscripts. I am highly thankful to Ms. Lee, Mei Hann, Editor (Editor, Life Science), Springer, Japan, for her prompt responses during the acquisition. I am also thankful to Sivachandran Ravanan, Project Coordinator of this book, and all other editorial staffs for their precious help in formatting and incorporating editorial changes in the manuscripts.

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About the Editor

Mirza Hasanuzzaman is Professor of Agronomy at Sher-e-Bangla Agricultural University in Dhaka, Bangladesh. He received his PhD in *Plant Stress Physiology and Antioxidant Metabolism* from the United Graduate School of Agricultural Sciences, Ehime University, Japan, as a recipient of a scholarship from the Japanese Government (MONBUKAGAKUSHO). Later, he completed his postdoctoral research at the Center of Molecular Biosciences, University of the Ryukyus, Okinawa, Japan, as a recipient of the Japan Society for the Promotion of Science (JSPS) postdoctoral fellowship. Subsequently, he received the Australian Government's Endeavour Research Fellowship for postdoctoral research as an Adjunct Senior Researcher at the Tasmanian Institute of Agriculture, University of Tasmania, Australia. Mirza Hasanuzzaman has supervised 20 MS students. His current work is focused on the physiological and molecular mechanisms of environmental stress tolerance. Prof. Hasanuzzaman has published over 120 research publications in peer-reviewed journals. He has edited 12 books and written 45 book chapters on important aspects of plant physiology, plant stress responses, and environmental problems in relation to agricultural plants. According to Scopus®, Prof. Hasanuzzaman's publications have received roughly 4800 citations with an h-index of 37 (As of April 2020). He is an editor and reviewer for more than 50 peer-reviewed international journals and was a recipient of the

"Publons Peer Review Award 2017, 2018 and 2019." He has been honored by different authorities for his outstanding performance in different fields like research and education, and has received the World Academy of Sciences Young Scientist Award (2014). He has attended and presented 25 papers at international conferences in many different countries (the USA, the UK, Germany, Australia, Japan, Austria, Sweden, Russia, Indonesia, etc.). Prof. Hasanuzzaman is an active member of 40 professional societies and is currently the Acting Research and Publication Secretary of the Bangladesh JSPS Alumni Association. He is also a fellow of The Linnean Society of London.

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Chapter 1
Climate Change Influences the Interactive Effects of Simultaneous Impact of Abiotic and Biotic Stresses on Plants

Ewa Surówka, Marcin Rapacz, and Franciszek Janowiak

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Since it is not feasible to formulate a comprehensive overview as the intricacy and immensity of the considered subject surpass the scope of this contribution, the chapter focuses on outlining the essential issues without an in-depth description of the underlying mechanisms.

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Abstract Under natural conditions, the defense responses of plants exposed to combined abiotic and biotic stress factors, which can randomly interact with each other, are in many aspects different from the response induced by an individual stress. Predicted climatic changes through affecting these simultaneously occurring interactions might change the microclimate surrounding plants, plants' susceptibility, the range of host microorganisms (i.e., symbionts or pathogens), and their simultaneous interaction with plants. The influence of climate change on interactions between environmental stresses and plants can lead to positive or negative impacts of one stress on the others and cause changes in strategies adopted by plants—either negative (i.e., susceptibility) or positive (i.e., tolerance)—thus causing modifications of primary and secondary metabolism of plants. Primary metabolism plays a key role in plants' adaptive/defense response through the influence on the modulation of secondary metabolism and the activation of the host's various defense mechanisms. Alterations in primary and secondary metabolism might include changes in the availability of nutrients, metabolically active compounds, or in carbon (C) and nitrogen (N) metabolism and C/N balance.

Keywords Climate change · C/N balance · Endophytes · Habitats · Holobiont · Invasive plants · Metaorganism · Microbiome · Rhizomicrobiome · Soil-plant-microbial interaction

Abbreviations

ACC deaminase	1-aminocyclopropane-1-carboxylate deaminase
AMF	Arbuscular mycorrhizal fungi
APSA	The Asia and Pacific Seed Association
Avr gene	Avirulence gene
CAM	Crassulacean acid metabolism
CC	Coiled-coil N-terminal domain
CCM	CO_2-concentrating mechanism
DAMPs	Damage-associated molecular patterns
eCO_2	Atmospheric CO_2 concentration
ET	Ethylene
ETI	Effector-triggered Immunity or R gene-mediated effector-triggered immunity
FAO	Food and Agriculture Organization of the United Nations
GCC	Global climate changes
GHG	Greenhouse gases
GLOBIO	Global Biodiversity model for policy support
HR	Hypersensitive response
IPCC	Intergovernmental Panel on Climate Change
ISR	Immune systemic resistance

ITPS	Intergovernmental Technical Panel on Soils
JA	Jasmonic acid
MAMPs	Microbial-associated molecular patterns
NB-LRR	Nucleotide binding (site)-leucine-rich repeat proteins
Oxfam	Oxford Committee for Famine Relief
Pacific ENSO	Pacific El Niño–Southern Oscillation
PAMPs	Pathogen-associated molecular patterns
PRRs	Membrane-bound pattern recognition receptors
PTI	PAMP-triggered immunity
SA	Salicylic acid
SAR	Systemic acquired resistance
TIR	Toll and interleukin-1 receptor type
UNFCCC	United Nations Framework Convention on Climate Change
WMO	World Meteorological Organization
WUE	Water use efficiency

1.1 Introduction: Climate Change Alters Habitats and Affects Ecosystem Functioning

According to specialists' predictions, in the coming decades, alterations in the interactive effects of simultaneous impact of abiotic and biotic stresses on plants due to global climate changes delineated by UNFCCC seem unavoidable. Such prognoses are based on climate prediction models of IPCC indicating that average surface temperatures will rise by about 3–5 °C in the next 50–100 years, as well as that precipitation will increase by up to 1.0% for mid- and high-latitude areas and 0.3% for tropical zones (IPCC 2013, 2018; Christensen et al. 2013; Pachauri et al. 2014; Hoegh-Guldberg et al. 2018). The rising temperatures across the globe are caused by GHG of natural and anthropogenic origin, majority of which is atmospheric carbon dioxide (CO_2), indicated as showing a consistent, almost linear correlation between its cumulative emissions and projected global temperature. CO_2 concentration has surged by over 40% since the industrial revolution, and it is predicted to increase further up to 770 ppm in 2100 (compared to present concentration of around 400 ppm), while the level of 450 ppm of CO_2 [atm] has been suggested as a critical threshold which would cause an increase in the global mean temperature of 2 °C above preindustrial values (Ahanger et al. 2013; IPCC 2013; Mahato 2014; Pachauri et al. 2014; FAO and ITPS 2015; Lefevre et al. 2017; Challinor et al. 2018; Winkler 2019). The extent and intensity of climate-related factor changes (e.g., rising of atmospheric CO_2 level, atmospheric N deposition, elevated temperature, altered rainfall or moisture, pressure, light intensity) and the interactions among multifactorial stress combinations are predicted to increase in the next decades (IPCC 2013, 2018; Pachauri et al. 2014; Hoegh-Guldberg et al. 2018).

The consequences of climate variability lead to the creation of environmental change conditions—frequent and extreme weather phenomena such as heat waves, drought, salinity, alkaline/acid soils, floods, sea level rise, and ocean acidification. They will cause direct/indirect and positive/negative effects on living organisms such as alterations in species composition and range; species invasions and extinctions; phenology, biodiversity, and ecosystem regime shifts; as well as the generation of new interactions in novel communities, novel intra- and interspecies interactions among plants and microbial communities, and changed feedback processes which may in turn affect species dynamics and interactions and can lead to altered ecological processes and ecosystem functions (van der Putten et al. 2013; Classen et al. 2015; Ravichandran and Thangavelu 2017; Hassani et al. 2018; Hawkins and Crawford 2018; Hoegh-Guldberg et al. 2018; Winkler 2019).

Although the resistance of organisms and ecosystems is highly changeable, climate-dependent biological alterations are likely to be commensurately quick (Brierley and Kingsford 2009; Lee et al. 2009; Pachauri et al. 2014; Classen et al. 2015; Zhang and Sonnewald 2017; Cassia et al. 2018). It has been shown that climate change is already altering many wildlife habitats not only locally but also all over the world and some species and whole ecosystems have already been lost. Consequently, biological alterations from genes to whole ecosystems (including land and marine ecosystems) in most regions of the globe will continue to proceed (Hansen et al. 2007; Galland et al. 2012; Smith et al. 2015; Karmakar et al. 2016; Llado et al. 2017; Hutchins and Fu 2017; Makinen et al. 2017; Santoyo et al. 2017), though these changes are unpredictable as climate-related systems/factors are nonlinear (Lenton et al. 2008; Lenton 2012; Challinor et al. 2018).

Climate variations can lead to severely transformed ecosystems with new dominant species and new ways in which soil and organisms interact (van der Putten 2012; van der Putten et al. 2013; Classen et al. 2015; Ravichandran and Thangavelu 2017; Hassani et al. 2018; Hawkins and Crawford 2018). Global climate change could lead to irreversible or catastrophic consequences in ecosystems (Llado et al. 2017; Santoyo et al. 2017).

1.2 New Ecological Entities “Metaorganism” and “Holobiont”

Natural communities are composed of individual organisms (plants, animals, and microorganisms living in an environment determined by physical conditions/abiotic factors) interacting among themselves and composing a complete ecosystem. Every species shows multiple levels of organization across biological units. They are linked directly or indirectly with a multitude of other species through many different types of highly integrated functional interactions with beneficial, neutral, or harmful effects, and they exert a crucial influence on the functioning and health of individual species, communities, and whole ecosystems (Luttge 2012, 2013;

Matyssek and Luttge 2013; Souza and Luttge 2015; Mitter et al. 2016; Souza et al. 2016). Ecosystems as complex systems tend to show cyclic fluctuations around approximate equilibrium state and undergo inevitable and dynamic alterations when climate change occurs or when new species appear as a result of migration, evolution, or human activity (Classen et al. 2015; Vandenkoornhuyse et al. 2015; Luttge and Thellier 2016; Bang et al. 2018).

The interdependence between multi-organismic associations in the ecosystem, including (1) individual organisms showing a high degree of internal functional integration as well as (2) dynamic communities of microorganisms being an essential and vital part of the functionalities of individual organisms or the whole ecosystem, is often established through their coexistence in ecological and evolutionary dimensions. This view led to the creation of the concept of a metaorganism (Bosch and McFall-Ngai 2011; McFall-Ngai et al. 2013; Vandenkoornhuyse et al. 2015; de Souza and Fiocchi 2016; Theis et al. 2016; Bang et al. 2018; Morris 2018; zu Castell et al. 2019). Multi-organismic cooperation which comprises a host organism (i.e., different plant tissues/organs and plant seeds) and its specific endocellular and extracellular associated microbiome (e.g., viruses, phages, eubacteria, archaea, fungi, protozoa) has been termed a holobiont (Mendes et al. 2013; Castell et al. 2016; Mitter et al. 2016; Smith and Dukes 2017; Morris 2018; Rosenberg and Zilber-Rosenberg 2018; Ying-Ning et al. 2017; zu Castell et al. 2019) and can function as an actual platform of selection and coevolution (anatomically, metabolically, immunologically, or developmentally) (Vandenkoornhuyse et al. 2015; Fladung 2016; Rosenberg and Zilber-Rosenberg 2018). The health and oftentimes the survival of the majority of holobionts depend on the network of interactions between all of their members (Mitter et al. 2016; Carrier and Reitzel 2017; Rosenberg and Zilber-Rosenberg 2018). Holobiont is represented by its hologenome consisting of two complementary components, host genome—highly conserved and microbiome genome—dynamic and effectively and rapidly changing, in response to environmental conditions, which might be selected for or against, thus enabling the promotion of acclimation and adaptation to changing environmental conditions (Berg et al. 2014; Souza and Luttge 2015; Larranaga and Ignacio Hormaza 2016; Souza et al. 2016; Rosenberg and Zilber-Rosenberg 2018; zu Castell et al. 2019). Thus, plant adaptation through genetic accommodation includes the variability of both mutualist-induced and epigenetically induced plasticity in the holobiont. Genetic accommodation and adaptation can impact both plant genome and all components of the holobiome, including genetic variability of microbiota, and is related to the occurrence of phenotypic variation induced by mutualists (Vannier et al. 2015; Carrier and Reitzel 2017; Ilangumaran et al. 2018). The evolutionarily advantageous development of relationships and cooperation among the components of the holobiont makes it possible to withstand environmental challenges (Smith and Dukes 2017; Ilangumaran et al. 2018). However, it should be noted that it is still under discussion whether metaorganisms constitute a hologenome as a unit of selection or whether they consist of separate entities which evolve independently (Carrier and Reitzel 2017).

1.3 Climate Change Affects Natural Habitats and Biodiversity of Plants and Microorganisms

The nature and type of vegetation are related to the availability of habitats, which are determined by latitudes and environmental factors (e.g., soil, light intensity, temperature, climate cycles). It is well established that with increasing latitudes, natural resources change, causing a decline of functional diversity of individual organisms, population, species, community, ecosystem, and biome scales (Rohde 1992; Cong et al. 2016). Additionally, rapid climate changes are anticipated to affect all the levels of biodiversity (decline or increase), from organism to biome levels (Sax and Gaines 2003; Dornelas et al. 2014; McGill et al. 2015; Gonzalez et al. 2016). As a consequence of the processes of biome or ecosystem degradation, the disruption of natural plant communities often coincides with or is preceded by a loss of physicochemical and biological soil properties.

1.3.1 Physicochemical Soil Properties

Soil is an integral structural part of every terrestrial ecosystem, substantially influencing biomes. Soil plays many important functions such as (1) affecting water quantity and quality; (2) providing water and nutrients, and functioning as a terrestrial regulator of carbon (C) and nitrogen (N) cycles according to the new climate regime established by the Paris Agreement of December 2015; (3) allowing an exchange of CO_2, oxygen, and other gasses (including GHG) which affect root growth and soil organisms; (4) providing physical support for plant vegetation and supporting a wide diversity of microbial, flora, and fauna taxa; (5) providing a substrate for organisms linked with vital ecosystem processes; and (6) influencing the harboring of root diseases and other pests (Makinen et al. 2017; Santoyo et al. 2017). The nature of soil habitats is affected by a complex interplay of direct and indirect interactions among soil properties.

The key potential changes in soil-forming factors and/or disturbances in the complex interplay of environmental factors that directly result from GCC could be in organic matter supply from biomass and the quality and quantity of resource input, alteration in the dominant soil type, and essential physicochemical soil properties (e.g., pH value, soil temperature regime, soil hydrology, the range of equilibrated mineral nutrient cycles/mineral nutrient limitations) (Smith et al. 2015; Karmakar et al. 2016; Llado et al. 2017; Makinen et al. 2017; Santoyo et al. 2017).

1.3.2 Soil Influence on Microbiota and Plant Diversity

It is well established that soil physicochemical properties, including soil pH, which is the master variable, affect many properties of the ecosystem, e.g., through changes in microorganism habitats and microorganism species composition such as bacteria, actinomycetes, fungi, algae, and protozoa in different physiological states (Blagodatskaya and Kuzyakov 2013; Lian et al. 2019; Tripathi et al. 2018) or through alterations in biomass or activities of soil microbial communities as well as microbial interactions like competition for resources including C and N (Balser et al. 2002; Wardle et al. 2006; van der Putten et al. 2007a; Raizada et al. 2008; Rengel 2011; Bach et al. 2018; Maron et al. 2018; Quatrini and Johnson 2018; Tripathi et al. 2018). A typical gram of soil has been suggested to contain about 9×10^7 bacteria, 2×10^5 fungi, 4×10^6 actinomycetes, 3×10^1 nematodes, 5×10^3 protozoa, and 3×10^4 algae. It has also been shown that soil pH plays an important role in bacterial and fungal growth and microbial biomass and composition and that most bacteria prefer nonacid microhabitats (Rousk et al. 2009; Ravichandran and Thangavelu 2017; Bach et al. 2018). The total microbial biomass is usually estimated at 50–2000 $\mu g\ C\ g^{-1}$ soil, and this is about 2–3% up to/not exceeding 4.5% of organic C content (Blagodatskaya and Kuzyakov 2013), and 10 g of soil holds about 10^{10} bacterial cells, representing upward of 10^6 species (Gans et al. 2005; Schloss and Handelsman 2006). According to Wang et al. (2017), healthy soils, when compared to infected soils, exhibit both higher diversity and content of beneficial microorganisms promoting plant growth as well as preventing plant diseases. Moreover, soil pH also affects soil enzyme activity, which may influence litter decomposition and alter soil nutrient availability (especially pools of C, N, and phosphorus (P)), dynamics of carbon and nitrogen cycles, ionic composition of soil solution, and aeration capacity (Sardans and Penuelas 2015; Ravichandran and Thangavelu 2017). Also, the richness and distribution of plant species are determined by soil physicochemical properties, particularly soil pH values (Gough et al. 2000; Cong et al. 2016; Llado et al. 2017).

In addition, Hou et al. (2018) estimated that climate change affects soil phosphorus cycle and the availability of P in global land ecosystems. It has been shown that soil-available PI, indexed by Hedley labile inorganic P fraction, fell significantly with rising mean annual temperature and rainfall. Authors also postulate that temperature and rainfall have opposite effects on soil P availability and can interact with soil particle size to regulate it. Although P is essential in plant nutrition, only 0.1% of total P in the soil is accessible to plants, making P the chief bottleneck for plant growth (Sharma et al. 2013). Thus, the changes in the availability of P can impact plants and related microbiota distribution.

Furthermore, climate change influences nitrogen cycle (Conniff 2017). According to the author, atmospheric N originating from intensive human activity and other sources is moved to the water and also lands/soils via a process called N deposition. Deposition of N has increased tenfold or more since preindustrial times and makes soils more fertile, leading to the contradictory effect of diminishing plant diversity by supplanting native species accustomed to nutrient-poor soils. For instance, across the United States upon investigating upward of 15,000 forest, woodland, grassland, and shrub land sites, it has been found that a quarter of them have already exceeded the N levels accompanying species loss. Moreover, a study in an arid South California habitat has revealed that N supplementation together with altering precipitation patterns brought about a shift from native shrubs to non-native grasses (Simkin et al. 2016; Conniff 2017; Gilliam 2019). Also, another series of recent studies showed that many European ecosystems were experiencing reductions in plant biodiversity due to N deposition (Dise et al. 2011; Payne et al. 2017). According to Lebeis (2015), nitrogen pool and its availability are affected more strongly by the environment than plants.

1.3.3 The Role of Microbiota in Habitat Modulation

Microbial communities, including bacteria and fungus species, in response to environmental changes modulate soil quality and properties such as soil pH, temperature, and relative humidity (Nannipieri 2006; Rousk et al. 2009; Ravichandran and Thangavelu 2017). Soil microbes are involved in (1) constant flow of low- and high-molecular-weight plant-derived organic compounds, (2) many biogeochemical processes (e.g., water or nutrient cycles), and (3) decomposition of organic matter (Herman et al. 2012; de Vries and Caruso 2016) and in the biological conversion of various nutrient pools, including carbon (Rumpel et al. 2015; Quiza et al. 2015; Legay et al. 2016; Okubo et al. 2016; Wang et al. 2017; Mandakovic et al. 2018).

Some soil microorganisms, mainly bacteria such as *Acidobacteria* or *Aciditerrimonas*, are associated with soil acidification and disease, while high abundance in the soil of advantageous microbes—such as *Agromyces*, *Acremonium*, *Bacillus*, *Bradyrhizobium*, *Chaetomium*, *Lysobacter*, *Micromonospora*, *Mesorhizobium*, *Microvirga*, and *Pseudonocardia*—is positively correlated with soil fertility and health (Unterseher et al. 2013; Purahong et al. 2016; Wang et al. 2017). Beneficial soil microbes play a role in preventing erosion, stabilizing soil aggregates, decomposing organic residues, solubilizing mineral phosphate, fixing atmospheric N, and improving nutrient cycling as well as in suppression of plant diseases and soil-borne pathogens (Quiza et al. 2015; Talaat and Shawky 2017). Also, microbial enzymes released into the soil, water, or plant microenvironments may affect biogeochemical processes (Nannipieri et al. 2012; Schimel and Schaeffer 2012; Alves et al. 2014; Khare and Yadav 2017). Thus, the altered belowground processes and the newly established interactions among soil microbiota due to climate change can have an immense influence on nutrient re-translocation within the ecosystem (Ehrenfeld 2003), especially the turnover of C and N pools (Balser et al. 2002; Gonzalez Megias and Mueller 2010; Reidinger et al. 2012; Brunner et al. 2015; Classen et al. 2015; Godschalx et al. 2015; Dawson and Schrama 2016; Ryalls et al. 2016; Heinen et al. 2018a, b; Agrawal et al. 2018; Maron et al. 2018; Ourry et al. 2018).

1.3.4 The Role of Plants in Modulation of Habitats

Plants, including invasive species, influence soil properties (Ehrenfeld 2003; ISAC 2006; Cong et al. 2016; Ravichandran and Thangavelu 2017). For example, *Wedelia trilobata* caused a significant rise in soil pH values at low levels of invasion, whereas high levels of invasion had no impact on soil pH values (Si et al. 2013). Other plants such as *Ambrosia artemisiifolia* L. (Li et al. 2014), *Solidago gigantea* (Herr et al. 2007), and *Lepidium latifolium* (Blank and Youn 2002) at an increased intensity of invasion caused a decrease of soil pH compared to sites of native plants. According to the authors, decreased soil pH values caused increased solubility of nutrients, e.g., P, and their higher availability for plants. Enhanced nitrification was proposed as a likely explanation for decreased pH under the invasion of *Berberis thunbergii* and *Microstegium vimineum* (Ehrenfeld and Scott 2001; Ehrenfeld 2003). Soil acidification during the invasion of *Avena barbata* and *Bromus hordeaceus* has a disadvantageous influence on the concentration of soil nitrate but an advantageous one on the concentration of soil ammonium (Hawkes et al. 2005). As discussed by Novoa et al. (2014) and Maron et al. (2018), the initial characteristics of the invaded ecosystems, including plants and microorganism community, play a key role.

1.4 Global Climate Change Affects Diversity of Plants and Microbiota and Interactions in Ecosystems

Apart from the influence of climate change on soil properties and natural resources including cycles of carbon and nitrogen, microelements pools, climate change modifies also microorganism communities essential for global nutrient cycling, plant biodiversity, as well as the network of close interactions between the soil, plants, and soil microorganisms (Fig. 1.1), which can occur as both native and non-native in the ecosystem (Ravichandran and Thangavelu 2017; Cowan et al. 2018; Sielaff et al. 2018). Microorganisms coexisting in nature are also engaged in intricate interactions with other organisms and their surroundings. These interactions, based among others on the exchange of electron donors or processes of auxotrophies, can affect community activities and composition (Zengler and Zaramela 2018). The altered close connections between different microbial communities occurring in varied habitats, e.g., in the soil, or in plant organs are likely to affect plant fitness, adaptability in natural systems, biodiversity, or the evolutionary path of individual species and whole ecosystems (Dai et al. 2016; Coats and Rumpho 2014; Maron et al. 2018; Zhang et al. 2018).

Changed levels of critical macro- and micronutrients (including C, N, P) due to climate change can cause modification of microbial community. It has been shown that bacteria and fungal communities correlate with microhabitats and specific soil geochemical features and play a distinct role in major nutrient cycles, though they both—bacteria and fungi—show differences in shaping C and N distribution in the soil (Mueller et al. 2015; Sun 2018).

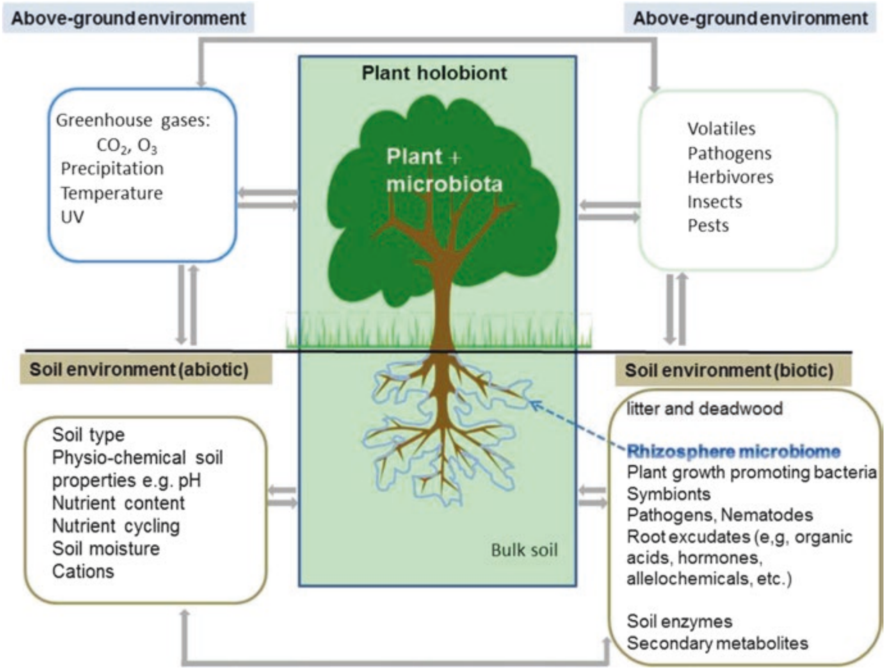

Fig. 1.1 The relationship between plant habitat and the ecosystem

Among different interactions in the ecosystem that can be affected by climate change, an important role is played by plant–soil microbiota feedback known as plant species-dependent profile of belowground microbiota, which in turn impacts the functioning of other plants growing subsequently in the same soil (van der Putten et al. 2013; Ravichandran and Thangavelu 2017; Heinen et al. 2018a, b). It has been shown that the feedback which influences plants via nutrient availability and changed microbiota both beneficially and pathogenically running the whole gamut of ecological possibilities (e.g., competitive, exploitative, neutral, commensal, mutualistic) can cause the establishment of new interactions between plants and belowground biotas, especially in the rhizosphere (Chakraborty 2005; Ruppel et al. 2013; Zhang and Sonnewald 2017; Bach et al. 2018; Jansson and Hofmockel 2018). Moreover, the responses of some organisms to climate change may affect microorganisms and plants that depend on them (Bellard et al. 2012; Montoya et al. 2012; Ravichandran and Thangavelu 2017). Plant species-mediated processes and plant interactions with microorganism community can further modify soil properties and biodiversity of plants (Kourtev et al. 2002; Yang et al. 2013; Li et al. 2014; Qin et al. 2014; Dawson and Schrama 2016; Ravichandran and Thangavelu 2017) as well as alter below- and aboveground organisms (Kos et al. 2015a, b; Heinen et al. 2018a, b) such as endophyte microbiomes colonizing root and shoot tissues (Wardle 2002; Wang et al. 2007, 2017; Zhang and Sonnewald 2017; Garcia and Kao-Kniffin 2018; Heinen et al. 2018a, b; Tripathi et al. 2018), insects, or herbivores (Brunner et al. 2015;

Classen et al. 2015; Smith et al. 2015; Agrawal et al. 2018; Ourry et al. 2018). Thus, climate change can affect eco-evolutionary dynamics of microorganisms and plants (Brunner et al. 2015; Ryalls et al. 2016) and is likely to cause an alteration in the functioning of ecosystem processes (Voroney 2007; Smith et al. 2015; Bach et al. 2018; Bardgett and van der Putten 2014; Eisenhauer et al. 2018; Guerrero-Ramirez et al. 2017; Heinen et al. 2018a, b; Jansson and Hofmockel 2018; Quatrini and Johnson 2018; Ramirez et al. 2018; Santoyo et al. 2017).

1.4.1 The Effect on Plants Adapted to Extremal Climate Conditions

The number of vascular species on Earth has been estimated to range between 223,000 and 420,000 (Scotland and Wortley 2003; Smith et al. 2008). On a large scale, plant species distribution variation (magnitude and direction of species range) along with plant functional characteristics and tolerance to stress factors (van der Putten et al. 2010; Cannone and Pignatti 2014; Parmesan and Hanley 2015; Gebrehiwot 2017) are attributed especially to species-specific responses to temperature, precipitation/water availability, or CO_2 level (Cong et al. 2016; Cassia et al. 2018). It has been shown that climate change can cause many species to fall outside their climatic niches by adjusting their metabolism, the type of adaptive responses, as well as the underlying mechanisms (Walther et al. 2002; Thuiller et al. 2005; Bellard et al. 2012; Cong et al. 2016).

Among changes in plant metabolism, the type of photosynthetic CO_2 fixation (type of photosynthesis, C_3, C_4, and CAM) plays a key role (Gray and Mogg 2001; Luttge 2010; McKee et al. 2012; Short et al. 2016). For instance, climate change can differentially impact plants performing various types of photosynthesis. It has been shown that the increasing CO_2 level will boost photosynthesis chiefly in C_3 plants—lacking CCM—in contrast to C_4 and CAM plants.

A concurrent increase in CO_2 level and temperature, which might be unfavorable for C_3 plants, may favor C_4 and CAM-performing plants having higher light saturation points, higher carboxylation efficiency, lower CO_2 compensation point, and lower WUE (Luttge 2010; Pathak et al. 2018) as well as showing better adaptation to a warmer and more arid climate (Luttge 2010; Yang et al. 2015). However, it should be noted that increasing atmospheric CO_2 level to some extent ameliorates the otherwise detrimental influence of higher temperature and diminished soil water content. The elevated atmospheric CO_2 level (1) has a fertilizing effect for C_3 species, in which photorespiratory costs are assuaged, and (2) causes partial stomata closure, thus improving water use efficiency in both C_3 and C_4 plants (Ainsworth and Long 2005; Lobell and Gourdji 2012).

Moreover, temperature changes also impact plant physiology and productivity, because elevated temperature (1) engenders faster plant growth and shorter plant life span, (2) affects the level of photosynthesis and respiration, and (3) leads to a substantial rise in vapor pressure deficit of air. Furthermore, extreme temperature can directly injure plant cells, while higher temperature together with increased atmospheric CO_2 level may encourage the growth and survival of many pests and diseases specific to plant species (Ziska et al. 2011; Lobell and Gourdji 2012). It has been shown that crops with C_4 metabolism, e.g., maize (*Zea mays*) or sugarcane (*Saccharum officinarum*), have higher optimal temperature for photosynthesis than C_3 crops, e.g., rice (*Oryza sativa*) or wheat (*Triticum*), but even C_4 crops experience a drop in photosynthesis at high temperature (Crafts-Brandner and Salvucci 2002). Elevated day temperatures can cause a rise or fall in net photosynthesis, depending on the current temperature relative to optimum, while elevated night temperatures increase respiration costs with no potential benefit for photosynthetic efficiency (Lobell and Gourdji 2012).

Moreover, GCC can affect in a different manner plants which are adapted to extreme environmental conditions and occupy unique ecological niches such as halophytes and glycophytes showing various salt sensitivities (Cheeseman 2015; Flowers and Colmer 2015; Flowers and Muscolo 2015; Short et al. 2016; Etesami and Beattie 2018). According to Parmesan and Hanley (2015), not only the plasticity of plant metabolism can allow species to adapt to different environmental conditions but also genotype–phenotype interplay as well as new ecological interactions favor a plastic response. Moreover, plants are able to quickly accustom to environmental conditions also due to microbiota structure and epigenetic mechanisms (Quiza et al. 2015; Vannier et al. 2015; Smith et al. 2017).

1.4.2 Climate Change and Plant Invasion

A critical ecological outcome of global warming and land use changes is plant species invasion, which creates new pressures on plant species, plant development, health, and competitiveness (Simon and Schmidt 2017). The process of plant invasion changes the natural native plant communities (Willis et al. 2010; Ratnayake 2014), especially by displacing native plant species and through the loss of plant and microbiota biodiversity, but also changes in interactions among plants and microbiota or among microorganisms (Vila and Weiner 2004; Ravichandran and Thangavelu 2017; Zhang and Sonnewald 2017; Zhang et al. 2018). According to Simon and Schmidt (2017), fundamental mainsprings of change are plant–plant interactions, which encompass competition, facilitation, and avoidance of competition, and their control by environmental factors (Trinder et al. 2013). It is established that upward of 13,000 plant species have been introduced and formed self-sufficient populations outside of their native range (van Kleunen et al. 2015), and that figure is expected to rise with globalized trade and resultant introductions (Bartz and Kowarik 2019). Nevertheless, Blackburn et al. (2011) and Dawson and Schrama (2016) showed that only a tiny proportion of introduced plant species became invasive and abundant on the local scale in invaded communities.

Invasive plants also benefit from elements of GCC (e.g., land use change, climate change, elevated atmospheric CO_2 level, and N deposition) (Ehrenfeld 2003; Kourtev et al. 2002; Theoharides and Dukes 2007). According to Sorte et al. (2013), invasive plants respond most positively to CO_2 and greater rainfall, while native species functioned more efficiently under elevated temperatures and diminished rainfall. Moreover, invasive and native plants compete for various resources (Werner et al. 2010; Eissfeller et al. 2013) and often contribute to a different quantity and quality of resource inputs to the soil (Ehrenfeld 2010). Native and invasive plants have various capabilities for water accumulation, organic matter decomposition, nutrient cycling (particularly C, N, and P) regulations, and inorganic compound accumulation (e.g., potassium (K), magnesium, and manganese) (Herr et al. 2007; Dassonville et al. 2008; Liao et al. 2008; Berg and Smalla 2009; Weidenhamer and Callaway 2010; Hickman et al. 2013; Berg et al. 2014; Chaparro et al. 2014; Lakshmanan et al. 2014; Quiza et al. 2015; Sardans et al. 2015; Wang et al. 2015; Zhang et al. 2016; Ilangumaran et al. 2018; Jacoby et al. 2017; Ravichandran and Thangavelu 2017; Heinen et al. 2018a, b). Differences in the rates and dynamics of biogeochemical processes activated by native and invasive plants (Si et al. 2013; Kuebbing et al. 2014; Sardans et al. 2015; Ravichandran and Thangavelu 2017) dissimilarly alter soil physicochemical properties, soil structure, and fertility (Ravichandran and Thangavelu 2017; Wallenstein 2017; Zhang et al. 2017; Jansson and Hofmockel 2018; Tripathi et al. 2018).

It is also worth noting that the problems indicated above for plant invasion are also applicable for the spread of indigenous weeds in cropping systems. As an example, in the last decades, an increasing problem with rush (*Juncus* sp.) is observed in Norwegian meadows and pastures. The main reasons are climate changes, which soothed the course of winters in the west coast of Norway. Rush species have good freezing tolerance until February and then their tolerance decreased (Ostrem et al. 2018). This drop in freezing tolerance appeared earlier than observed in competing perennial grasses (Hoglind et al. 2010). Thus, rushes may start their vegetation earlier, which increases their level of competitiveness.

1.4.3 The Role of Links Between Genotypes and Phenotypes in Adaptation to Climate Changes

The links between genotypes, phenotypes, and changing environment are also thought to play a major role in adaptive responses and in plasticity of evolutionary trajectories (El-Soda et al. 2014). Genetic diversity can be an important determinant of species' sensitivity (Kelly 2019). Plant phenotypic plasticity/variation, which may allow species to counter the detrimental effects of extreme conditions, is also controlled by epigenetics and plant symbiotic microbiota (Vannier et al. 2015; Chevin and Hoffmann 2017). Transgenerational epigenetic inheritance enables a prompt response to environmental stresses, through changes in gene expression as well as in posttranscriptional and posttranslational modifications by means of inherited change in small RNA expression patterns, DNA methylation, or histone modification. Environmentally induced phenotypes may be sustained for several generations, due to the transmission of molecular factors determining the way in which genetic information is expressed (Shaw and Etterson 2012; Zhang et al. 2013; Vannier et al. 2015; Chevin and Hoffmann 2017; Lind and Spagopoulou 2018). Plant-associated (micro-) organisms (symbiotic microbiota) provide essential active biomolecules, modulate plant metabolism, and modulate the immune system of the host; thus, they are involved in dynamic adjustment to the constraints of the environment, plant survival, and adaptation (Vandenkoornhuyse et al. 2015; Vannier et al. 2015).

1.5 Ecological Interactions Between the Soil, Plants, and Microorganisms Promoting Plastic Response to Climate Change

Microbial communities play a key role in the regulation of ecosystem homeostasis, since they influence abiotic and biotic ecosystem components extensively and in various ways as well as affect the balance between any sort of interactions (i.e., positive, negative). Microorganisms can benefit plants through the impact on plant–water relations, ionic balance, photosynthetic capacity, protein assimilation, or hormonal status (Talaat and Shawky 2017). On the other hand, microbial community structure is under direct influence and regulation by abiotic and biotic ecosystem components, for instance, by different plant–microorganism relationships classified as neutralism, synergism, commensalism, mutualism, amensalism, competition, or parasitism (Ilangumaran et al. 2018). Interaction of plants with microorganisms confers (a)biotic stress tolerance to plants, e.g., alleviates negative effects of plant pathogen attacks/infections (Dimkpa et al. 2009; Dodd and Perez-Alfocea 2012) or soil-borne pathogens under unfavorable environmental conditions (Bell et al. 2015; Quiza et al. 2015; Talaat and Shawky 2017).

In addition, global climate change by altering the distribution of organisms such as plants, animals, and microorganisms (above- and belowground biotas), as well as modifying their metabolism (Dawson and Schrama 2016; Jacoby et al. 2017), can alter or interrupt even long-term coevolved associations (e.g., by promoting the invasion of plants) between plants and microbiomes (e.g., plant–herbivore or plant–pathogen interactions) or between microbiomes living in the soil and aboveground (Kerchev et al. 2012; van der Putten 2012; Classen et al. 2015; Bang et al. 2018; Ilangumaran et al. 2018; Tripathi et al. 2018), e.g., by root secretions (Wolfe and Klironomos 2005; Wallenstein 2017; Zhang et al. 2017, 2018).

Moreover, altered plant biodiversity and plant–plant interactions (e.g., competition between native and invasive plant species) (1) play a key role in regulating the impact of environmental change drivers—any natural or human-induced factors that cause change in the ecosystem directly (GLOBIO), (2) can affect the pattern of plant species or microbial communities structure, and (3) can in turn influence plant performance through positive and negative feedbacks (van der Putten et al. 2007a, b; Nannipieri et al. 2012; Philippot et al. 2013; Maron et al. 2016; Marupakula et al. 2017; Ravichandran and Thangavelu 2017). For example, feedback between plants and soil occurs when soil interacts with changing vegetation to create microorganisms that help or harm specific species (Maron et al. 2016). Positive feedback is favored mostly by mycorrhizal fungi, nitrogen-fixing bacteria, and beneficial soil microbes, and it promotes intraspecific and interspecific competition and favors the predominance of plants, while negative feedback is mediated by soil-borne pathogens, herbivores, and parasites (Larios and Suding 2015; Ravichandran and Thangavelu 2017). Maron et al. (2016) underlines that plant–soil feedbacks and interspecific competition are common interactions which have a strong impact on productivity, abundance, and diversity of plants and can play a crucial part in the coexistence of plant species and ecosystem services. According to Bukowski et al. (2018), the taxonomic level of organisms is an important factor in maintaining the coexistence of plants and soils as a potential stabilizing mechanism. Moreover, plants such as native and invasive species may create a feedback with soil microbiota but with different influence on the microbial communities' composition below- and aboveground (Wang et al. 2007; Li et al. 2014; Ravichandran and Thangavelu 2017).

Altered biodiversity of plants and soil microbiota as well as their interactions can further cause changes in (1) the competitiveness of plants, (2) the interaction between plants and their environment, (3) the capabilities of plants to adapt to specific local habitats, (4) the dynamic responses to changes in resource availability, (5) the tolerance/resistance of plants to abiotic and biotic stresses, and (6) the changed feedback effects (positive or negative) (Rout and Callaway 2012; Suding et al. 2013; Kuebbing et al. 2014; Ravichandran and Thangavelu 2017). Altered biodiversity of plants and soil microbiota as well as their interactions can also (1) alter the stability of microbial community; (2) change interactions of competitiveness; (3) affect the actual ratio of beneficial and pathogenic soil microbes, including bacteria and fungi; and (4) alter soil enzyme activities (Kourtev et al. 2002; Yang et al. 2013; Li et al. 2014; Qin et al. 2014; Quiza et al. 2015; Dawson and Schrama 2016; Lareen et al. 2016; Wang et al. 2016; Ravichandran and Thangavelu 2017). Thus, they lead to changed interspecific competition and plant–soil feedback interaction (Maron et al. 2016); contribute to new plant–microbe interactions including parasites or pathogens, mutualists, symbionts and saprophytes, or decomposers; and can cause the development of disease states of plants (Quiza et al. 2015; Guo et al. 2018; Tripathi et al. 2018) and change ecosystem functioning (Brooker 2006; Mitchell et al. 2006; Wang et al. 2015).

1.5.1 The Rhizomicrobiomes

Among microorganisms, in particular mutualistic microbiota, such as endophytic or arbuscular mycorrhiza, which are selected by the plant, persist through generations and have an impact on the reproductive strategies in the host plant, plant competition, and successive generations. It has been shown that with raised CO_2 and/or N level, also other factors will come into play such as elevated moisture or temperature, and they can affect microbial biomass, the composition and structure of microbial communities, as well as microbial metabolism (Llado et al. 2017; Santoyo et al. 2017; Maron et al. 2018). Soil microbial communities affect processes vital for the survival of a living organism and shape its capabilities for interacting with its environment. Soil microbiome can (1) modify the plant's ability to reproduce and acquire resources, (2) promote plant development and productivity, (3) control plant resistance to abiotic constraints, (4) alleviate the influence of environmental stresses on plants and have significant impact on plant stress tolerance, (5) enhance plant survival, and (6) control plant and microbiota populations as well as plant–microorganism relationships (Quiza et al. 2015; Vandenkoornhuyse et al. 2015; Smith et al. 2017; Guo et al. 2018; Ilangumaran et al. 2018; Tripathi et al. 2018).

Microorganisms also affect plant phenotype (induced by mutualists) and support its fitness in rapid buffering of environmental changes. In the creation of phenotypic variants in response to environmental conditions, an important role is also played by mechanisms such as epigenetics. The same selection factors that affect specific organisms also have equivalent influence on phytomicrobiome and its interactions with the host plant in a resistant holobiont (as the unit of selection). The plasticity of adaptation of all components of the holobiome (interspecies induction changes) is mediated through epigenetic mechanisms (Vandenkoornhuyse et al. 2015; Vannier et al. 2015). Additionally, the enhancement of the activity of microbial soil enzymes—such as dehydrogenases, oxidoreductases (e.g., catalase), and enzymes involved in C (invertase) and N (urease) or phosphatases—not only improves soil quality but also promotes plant productivity (Ilangumaran et al. 2018; Utobo and Tewari 2015).

The rhizosphere, distinguished from the bulk soil zone (edaphosphere), is a versatile and dynamic ecological environment in the soil and a vital region of the plant ecosystem, extending from 2 to 80 mm away from plant root surface (Prasad et al. 2019). The rhizosphere consists of three main zones—endorhizosphere, rhizoplane, and ectorhizosphere. Among the main zones, the endorhizosphere comprises the cortical and endodermal tissue of the root, the rhizoplane includes root epidermis and associated mucilage, while the ectorhizosphere encompasses the soil close to the root (De-la-Pena and Loyola-Vargas 2014; Garcia and Kao-Kniffin 2018). In the rhizosphere, complex, intensive, direct, and indirect interactions between plants and the corresponding organisms closely associated with plant roots (rhizomicrobiome) take place, e.g., plant–plant, microbe–microbe, and plant–microbe, as well as interactions with other eukaryotic micro-, meso- and macro-soil inhabitants (Peiffer et al. 2013; Quiza et al. 2015; Garcia and Kao-Kniffin 2018). The rhizosphere microbiota (free-living or intricately linked to their plant hosts), which establishes mutualistic symbioses with the roots of most terrestrial plants (more than 80% of plant species), may have a microbial cell count of up to 1.011 per root gram (Egamberdieva et al. 2008) and over 30,000 prokaryotic species (Mendes et al. 2013). The root microbiome has also been described as a "secondary genome" which supplies host plants with microbe-derived compounds (Rout and Southworth 2013). The plant–microbe interactions may have a positive, negative, or neutral effect on plant growth and productivity (Ordookhani and Zare 2011). In the rhizosphere, among others, (1) plants and microbes compete to retrieve essential macro- and micronutrients from a limited nutrient pool and (2) bacterial communities compete for nutrients released near plant roots (Bulgarelli et al. 2013; Chaparro et al. 2014). Moreover, the rhizosphere zone due to the presence of root exudates undergoes chemical transformations, enhances microbial activity or metabolites of microbial degradation, as well as promotes a typically diversified and dense microbial population, including bacteria, whose population in the rhizosphere is generally 10–100 times higher than in bulk soil, and also fungi, protozoa, and algae coexisting among them.

Among this microbiota, plant growth-promoting bacteria are most numerous in the rhizosphere. They can bind to the outer surface of the plant, such as roots (rhizosphere) or leaves (phyllosphere), or can inhabit the inner surfaces of the plant to form endophytic compounds. Bacterial endophytes can only be located in roots or stems and can be equally distributed in plant tissues or form specific structures, such as nodules, depending on bacteria and plants. Plant growth-promoting bacteria support the growth and development of plants, improve plant health, and protect plants against environmental stress such as flooding, drought, salt, metals, organic pollutants, as well as bacterial and fungal pathogens. The key component in the potent functioning of these bacteria is the ability to produce, among others, ACC-deaminase, which decreases plant ET level, often induced as a result of various stresses (Bahadur et al. 2017; Verma et al. 2017; Prasad et al. 2019).

Important members of the root microbiome are arbuscular mycorrhizal (AM) fungi. Moreover, some bacteria associated with the mycorrhizosphere (mycorrhiza helper bacteria, component of AM symbiosis) seem to be involved in the establishment and function of AM fungi and AM symbiosis. Spore germination, hyphal growth, and AM fungal colonization may be promoted by the mycorrhizospheric bacteria, such as the bacteria associated with the hyphae or spores of AM fungi, together with bacteria living in the root nodules, the endosphere, and the rhizosphere. In addition, synergistic interactions between plant growth-promoting rhizobacteria and AM fungi can enhance plant yield quality (Gorzelak et al. 2015; Akyol et al. 2019). It has also been found that various AM fungal species are linked to different bacteria (Selvakumar et al. 2016); thus, the introduction of new AM fungi species can also introduce related bacteria which can lead to changes of the contents and structures of the pools of root microbiomes (Akyol et al. 2019). AM fungi may stimulate or inhibit the growth of some microbes (Marschner and Timonen 2006) by providing carbon compounds, exuding inhibitory or stimulatory compounds, or simply competing for nutrients (Akyol et al. 2019). The cooperation between plants and AM fungi enables the provision of multiple ecosystem services from the biogeochemical cycle completion to the retention of biological soil fertility. It has been shown that AMF can also act as a direct C source for the host in the soil and contribute directly to its C pools to pass over the decomposition process (Asmelash et al. 2016). In exchange, AMF improve the availability of mineral nutrients for plants, including calcium (Ca), copper (Cu), sulfur (S), N, K, P, and zinc (Zn), among which some nutrients such as P or Zn are known as limiting factors for plant growth as well as nutrients affected by climate change (Smith et al. 2017; Akyol et al. 2019). AMF increase plant tolerance to (a)biotic stresses or cause changes in plant secondary metabolism by stimulating the biosynthesis of, e.g., polyphenols or carotenoids which promote plant productivity (Doornbos et al. 2012; Turrini et al. 2018).

Soil microbial communities can be affected by climate change, especially CO_2 concentration, N deposition level, and temperature (Garrett et al. 2006; Wilson et al. 2016). According to Wilson et al. (2016), the effects of climate change on AMF–plant symbioses are mediated by vegetation dynamics as well as soil water and nutrient availability. Moreover, altered soil microbial communities through root exudates, litter, and mineralized nutrients can change plant biodiversity or plant interactions with symbiotic mutualists, pathogens, and herbivores in the rhizosphere, as well as with decomposer organisms (Quiza et al. 2015; Smith et al. 2017; Zhang et al. 2018; Akyol et al. 2019). All these processes can be highly impacted by invasive species since they introduce new properties, such as N fixation, chemical control of local symbiotic mycorrhizal fungi, and pathogen resistance, or change the belowground resource input when they produce organic matter of different quality (van der Putten et al. 2007a, b; Zhang et al. 2018). Invasive microorganisms can also alter these ecosystem processes when they interfere with local patterns of symbiosis, pathogenicity, or decomposition processes (Ehrenfeld 2003; van der Putten et al. 2007a, b; Zhang et al. 2018). Moreover, soil biota exerts different impacts on native and invasive ranges. For instance, microorganisms which are detrimental or pathogenic to the native plant species can be beneficial for the invading species and promote plant invasion (Inderjit 2005; Coats and Rumpho 2014; Dai et al. 2016). The microbiome of cultivated barley (*Hordeum vulgare*) differs from that of its wild ancestors in both function and diversity, with genes connected with host–microbe interaction showing evidence of positive selection (Bulgarelli et al. 2015). Zachow et al. (2014) showed that the rhizosphere bacterial community of *Beta vulgaris* ssp. Maritima, a wild ancestor of beet, has a greater degree of diversity resistance to abiotic stress and lower proportion of isolates with anti-phytopathogenic activity than that of modern sugar beet. Zhang et al. (2018) stated that CO_2 efflux, N mineralization rate, and enzyme activities are higher in invasive compared to native rhizosphere soils. They indicated that invasive plants may in particular support decomposers, which entails stimulation of nutrient release via litter effect and enhancing nutrient uptake by decrease in root grazing together with forming more symbioses in the rhizosphere, which in consequence facilitates plant invasion.

Moreover, the biological and chemical features of the rhizosphere zone can be influenced by root exudation patterns caused by changed plant status as well as high diversity and activity of microbial community, including AMF (Bulgarelli et al. 2013; Chaparro et al. 2014; Akyol et al. 2019). Soil microbiomes, especially in the rhizosphere zone, impact the ability to process chemical elements, as well as the function, productivity, stability, and sustainability of ecosystems (Panke-Buisse et al. 2015; Vannier et al. 2015; Ravichandran and Thangavelu 2017; Wang et al. 2017).

1.5.2 The Endosymbionts

"Phytomicrobiome" is the collective term for the microorganisms which colonize plants. The phytomicrobial genomes broaden the genetic pool of plants, and plants control their phytomicrobial composition (Smith et al. 2017). The complex ecological interactions between plant and endo- and intracellular microorganisms described as the "plant–microbiome (phytomicrobiome) interactions" (Quiza et al. 2015; Ying-Ning et al. 2017), of which many are inextricable, e.g., endosymbionts, occur inside the tissues of the host plant (Ilangumaran et al. 2018). The phytomicrobiome is composed of functionally and taxonomically distinct sets of microbiomes which adapted to different compartments of the plant including flowers (anthosphere), fruit (carposphere), leaves (phyllosphere), and stem (caulosphere), within the plant (endosphere) and on the roots (rhizosphere), as well as interact with the host plant in a particular way (Turner and Condron 2013; Smith et al. 2015; Ilangumaran et al. 2018). These interactions include processes within plant endosphere (the microbial habitat inside both above- and belowground plant organs), phyllosphere (aboveground plant surfaces), and rhizosphere (Parmesan and Hanley 2015; Quiza et al. 2015; Franklin et al. 2016; Compant et al. 2019). The microorganisms such as the "phytomicrobiome" have also been described as key components of plants because they contribute to a significant portion of the "secondary genome" of the host plant, hence the functioning of both these organisms as a metaorganism or holobiont (Bosch and McFall-Ngai 2011; Lakshmanan et al. 2014; Quiza et al. 2015; Vandenkoornhuyse et al. 2015). The distribution and composition of microbial communities (phytomicrobiome) living inside both above- and belowground plant organs have been correlated with the overall condition of the plant, productivity and stress tolerance/resistance (Ma et al. 2011; Adesemoye and Egamberdieva 2013; Chaparro et al. 2014; Glick 2014; Panke-Buisse et al. 2015; Quiza et al. 2015; Santoyo et al. 2016; Smith et al. 2017; Compant et al. 2019), their involvement in facilitating the uptake of soil nutrients, and mobilization of nutrients or atmospheric N fixation (Smith et al. 2017; Ilangumaran et al. 2018).

1.5.3 Plant–Pathogen Interaction

Global warming leads to the exposure of plants to a greater range and number of simultaneous abiotic and biotic stresses. Moreover, (a)biotic stresses or their combinations can interact unpredictably (e.g., additively, synergistically) under global climate change and cause negative as well as positive effects on plants (Pandey et al. 2017). Changes in plant diversity and also plant-associated communities of microorganisms will likewise significantly model habitats and thus influence occurrence of pathogens (Zhang and Sonnewald 2017). Climate change can also affect the balance among different signals that are perceived or induced by plants/other organisms, e.g., environmental (nutrients, light, temperature, CO_2 level, salinity, species/populations of plant and microbiota, etc.) or metabolic (carbohydrates, amino acids, phytohormones), as well as affect source-to-sink transport and/or source–sink relationship in plants. These changes would directly or indirectly affect the nutrition status, metabolic state, or signaling pathways of plants and other organisms. Plants with changed metabolism may have modified sensitivity to abiotic and biotic (e.g., pathogens, viruses, nematodes) stresses. For instance, under altered environmental conditions, the source–sink balance at the whole plant level can be changed by a pathogen that may form strong and competitive metabolic sinks at the site of infection having negative impact on growth and development of the plant (Zhang and Sonnewald 2017). Moreover, the dynamic host plant–pathogens–environment interplay (including the so-called disease triangle) altered by global climate change (Pachauri et al. 2014; Das et al. 2017; Pathak et al. 2018) may cause pathogen dispersal over great distances and transmission of pathogen-related diseases from one geographic region to another, negatively affecting plant population development and production potential (Atkinson and Urwin 2012; Andersen et al. 2018).

Plants' ability to withstand aggressive attacks of pathogens/pathogen infection depends not only on the ongoing primary and secondary global changes in the lithosphere, hydrosphere, or atmosphere (especially CO_2, temperature, humidity) but also on changes in microbiome populations (e.g., above- and belowground microflora diversities) playing a crucial role in the maintenance of ecological balance or other organisms such as, e.g., insects (Das et al. 2017; Trębicki et al. 2017; Pathak et al. 2018; Zhou et al. 2019).

The plant–pathogen interaction can be regarded as a two-way process mediated by plant- and pathogen-derived metabolites/stimulants, in which the plant recognizes and responds to the attack of the pathogen (classified as biotrophic, hemibiotrophic, or necrotrophic based on its lifestyle and impact on the host cells), while the pathogen influences plant metabolism to optimize conditions for its own pattern of growth and development (Avila Mendez and Romero 2017). The "disease triangle" is a conceptual model in plant pathology that underlines multifaceted processes between plants, pathogens, and the environment. Naturally, disease may happen when these three components/agents, i.e., conducive environmental conditions, a susceptible plant host, and a virulent pathogen, coexist at the same time, while the lack of an environment conducive to the development of any of three factors means that the disease does not develop (Velasquez et al. 2018).

The plant defense/immune system consists of two branches. The first level of the defense system is a general reaction of resistance to common pathogen features, and it is triggered in plants by the perception of molecular patterns (i.e., MAMPs or PAMPs) associated with microbes or pathogens. Moreover, following a pathogen attack, an additional plant surveillance system consists in the release or production of endogenous damage-associated molecular patterns (DAMPs), which are able to activate the innate immune system. MAMP/PAMP/DAMP recognized by plant cell surface receptor proteins known as pattern recognition receptors (PRRs) initiates physiological modulation of the cell. PRRs induce local and systemic immunity. The identification of PAMPs or MAMPs results in plant immunity called PAMP/pattern-triggered immunity (PTI), which enhances plant resistance to a broad spectrum of pathogens (including nonhost pathogens). When PTI and host resistance genes are suppressed by pathogens to promote pathogenesis, the second branch of the immune system (pathogen-specific branch) called ETI or R gene-mediated effector-triggered immunity is initiated. It refers to virulence factors or specific pathogen effectors. It is induced after specific recognition of the pathogen race-specific avirulence (*Avr*) gene by specific resistance (R) gene of the host plant. In order to recognize effectors secreted by pathogens (i.e., biotrophs, several necrotrophs), plants utilize cell surface-localized NB-LRR proteins (referred to as R proteins). The amino terms of these proteins are TIR-type receptors or the non-TIR group referred to as the CC domains. ETI is highly specific and often results in the HR and SAR. PTI and ETI share signaling mechanisms including PR gene expression, generation of reactive oxygen species, or phytohormone-dependent signaling pathways. A coevolution of host plants and pathogens is reflected by the multiple layers of plant immunity (Delaunois et al. 2014; Gill et al. 2015; Avila Mendez and Romero 2017; Chowdhury et al. 2017; Jwa and Hwang 2017; Lee et al. 2017; Andersen et al. 2018; Saijo et al. 2018; Lorang 2019; Noman et al. 2019; Rodriguez et al. 2019). Other plant–pathogen interaction models such as the invasion model, multicomponent model, and zigzag model have also been described (Andolfo and Ercolano 2015; Avila Mendez and Romero 2017).

Plant disease development is determined by the three-way interaction of the plant, the pathogen, and the environment. The optimal environmental conditions, such as CO_2 concentration, temperature, relative humidity, and soil fertility, enable plant and pathogen growth, development and reproduction, as well as the outbreak of disease. The altered environmental conditions due to climate change may have positive, negative, or neutral impact on the shift in the nature of some plant–pathogen interactions as well as the development of plant diseases (Elad and Pertot 2014; Zeilinger et al. 2016; Peyraud et al. 2017; Pathak et al. 2018; Velasquez et al. 2018). Among others, this is also due to the fact that both plants and pathogens, which function as two coevolving groups, are joined in continual antagonism, which includes changing selection cycles leading to the increase of the resistance or virulence, respectively (Wroblewski et al. 2009). The environmental changes can impact pathogen biology, including vigor, survival, rate of multiplication, sporulation, direction, and distance of inoculum dispersal as well as the rate of spore germination, thus affecting the dynamics of pathogen populations. Moreover, pathogens evolve new virulence through migration, selection, mutation, or recombination of virulence genes (Yanez-Lopez et al. 2012; Ferrocino et al. 2013; Bourguet et al. 2016; Wu et al. 2016; Pathak et al. 2018; Velasquez et al. 2018). Also the intrinsic genetic characteristics of both plant host and pathogens, and genetic changes in pathogens as a result of better adaptation to stress conditions or alteration in pathogen vector bionomics due to direct or indirect modification as well as rapid microorganism migration/spread, determine the range of plant diseases (Lamichhane and Venturi 2015; Croll and McDonald 2017). Since a number of plant disease resistance pathways, such as PTI, ETI, RNA interference, and the network of phytohormone signaling pathways enabling plants to activate defense responses, are all influenced by environmental factors (Velasquez et al. 2018), changing environmental conditions can cause, e.g., a negative interactive effect of plant and pathogen, by lowering plant disease resistance/plant innate immunity, which results in plants becoming more susceptible to viral, bacterial, fungal, and nematode pathogens as well as insects (Gao et al. 2015; Pathak et al. 2018; Velasquez et al. 2018). Climate affects all stages of pathogen and host plant life and undoubtedly gives rise to a challenge to many pathosystems (Ahanger et al. 2013; Elad and Pertot 2014; Helfer 2014; Lamichhane and Venturi 2015; Newbery et al. 2016; Caubel et al. 2017; Das et al. 2017; Pathak et al. 2018). As a result, pathogens will become resistant to current host defense responses and/or better adapted to infect a new host species, will enter and spread in new hosts, new virulent variants of pathogen races will appear, and the geographical distribution of pathogens will expand (Altizer et al. 2013; Newbery et al. 2016; Peyraud et al. 2017; Zhang and Sonnewald 2017).

The degree of complexity of environmental impact on plants and microorganisms increases when the effects of simultaneous abiotic and biotic factors combine as well as when there are significant overlaps between multiple stress signal transduction pathways. It should be noted that in many cases, the first stress factor(s) followed by other stress factor(s) in sequence may either "endure" due to priming or "predispose" the plants to the subsequent stress (Pandey et al. 2017; Chojak-Kozniewska et al. 2018). The response to the previous stress factor alters the response to the following/repeated or new abiotic or biotic stress factor(s) through key processes such as stress memory and priming effects, by which plants modify responses to subsequent challenges in the future (Atkinson and Urwin 2012; Prasch and Sonnewald 2015; Nejat and Mantri 2017; Chojak-Kozniewska et al. 2018; Libik-Konieczny et al. 2019). For instance, plants influenced by abiotic stresses, thus experiencing oxidative stress, are probably more resistant to biotrophic or hemibiotrophic pathogens and may be less resistant to necrotrophic fungal pathogens (Libik-Konieczny et al. 2011, 2012, 2019). Also, pathogens can improve plant resistance to abiotic stresses. Several pathogens cause the closure of stomata making infected plants more drought-tolerant (Zhang and Sonnewald 2017).

The effect of climate change on plant–pathogen interaction may be in some cases very complicated. This is observed for plant winter pathogens causing snow mold symptoms (Rapacz et al. 2014). The reduction of snow cover, which decreases the incubation period for fungi, would result in a significant decrease in the occurrence and severity of infections (Roos et al. 2011). On the other hand, the extreme/episodic weather events predicted, inclusive of years of heavy snowfall and colder winters, will favor these species of snow mold fungi which are able to live saprophytically in the soil, and even the inoculum of sclerotia-forming species can survive for long periods in the soil without favorable growth conditions waiting to attack plants under advantageous conditions (Hsiang et al. 1999). Thus, it is likely that climate change will considerably influence the biodiversity of snow mold fungi. Additionally, changes in weather conditions in autumn and winter may considerably affect plant metabolism and thus plant–snow mold interactions (Gaudet and Chen 1988).

Climate change will increase pathogen density in relation to plant population, favoring disease transmission and increasing the range of plant diseases caused by particular pathogen species, as well as affect the optimal conditions for and the mechanism of infection, host susceptibility and specificity, and thus plant–pathogen interactions (Atkinson and Urwin 2012; Ahanger et al. 2013; Elad and Pertot 2014; Gautam et al. 2013; Bebber et al. 2014; Elderd and Reilly 2014; Abdullah et al. 2017). Climate change is also likely to directly and indirectly influence future outbreaks of viral diseases in wild and cultivated plants through effect on hosts, viruses, and vectors (Jones 2016). The stability of plants in a particular environment determines the dynamic of plant disease (epidemics) (Peyraud et al. 2017; Islam 2018). The altered environmental conditions and deviation from factors determining "disease optimum" can cause changes in plant disease in time and space, e.g., fewer disease symptoms occurring in plants (Gill et al. 2015; Avila Mendez and Romero 2017; Lee et al. 2017; Peyraud et al. 2017; Saijo et al. 2018). The altered ecophysiology of plants and pathogens as well plant–pathogen interactions due to climate changes can also lead to altered management of energy and nutrient flow through systems/communities in the ecosystem, thereby affecting whole ecosystem functioning and resilience (Atkinson and Urwin 2012; Elad and Pertot 2014).

Examples of global climate change on different members of ecosphere (soil, plants, and microbiota) have been presented in Table 1.1 and also in many reviews. Its influence on plants has been presented in, e.g., Bodner et al. (2015), Mueller et al. (2015), and Pathak et al. (2018) and on pathogens in Newbery et al. (2016), Noctor and Mhamdi (2017), Short et al. (2016), Chala and Meseret (2018), Pathak et al. (2018), and Velasquez et al. (2018).

1.6 Plant and Microbiota Internal Factors Enabling the Response to Complex Environmental Challenges

The interactions between plants and diverse microorganisms which occur in the rhizosphere, phyllosphere or endosphere are based on different mechanisms, signals (e.g., chemical), or bioactive molecules secreted by both plants and microorganisms (Evangelisti et al. 2014; Quiza et al. 2015; Ilangumaran et al. 2018). Bioactive molecules secreted by plants are known as plant exudates, root-secreted molecules, while by microorganisms as plant growth-promoting factors. These biologically active/signaling substances include primary and secondary plant metabolites such as sugars, amino acids, proteins, amides, fatty acids, vitamins, organic acids compounds, aromatic or phenolic compounds (phytoalexins, flavonols, indole compounds, flavonoids), phytohormones (e.g., SA), glucosinolates, extracellular enzymes, volatile substances, and soil enzymes (Mendes et al. 2013; Oburger et al. 2013; Turner and Condron 2013; De-la-Pena and Loyola-Vargas 2014; Yergeau et al. 2014; Quiza et al. 2015; Page et al. 2015; Smith et al. 2015; Zhang et al. 2015; Wang et al. 2017; Ilangumaran et al. 2018). Among metabolites secreted to the soil, plant root exudates are the most important compounds in the rhizosphere. Dynamic composition (quality and amount) of compounds exudated to the soil depends on the plant species, plant physiological stage, plant nutritional status, microbial activity in the rhizosphere, and

Table 1.1 Examples of the impact of short- and long-term changes of the environmental factors due to global climate change

Climate-dependent changed environmental factors/ climatic events	Geographical region/effect on environment and plants	References
Alteration in rainfall pattern due to El Niño–Southern Oscillation (ENSO), i.e., irregular and periodic variation of sea surface temperatures and winds over the eastern tropical Pacific Ocean or La Niña (colder counterpart of El Niño)	• Ethiopia, 1997–1998 • High degree of loss of the crop of late-planted lentil due to rust • Ethiopia, 2008–2011 • Drought, poor harvests, or complete crop failure, e.g., teff, maize, sorghum, wheat, and barley • The Marshall Islands, El Niño-driven drought, 2015–2016 • Damage and losses in crops, e.g., taro, pumpkins, and fruit trees such as coconut, papaya, bananas, and citrus	Varma and Winslow (2004) http://www.fao.org/3/a-i6049e.pdf
Infrequent late rainfall	• West Asia, North Africa, 1979–2007 • Severe *Ascochyta* blight and infection caused by fungus *Ascochyta rabiei* in chickpea, resulting in yield and quality losses	Abang and Malhotra (2008)
Floods due to the El Niño	• Sri Lanka, 2016–2017 • Soil erosion and sludge accumulation in low agricultural lands, water pollution in excavated wells • Negative influence on agricultural production, e.g., tea and rice	http://www.fao.org/3/a-i6049e.pdf
Tropical Cyclone Pam due to the El Niño El Niño-dependent drought in agricultural areas; rain shadow areas	• Vanuatu, 2015 • Serious damage to marine and coastal ecosystems such as coral reefs, mangroves, and tropical forests • Reduction of farmlands • Losses in crops yields, e.g., manioc, sweet potato, and aroids	http://www.fao.org/3/a-i6049e.pdf http://www.fao.org/3/a-i4251e.pdf
Meteorological drought	• The Czech Republic, 1961–2000 • Reduction of yields of spring barley (determined by Palmer Z-index) • Seasonal water balance has a significant influence on cereal production (mainly in south eastern Czech Republic)	Trnka et al. (2007)
Elevated CO_2	• Atmospheric CO_2 and soil nutritional value affect the responses of plants to rhizosphere colonization by soil bacteria • Plant growth and systemic resistance depend on the concentration of atmospheric CO_2 and the type of soil (ranging from growth stimulation to growth suppression with induced resistance at elevated CO_2) • Interaction between CO_2 content in the atmosphere and soil nutritional status affects the responses of plants to rhizobacteria	Williams et al. (2018)

(continued)

Table 1.1 (continued)

Climate-dependent changed environmental factors/ climatic events	Geographical region/effect on environment and plants	References
Elevated CO_2	- Giessen, Germany - Elevated CO_2 content stimulates the use of rhizosphere C by arbuscular mycorrhizal fungi in permanent grassland - Movements of soil microbial community and translocation of carbon within metabolically active microorganisms in the rhizosphere - New rhizodeposit C is rapidly processed by fungal communities and only much later by bacterial communities	Denef et al. (2007)
Elevated CO_2 level	- Eastern Denmark, heathland area - More carbon passes through fungal channels than bacterial channels when belowground allocation of photosynthetically derived C increases without a corresponding increase of N in the soil - Different plant species are associated with distinct communities of belowground decomposers - Increased CO_2 level and climate regimes affect vegetation shifts; belowground communities have consequences for dynamics of plant decomposition	Dam et al. (2017)
Warming and elevated CO_2	- North American, mixed-grass prairie - Interaction of climate warming and increased atmospheric CO_2 level changes seasonality and lowers variability of soil water in semiarid grassland	Blumenthal et al. (2018)
Climate change	- Concord, Massachusetts, USA - Some species are unable to respond to climate change by altering their flowering phenology decline - Climate change has an impact on shaping the phylogenetic model of species loss	Willis and Davis (2014); Willis et al. (2009)
Climate change	- Concord, Massachusetts, USA - Non-native, and particularly invasive, species have been able to respond to climate change by adjusting their flowering time - Climate change has probably played, and can continue to play, an important role in facilitating non-native species acclimatization/domestication and invasion at the community level	Willis et al. (2010)

(continued)

Table 1.1 (continued)

Climate-dependent changed environmental factors/ climatic events	Geographical region/effect on environment and plants	References
Climate change	• Northeastern United States and Eastern Canada, forest areas • Significant reduction in the suitable habitat for spruce forests and extension of suitable habitat for oak-dominated forests • Productivity gains that could result from long growing seasons and from carbon dioxide and N fertilization • Interruption of the assemblages of species • Forest fragmentation by invasive (nuisance) species • Changes in evapotranspiration, rates of mineralization, soil respiration, and alterations in key ecosystem processes • New species, including pests and pathogens, may be better adapted to changing climatic conditions, improving their competitiveness vis-à-vis native species	Rustad et al. (2012)
Climate change	• A newly emerging virulent race is the Ug99 (wheat virus Ug99) wheat stem rust strain, which is becoming, after three decades (from the 1950s in North America), a serious threat to world wheat production. The Ug99 strain overcomes the resistance of Sr31 and Sr38 genes, which were previously effective resistance genes • New virulent breed of stem rust has been identified in Uganda's wheat fields (1999) and then in Kenya, Ethiopia, Yemen, and Iran	Singh et al. (2015); Eshete (2018)

The influence of global climate change (especially El Niño weather phenomenon) on forests, crop production/agriculture, and ecosystems during the last decades and future forecast predictions on the Global Climate are presented in
FAO Report (2016) (http://www.fao.org/3/a-i6049e.pdf)
Oxfam Media Briefing Report (2015) https://oxfamilibrary.openrepository.com/bitstream/handle/10546/578822/mb-El-Nino-uncharted-waters-updated.pdf;jsessionid=F5365A5B862B785C77D25C14084073CA?sequence=13
WMO OMM Report (2016) https://unfccc.int/sites/default/files/wmostatement_on_the_status_of_the_global_climate_2016.pdf
Pacific ENSO Bulletin (2015) https://www.weather.gov/media/peac/PEU/PEU_v21_n4.pdf
and in publication of the Asia and Pacific seed association "Asoan Seed" (vol. 24, (1), 2018) apsaseed.org; https://apsaseed.org/AsianSeed2018/AS_V24_I01_single.pdf
Understanding the drought impact of El Niño on the global agricultural areas: An assessment using FAO's, Agricultural Stress Index (ASI), Oscar Rojas, NRC (FAO), Yanyun Li, EST (FAO), Renato Cumani, NRL (FAO); http://www.fao.org/3/a-i4251e.pdf

type of environmental stresses (Berg and Smalla 2009; Oburger et al. 2013; Chaparro et al. 2014; Quiza et al. 2015; Okubo et al. 2016; Jacoby et al. 2017; Ravichandran and Thangavelu 2017; Wang et al. 2017; Ilangumaran et al. 2018; Heinen et al. 2018a, b). These bioactive compounds, which include among others signaling molecules of host microbes and microbiomes living in other habitats, play a key role in the interactions between plant roots and soil microbes and can alter soil dynamics and microbiological diversity, select best microbial cooperators for the plant, and influence microbial metabolic activity or soil extracellular enzyme activity interactions (Venturi and Keel 2016; Garcia and Kao-Kniffin 2018). Thus, root exudates modify ecological interactions between plants and microorganisms (e.g., symbiotic, mutualistic, competitions), which determine plant health and productivity, modulate plant tolerance or resistance, as well as enable plants to adapt to the changing environment (Dangl et al. 2013; Morel and Castro-Sowinski 2013; Oburger et al. 2013; Chaparro et al. 2014; Quiza et al. 2015; Vandenkoornhuyse et al. 2015; Vannier et al. 2015; Okubo et al. 2016; Ravichandran and Thangavelu 2017; Wang et al. 2017; Ilangumaran et al. 2018). Moreover, plant exudates can inhibit the growth of competing plant species, e.g., native and invasive plants, thereby influencing plant invasion (Ravichandran and Thangavelu 2017; Wang et al. 2017; Ilangumaran et al. 2018). Furthermore, plants have evolved many molecules involved in an integrated signal transduction network working in concert to coordinate the balance between the use of assimilates in plant development and the defense response under both abiotic and biotic stress conditions (Ruan 2014). The signal transduction is transmitted through molecular components such as ROS, nitric oxide (Farnese et al. 2016), sugars, and Ca^{2+} signatures (Niu and Liao 2016), which have been reported to be induced by internal developmental triggers or different environmental stresses (Iqbal et al. 2013). As compounds of a complex network of interconnected systems, they cross talk with molecular mechanisms including transcription factors, kinase cascades, and gene regulation (Atkinson and Urwin 2012; Vile et al. 2012; Sham et al. 2015; Zhang and Sonnewald 2017) and integrate the signal (Matsuda et al. 2016), regulate stress response, store information in plants, and affect plant performance (Luttge and Thellier 2016). Microorganisms are also involved in stress tolerance of glycophytes (Rosenblueth and Martinez-Romero 2006) and halophytes (Ruppel et al. 2013) through participation in the production of bioactive compounds, phytohormones, siderophores, osmolytes, or antioxidants. Among bioactive compounds, phytohormones produced by microorganisms are critical for plant defense against abiotic and biotic stresses through regulation of signaling pathways or the cross talk mediated by phytohormones (e.g., SA, JA and ET) leading to plant systemic acquired resistance (SAR) or immune systemic resistance (ISR) induction and to the reduction of phytotoxic microbial communities (Miura and Tada 2014; Quiza et al. 2015; Pozo et al. 2015; Ilangumaran et al. 2018). At the same time, antibiotics produced by microorganisms, volatile signals, and surface factor compounds recognized by the host plant are able to act as the primary barrier of plant defense and activate an immune response system via plant cell receptors which govern microbe recognition and the response to the infection. The plant immune system includes receptors of extracellular cell surface pattern recognition activated by the identification of evolutionarily conserved pathogen or molecular pattern associated with microorganisms, which leads to a complex response limiting microbial colonization or shaping the soil microbiome in the rhizosphere by means of intracellular signaling and translational reprogramming (Dangl et al. 2013; Quiza et al. 2015).

1.7 Carbon and Nitrogen Balance Under Climate Change

The land and ocean biogeochemical cycles are key components of the Earth's climate system. Changed environmental conditions provide plants with modified critical nutrients, including C and N (Fig. 1.2). Many studies highlighted the potential for climate change to induce a significant loss of C from vulnerable reservoirs. For example, the dieback of the Amazon forests induced by climate change has been suggested for decades, though with inconclusive evidence. Similarly, warming at high latitudes leads to permafrost thawing with a risk of CO_2 and CH_4 release to the atmosphere. Further climate change also alters ecosystem disturbance regimes, which can significantly decrease carbon sinks and sporadically release CO_2 to the atmosphere. Moreover, a direct result of global climate change, especially due to increased CO_2 level, elevated moisture, or temperature, are changes in the stock of soil organic C and/or N due to changes in organic matter supply from biomass and the quality and quantity of resource input (Lal 2010; Scharlemann et al. 2014; Santoyo et al. 2017) as well as the alteration in soil C/N ratio, which is regulated among others by soil-plant-microbe interactions, especially microbial biomass, structure of microbial communities, and microbial metabolism (Bradford et al. 2013; Steinweg et al. 2013; Smith et al. 2015; Alster et al. 2016; Karmakar et al. 2016; Llado et al. 2017; Makinen et al. 2017; Santoyo et al. 2017; Maron et al. 2018). Moreover, the elevated CO_2 or N deposition as a result of global climate change may lead to N or C limitation in habitats/ecosystems (by increasing available soil C or N, respectively) (Balser et al. 2002; Llado et al. 2017) and/or changes in their accumulation and/or regulation (Smith et al. 2015; Karmakar et al. 2016; Llado et al. 2017; Makinen et al. 2017; Santoyo et al. 2017; Maron et al. 2018). Various estimates of the amount of photosynthetically fixed C that is exuded by the roots of different plant species into the rhizosphere as rhizodeposits, i.e., soluble exudates, insoluble secretions, rhizosphere C flow, and detrital root material, are contradictory and range from 5% up to around 30% (Glick 2014) or between 10 and 20% (Badri and Vivanco 2009; Lloyd et al. 2016). A large volume of existing evidence suggests that climate change enhances root exudation of organic compounds into the soil and increased exudate inputs may cause a net loss of soil carbon (Keiluweit et al. 2015). According to Keiluweit et al. (2015), the stimulation of microbiological mineralization of C may be explained by the assumption that exudates provide an easily accessible source of energy for the decomposition of soil carbon (co-metabolism). These authors also showed that an alternative mechanism (biotic–abiotic coupled mechanisms) can cause similar or higher C loss and that a common root exudate, oxalic acid, promotes C loss by releasing organic compounds

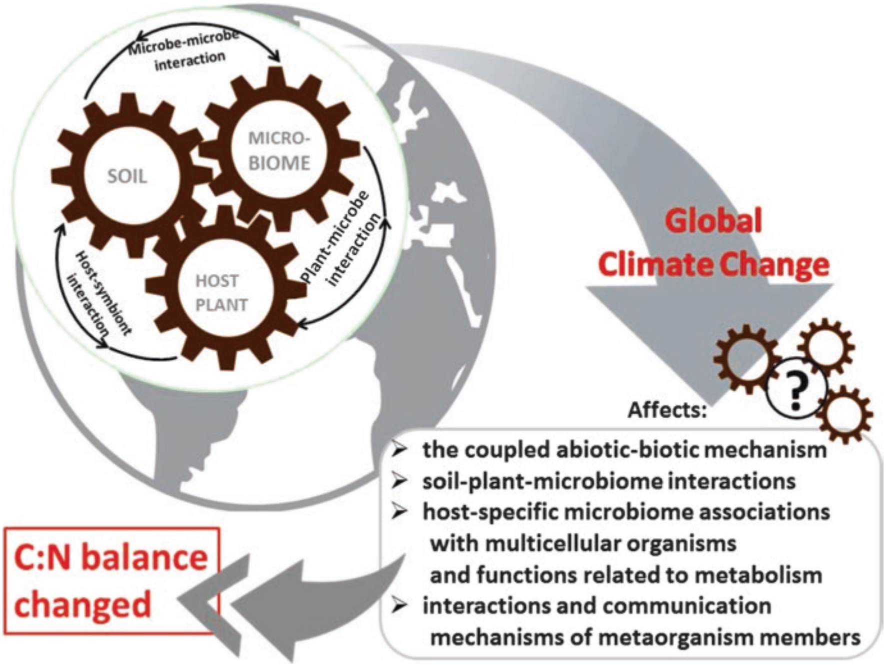

Fig. 1.2 The effect of global climate change on soil-plant-microbiota interactions

from protective associations with minerals. By increasing microbial access to previously protected minerals, this indirect mechanism has accelerated C loss more than by simply increasing the supply of more energy-efficient substrates.

It has also been shown that soil microbiomes, including bacterial and fungal communities, correlate with specific soil geochemical features (including C and N cycles) and influence plant biodiversity (Kourtev et al. 2002; Yang et al. 2013; Li et al. 2014; Qin et al. 2014; Dawson and Schrama 2016; Ravichandran and Thangavelu 2017), though both bacteria and fungi show differences in shaping C and N distribution in the soil (Mueller et al. 2015; Sun 2018). Soil type and plant vitality determine the deposition of C substrate from roots and the competition with roots for N driven by microbial demand for this nutrient (Lloyd et al. 2016). Nair and Ngouajio (2012) showed that soil microbial biomass carbon and nitrogen (including bacteria and fungus species abundance) function as a living nutrient pool in the soil. Soil total C correlates more with soil bacterial (especially the anaerobic and facultative anaerobic groups) than with fungal communities (Sun 2018).

Yu et al. (2018) found that the possible effect of multiple climate change factors on soil microbial communities in semiarid grassland ecosystems may be connected with the suppression of N cycling under warmer temperatures and the enhancement of carbon and nitrogen cycling processes under either elevated CO_2 alone or together with warmer temperatures. The different effects on C and N regulation result from changes in the expression of key functional genes involved in C degradation and fixation, methane metabolism, N fixation, denitrification, and N mineralization. The expression of all these genes has been shown to be upregulated under elevated CO_2, while the expression of genes involved in denitrification and ammonification is downregulated under warmer temperatures alone. Chen et al. (2019) found that N deposition stimulates soil C accumulation by reducing lignin-modified enzyme activity of microorganisms and further suggested that reduced microbial decomposition is a key process contributing to soil C sequestration with N addition, hence soil C/N ratio. Mueller et al. (2015) showed the resistance of fungi and the sensitivity of bacteria to N changes and suggested that the increased N inputs predicted for many dry ecosystems could shift the nutrient cycle toward paths driven mainly by fungal communities. The influence of changed N level or N mineralization rate on the alteration in soil microbial communities, which in turn affects soil N cycle, and thus plant growth and productivity has also been shown by, e.g., Smithwick et al. (2012), Philippot et al. (2013), and Mueller et al. (2015). Furthermore, plant growth conditions influence (a) the rate of photosynthesis; (b) rhizodeposition, which provides sufficient energy for microbes to obtain nutrients from soil organic matter mineralization; and (c) plant and microbial competition for N and other nutrients in the rhizosphere. In addition, the possible improvement of soil quality in terms of N and organic matter content as well as soil aggregation promoting hydrostability in the rhizosphere was also shown. The benefits included increased N content and higher amounts of organic matter and soil aggregation in the soil around the roots (Requena et al. 2001).

1.8 Conclusion

To summarize, global climate change affects the coupled soil abiotic–biotic mechanisms and leads to changes in carbon and nitrogen processes/cycles in habitats and ecosystems or accelerates these alterations. They are accompanied by changes in plant biodiversity, microbiome community structure, and soil-plant-microbiome interactions. When considering the impact of climate change, one should take into account its effects on the host plant, specific associations of host microbial organisms with multicellular organisms, and their functions related to metabolism, immunity, and environmental adaptation, inter alia, as the interactions and communication mechanisms among members of the metaorganism are expected to play a crucial role in maintaining the fitness of plants, the stability of the microbiome, and the flexibility and resistance to environmental disturbances.

References

Abang M, Malhotra R (2008) Chickpea and climate change. ICARDA Caravan; Special Issue on Climate Change 25:9–12

Abdullah AS, Moffat CS, Lopez-Ruiz FJ, Gibberd MR, Hamblin J, Zerihun A (2017) Host-multi-pathogen warfare: pathogen interactions in co-infected plants. Front Plant Sci 8:1806. https://doi.org/10.3389/fpls.2017.01806

Adesemoye AO, Egamberdieva D (2013) Beneficial effects of plant growth-promoting rhizobacteria on improved crop production: prospects for developing economies. In: Maheshwari DK, Saraf M, Aeron A (eds) Bacteria in agrobiology: crop productivity. Springer, Berlin, pp 45–63. https://doi.org/10.1007/978-3-642-37241-4_2

Agrawal AA, Hastings AP, Fines DM, Bogdanowicz S, Huber M (2018) Insect herbivory and plant adaptation in an early successional community. Evolution 72(5):1020–1033. https://doi.org/10.1111/evo.13451

Ahanger RA, Bhat HA, Bhat TA, Ganie S, Lone AA, Wani IA, Ganai SA, Haq S, Khan OA, Junaid JM (2013) Impact of climate change on plant diseases. Int J Mod Plant Anim Sci 1(3):105–115

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. New Phytol 165(2):351–371. https://doi.org/10.1111/j.1469-8137.2004.01224.x

Akyol TY, Niwa R, Hirakawa H, Maruyama H, Sato T, Suzuki T, Fukunaga A, Sato T, Yoshida S, Tawaraya K, Saito M, Ezawa T, Sato S (2019) Impact of introduction of arbuscular mycorrhizal fungi on the root microbial community in agricultural fields. Microbes Environ 34(1):23–32. https://doi.org/10.1264/jsme2.ME18109

Alster CJ, Baas P, Wallenstein MD, Johnson NG, von Fischer JC (2016) Temperature sensitivity as a microbial trait using parameters from macromolecular rate theory. Front Microbiol 7:1821. https://doi.org/10.3389/fmicb.2016.01821

Altizer S, Ostfeld RS, Johnson PTJ, Kutz S, Harvell CD (2013) Climate change and infectious diseases: from evidence to a predictive framework. Science 341(6145):514–519. https://doi.org/10.1126/science.1239401

Alves PDD, Siqueira FF, Facchin S, Horta CCR, Victoria JMN, Kalapothakis E (2014) Survey of microbial enzymes in soil, water, and plant microenvironments. Open Microbiol J 8:25–31. https://doi.org/10.2174/1874285801408010025

Andersen EJ, Ali S, Byamukama E, Yen Y, Nepal MP (2018) Disease resistance mechanisms in plants. Genes 9(7):E339. https://doi.org/10.3390/genes9070339

Andolfo G, Ercolano MR (2015) Plant innate immunity multicomponent model. Front Plant Sci 6:987. https://doi.org/10.3389/fpls.2015.00987

Asmelash F, Bekele T, Birhane E (2016) The potential role of arbuscular mycorrhizal fungi in the restoration of degraded lands. Front Microbiol 7:1095. https://doi.org/10.3389/fmicb.2016.01095

Atkinson NJ, Urwin PE (2012) The interaction of plant biotic and abiotic stresses: from genes to the field. J Exp Bot 63(10):3523–3543. https://doi.org/10.1093/jxb/ers100

Avila Mendez K, Romero HM (2017) Plant responses to pathogen attack: molecular basis of qualitative resistance. Rev Facult Nac Agron Medellin 70:8225–8235

Bach EM, Williams RJ, Hargreaves SK, Yang F, Hofmockel KS (2018) Greatest soil microbial diversity found in micro-habitats. Soil Biol Biochem 118:217–226. https://doi.org/10.1016/j.soilbio.2017.12.018

Badri DV, Vivanco JM (2009) Regulation and function of root exudates. Plant Cell Environ 32(6):666–681. https://doi.org/10.1111/j.1365-3040.2009.01926.x

Bahadur I, Maurya BR, Meena VS, Saha M, Kumar A, Aeron A (2017) Mineral release dynamics of tricalcium phosphate and waste muscovite by mineral-solubilizing *Rhizobacteria* isolated from indo-gangetic plain of India. Geomicrobiol J 34(5):454–466. https://doi.org/10.1080/01490451.2016.1219431

Balser TC, Kinzig AP, Firestone MK (2002) Linking soil microbial communities and ecosystem functioning. In: Kinzig AP, Pacala SW, Tilman D (eds) The functional consequences of biodiversity. Empirical progress and theoretical extensions (MPB-33). Princeton University Press, Princeton NJ, pp 265–293

Bang C, Dagan T, Deines P, Dubilier N, Duschl WJ, Fraune S, Hentschel U, Hirt H, Huelter N, Lachnit T, Picazo D, Pita L, Pogoreutz C, Raedecker N, Saad MM, Schmitz RA, Schulenburg H, Voolstra CR, Weiland-Braeuer N, Ziegler M, Bosch TCG (2018) Metaorganisms in extreme environments: do microbes play a role in organismal adaptation? Zoology 127:1–19. https://doi.org/10.1016/j.zool.2018.02.004

Bardgett RD, van der Putten WH (2014) Belowground biodiversity and ecosystem functioning. Nature 515(7528):505–511. https://doi.org/10.1038/nature13855

Bartz R, Kowarik I (2019) Assessing the environmental impacts of invasive alien plants: a review of assessment approaches. Neobiota 43:69–99. https://doi.org/10.3897/neobiota.43.30122

Bebber DP, Holmes T, Gurr SJ (2014) The global spread of crop pests and pathogens. Glob Ecol Biogeogr 23(12):1398–1407. https://doi.org/10.1111/geb.12214

Bell M, Charles-Edwards E, Ueffing P, Stillwell J, Kupiszewski M, Kupiszewska D (2015) Internal migration and development: comparing migration intensities around the world. Popul Dev Rev 41(1):33–58. https://doi.org/10.1111/j.1728-4457.2015.00025.x

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15(4):365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Berg G, Smalla K (2009) Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiol Ecol 68(1):1–13. https://doi.org/10.1111/j.1574-6941.2009.00654.x

Berg G, Grube M, Schloter M, Smalla K (2014) The plant microbiome and its importance for plant and human health. Front Microbiol 5:491. https://doi.org/10.3389/fmicb.2014.00491

Blackburn TM, Pysek P, Bacher S, Carlton JT, Duncan RP, Jarosik V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26(7):333–339. https://doi.org/10.1016/j.tree.2011.03.023

Blagodatskaya E, Kuzyakov Y (2013) Active microorganisms in soil: critical review of estimation criteria and approaches. Soil Biol Biochem 67:192–211. https://doi.org/10.1016/j.soilbio.2013.08.024

Blank RR, Youn JA (2002) Influence of the exotic invasive crucifer, *Lepidium latifolium* on soil properties and elemental cycling. Soil Sci 167(12):821–829. https://doi.org/10.1097/01.ss.0000043032.84859.8d

Blumenthal DM, Mueller KE, Kray JA, LeCain DR, Pendall E, Duke S, Zelikova TJ, Dijkstra FA, Williams DG, Morgan JA (2018) Warming and elevated CO_2 interact to alter seasonality and reduce variability of soil water in a semiarid grassland. Ecosystems 21(8):1533–1544. https://doi.org/10.1007/s10021-018-0237-1

Bodner G, Nakhforoosh A, Kaul HP (2015) Management of crop water under drought: a review. Agron Sustain Dev 35(2):401–442. https://doi.org/10.1007/s13593-015-0283-4

Bosch TCG, McFall-Ngai MJ (2011) Metaorganisms as the new frontier. Zoology 114(4):185–190. https://doi.org/10.1016/j.zool.2011.04.001

Bourguet D, Delmotte F, Franck P, Guillemaud T, Reboud X, Vacher C, Walker AS, Consortium REX (2016) Combining selective pressures to enhance the durability of disease resistance genes. Front Plant Sci 7:1916. https://doi.org/10.3389/fpls.2016.01916

Bradford SA, Morales VL, Zhang W, Harvey RW, Packman AI, Mohanram A, Welty C (2013) Transport and fate of microbial pathogens in agricultural settings. Crit Rev Environ Sci Technol 43(8):775–893. https://doi.org/10.1080/10643389.2012.710449

Brierley AS, Kingsford MJ (2009) Impacts of climate change on marine organisms and ecosystems. Curr Biol 19(14):R602–R614. https://doi.org/10.1016/j.cub.2009.05.046

Brooker RW (2006) Plant-plant interactions and environmental change. New Phytol 171(2):271–284. https://doi.org/10.1111/j1.469-8137.2006.01752.x

Brunner SM, Goos RJ, Swenson SJ, Foster SP, Schatz BG, Lawley YE, Prischmann-Voldseth DA (2015) Impact of nitrogen fixing and plant growth-promoting bacteria on a phloem-feeding soybean herbivore. Appl Soil Ecol 86:71–81. https://doi.org/10.1016/j.apsoil.2014.10.007

Bukowski AR, Schittko C, Petermann JS (2018) The strength of negative plant-soil feedback increases from the intraspecific to the interspecific and the functional group level. Ecol Evol 8(4):2280–2289. https://doi.org/10.1002/ece3.3755

Bulgarelli D, Schlaeppi K, Spaepen S, van Themaat EVL, Schulze-Lefert P (2013) Structure and functions of the bacterial microbiota of plants. Annu Rev Plant Biol 64:807–838. https://doi.org/10.1146/annurev-arplant-050312-120106

Bulgarelli D, Garrido-Oter R, Munch PC, Weiman A, Droge J, Pan Y, McHardy AC, Schulze-Lefert P (2015) Structure and function of the bacterial root microbiota in wild and domesticated barley. Cell Host Microbe 17(3):392–403. https://doi.org/10.1016/j.chom.2015.01.011

Cannone N, Pignatti S (2014) Ecological responses of plant species and communities to climate warming: upward shift or range filling processes? Clim Chang 123(2):201–214. https://doi.org/10.1007/s10584-014-1065-8

Carrier TJ, Reitzel AM (2017) The hologenome across environments and the implications of a host-associated microbial repertoire. Front Microbiol 8:802. https://doi.org/10.3389/fmicb.2017.00802

Cassia R, Nocioni M, Correa-Aragunde N, Lamattina L (2018) Climate change and the impact of greenhouse gasses: CO_2 and NO, friends and foes of plant oxidative stress. Front Plant Sci 9:273. https://doi.org/10.3389/fpls.2018.00273

Castell WZ, Fleischmann F, Heger T, Matyssek R (2016) Shaping theoretic foundations of holobiont-like systems. In: Luttge U, Canovas FM, Matyssek R (eds) Progress in botany 77. Progress in botany, vol 77, pp 219–244. https://doi.org/10.1007/978-3-319-25688-7_7

Caubel J, Launay M, Ripoche D, Gouache D, Buis S, Huard F, Huber L, Brun F, Bancal MO (2017) Climate change effects on leaf rust of wheat: implementing a coupled crop-disease model in a French regional application. Eur J Agron 90:53–66. https://doi.org/10.1016/j.eja.2017.07.004

Chakraborty S (2005) Potential impact of climate change on plant-pathogen interactions. Australas Plant Pathol 34(4):443–448. https://doi.org/10.1071/ap05084

Chala D, Meseret T (2018) Effect of elevated CO2 and temperature on crop-disease interactions under rapid climate change. Int J Environ Sci Nat Resour 13(1):555851. https://doi.org/10.19080/IJESNR.2018.13.555851

Challinor AJ, Muller C, Asseng S, Deva C, Nicklin KJ, Wallach D, Vanuytrecht E, Whitfield S, Ramirez-Villegas J, Koehler AK (2018) Improving the use of crop models for risk assessment and climate change adaptation. Agric Syst 159:296–306. https://doi.org/10.1016/j.agsy.2017.07.010

Chaparro JM, Badri DV, Vivanco JM (2014) Rhizosphere microbiome assemblage is affected by plant development. ISME J 8(4):790–803. https://doi.org/10.1038/ismej.2013.196

Cheeseman JM (2015) The evolution of halophytes, glycophytes and crops, and its implications for food security under saline conditions. New Phytol 206(2):557–570. https://doi.org/10.1111/nph.13217

Chen LY, Liu L, Qin SQ, Yang GB, Fang K, Zhu B, Kuzyakov Y, Chen PD, Xu YP, Yang YH (2019) Regulation of priming effect by soil organic matter stability over a broad geographic scale. Nat Commun 10. https://doi.org/10.1038/s41467-019-13119-z

Chevin LM, Hoffmann AA (2017) Evolution of phenotypic plasticity in extreme environments. Philos Trans R Soc Lond B Biol Sci 372(1723):20160138. https://doi.org/10.1098/rstb.2016.0138

Christensen JH, Krishna Kumar K, Aldrian E, An S-I, Cavalcanti IFA, de Castro M, Dong W, Goswami P, Hall A, J.K. Kanyanga, Kitoh A, Kossin J, Lau N-C, Renwick J, Stephenson DB, Xie S-P, Zhou T (2013) Climate phenomena and their relevance for future regional climate change. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) IPCC, 2013: climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, 1535 pp

Chojak-Kozniewska J, Kuzniak E, Zimny J (2018) The effects of combined abiotic and pathogen stress in plants: insights from salinity and *Pseudomonas syringae* pv *lachrymans* interaction in cucumber. Front Plant Sci 9:1691. https://doi.org/10.3389/fpls.2018.01691

Chowdhury S, Basu A, Kundu S (2017) Biotrophy-necrotrophy switch in pathogen evoke differential response in resistant and susceptible sesame involving multiple signaling pathways at different phases. Sci Rep 7:17251. https://doi.org/10.1038/s41598-017-17248-7

Classen AT, Sundqvist MK, Henning JA, Newman GS, Moore JAM, Cregger MA, Moorhead LC, Patterson CM (2015) Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: what lies ahead? Ecosphere 6(8):1–21. https://doi.org/10.1890/es15-00217.1

Coats VC, Rumpho ME (2014) The rhizosphere microbiota of plant invaders: an overview of recent advances in the microbiomics of invasive plants. Front Microbiol 5:368. https://doi.org/10.3389/fmicb.2014.00368

Compant S, Samad A, Faist H, Sessitsch A (2019) A review on the plant microbiome: ecology, functions, and emerging trends in microbial application. J Adv Res 19:29–37. https://doi.org/10.1016/j.jare.2019.03.004

Cong J, Su X, Liu X, Xue Y, Li G, Li D, Zhang Y (2016) Changes and drivers of plant community in the natural broadleaved forests across geographic gradient. Acta Ecol Sin 36(5):361–366

Conniff R (2017) The nitrogen problem: why global warming is making it worse. Yale Environ 360. https://e360.yale.edu/features/the-nitrogen-problem-why-global-warming-is-making-it-worse

Cowan D, Hughes K, Pointing S, Mataloni G, Blamey J, Kong W (2018) Non-native microbial introductions: what risk to Antarctic ecosystems? Antarct Environ Portal. https://doi.org/10.18124/D40S5T

Crafts-Brandner SJ, Salvucci ME (2002) Sensitivity of photosynthesis in a C4 plant, maize, to heat stress. Plant Physiol 129(4):1773–1780. https://doi.org/10.1104/pp.002170

Croll D, McDonald BA (2017) The genetic basis of local adaptation for pathogenic fungi in agricultural ecosystems. Mol Ecol 26(7):2027–2040. https://doi.org/10.1111/mec.13870

Dai Z-C, Fu W, Wan L-Y, Cai H-H, Wang N, Qi S-S, Du D-L (2016) Different growth promoting effects of endophytic bacteria on invasive and native clonal plants. Front Plant Sci 7:706. https://doi.org/10.3389/fpls.2016.00706

Dam M, Bergmark L, Vestergard M (2017) Elevated CO_2 increases fungal-based micro-foodwebs in soils of contrasting plant species. Plant Soil 415(1–2):549–561. https://doi.org/10.1007/s11104-017-3191-3

Dangl JL, Horvath DM, Staskawicz BJ (2013) Pivoting the plant Immune system from dissection to deployment. Science 341(6147):746–751. https://doi.org/10.1126/science.1236011

Das T, Majumdar MH, Devi R, Rajesh T (2017) Climate change impacts on plant diseases. SAARC J Agric 14(2):200–209. https://doi.org/10.3329/sja.v14i2.31259

Dassonville N, Vanderhoeven S, Vanparys V, Hayez M, Gruber W, Meerts P (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. Oecologia 157(1):131–140. https://doi.org/10.1007/s00442-008-1054-6

Dawson W, Schrama M (2016) Identifying the role of soil microbes in plant invasions. J Ecol 104(5):1211–1218. https://doi.org/10.1111/1365-2745.12619

de Souza HSP, Fiocchi C (2016) Immunopathogenesis of IBD: current state of the art. Nat Rev Gastroenterol Hepatol 13(1):13–27. https://doi.org/10.1038/nrgastro.2016.186

de Vries FT, Caruso T (2016) Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web. Soil Biol Biochem 102:4–9. https://doi.org/10.1016/j.soilbio.2016.06.023

De-la-Pena C, Loyola-Vargas VM (2014) Biotic interactions in the rhizosphere: a diverse cooperative enterprise for plant productivity. Plant Physiol 166(2):701–719. https://doi.org/10.1104/pp.114.241810

Delaunois B, Jeandet P, Clement C, Baillieul F, Dorey S, Cordelier S (2014) Uncovering plant-pathogen crosstalk through apoplastic proteomic studies. Front Plant Sci 5:249. https://doi.org/10.3389/fpls.2014.00249

Denef K, Bubenheim H, Lenhart K, Vermeulen J, Van Cleemput O, Boeckx P, Muller C (2007) Community shifts and carbon translocation within metabolically-active rhizosphere microorganisms in grasslands under elevated CO_2. Biogeosciences 4(5):769–779. https://doi.org/10.5194/bg-4-769-2007

Dimkpa C, Weinand T, Asch F (2009) Plant–rhizobacteria interactions alleviate abiotic stress conditions. Plant Cell Environ 32(12):1682–1694

Dise NB, Ashmore M, Belyazid S, Bleeker A, Bobbink R, de Vries W, Erisman JW, Spranger T, Stevens CJ, van den Berg L (2011) Nitrogen as a threat to European terrestrial biodiversity. In: Bleeker A, Grizzetti B, Howard CM et al (eds) The European nitrogen assessment: sources, effects and policy perspectives. Cambridge University Press, Cambridge, pp 463–494. https://doi.org/10.1017/cbo9780511976988.023

Dodd IC, Perez-Alfocea F (2012) Microbial amelioration of crop salinity stress. J Exp Bot 63(9):3415–3428. https://doi.org/10.1093/jxb/ers033

Doornbos RF, van Loon LC, Bakker P (2012) Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. A review. Agron Sustain Dev 32(1):227–243. https://doi.org/10.1007/s13593-011-0028-y

Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science 344(6181):296–299. https://doi.org/10.1126/science.1248484

Egamberdieva D, Kamilova F, Validov S, Gafurova L, Kucharova Z, Lugtenberg B (2008) High incidence of plant growth-stimulating bacteria associated with the rhizosphere of wheat grown on salinated soil in Uzbekistan. Environ Microbiol 10(1):1–9

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6(6):503–523. https://doi.org/10.1007/s10021-002-0151-3

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650

Ehrenfeld JG, Scott N (2001) Invasive species and the soil: effects on organisms and ecosystem processes. Ecol Appl 11(5):1259–1260. https://doi.org/10.1890/1051-0761(2001)011[1259:isatse]2.0.co;2

Eisenhauer N, Hines J, Isbell F, van der Plas F, Hobbie SE, Kazanski CE, Lehmann A, Liu M, Lochner A, Rilling MC, Vogel A, Worm K, Reich PB (2018) Plant diversity maintains multiple soil functions in future environments. Elife 7:e41228. https://doi.org/10.7554/eLife.41228

Eissfeller V, Beyer F, Valtanen K, Hertel D, Maraun M, Polle A, Scheu S (2013) Incorporation of plant carbon and microbial nitrogen into the rhizosphere food web of beech and ash. Soil Biol Biochem 62:76–81. https://doi.org/10.1016/j.soilbio.2013.03.002

Elad Y, Pertot I (2014) Climate change impacts on plant pathogens and plant diseases. J Crop Improv 28(1):99–139. https://doi.org/10.1080/15427528.2014.865412

Elderd BD, Reilly JR (2014) Warmer temperatures increase disease transmission and outbreak intensity in a host-pathogen system. J Anim Ecol 83(4):838–849. https://doi.org/10.1111/1365-2656.12180

El-Soda M, Malosetti M, Zwaan BJ, Koornneef M, Aarts MGM (2014) Genotype x environment interaction QTL mapping in plants: lessons from *Arabidopsis*. Trends Plant Sci 19(6):390–398. https://doi.org/10.1016/j.tplants.2014.01.001

Eshete BB (2018) Status and challenges of wheat stem rust (*Puccinia graminis* F.sp. *Tritici*) and threats of new races in Ethiopia. Int J For Hortic 4(4):22–31

Etesami H, Beattie GA (2018) Mining halophytes for plant growth-promoting halotolerant bacteria to enhance the salinity tolerance of non-halophytic crops. Front Microbiol 9:148. https://doi.org/10.3389/fmicb.2018.00148

Evangelisti E, Rey T, Schornack S (2014) Cross-interference of plant development and plant-microbe interactions. Curr Opin Plant Biol 20:118–126. https://doi.org/10.1016/j.pbi.2014.05.014

FAO, ITPS (2015) Status of the World's Soil Resources (SWSR)–main report. Food and Agriculture Organization of the United Nations and Intergovernmental Technical Panel on Soils, Rome, p 650

Farnese FS, Menezes-Silva PE, Gusman GS, Oliveira JA (2016) When bad guys become good ones: the key role of reactive oxygen species and nitric oxide in the plant responses to abiotic stress. Front Plant Sci 7:471. https://doi.org/10.3389/fpls.2016.00471

Ferrocino I, Chitarra W, Pugliese M, Gilardi G, Gullino ML, Garibaldi A (2013) Effect of elevated atmospheric CO_2 and temperature on disease severity of *Fusarium oxysporum* F.sp. *lactucae* on lettuce plants. Appl Soil Ecol 72:1–6. https://doi.org/10.1016/j.apsoil.2013.05.015

Fladung M (2016) Transposon activation tagging in plants for gene function discovery. In: Luttge U, Canovas FM, Matyssek R (eds) Progress in botany 77. Progress in botany, vol 77, pp 265–289. https://doi.org/10.1007/978-3-319-25688-7_9

Flowers TJ, Colmer TD (2015) Plant salt tolerance: adaptations in halophytes. Ann Bot 115(3):327–331. https://doi.org/10.1093/aob/mcu267

Flowers TJ, Muscolo A (2015) SPECIAL ISSUE: physiology and ecology of halophytes—plants living in salt-rich environments introduction to the special issue: halophytes in a changing world. AoB Plants 7:plv020. https://doi.org/10.1093/aobpla/plv020

Franklin AM, Aga DS, Cytryn E, Durso LM, McLain JE, Pruden A, Roberts MC, Rothrock MJ, Snow DD, Watson JE, Dungan RS (2016) Antibiotics in agroecosystems: introduction to the special section. J Environ Qual 45(2):377–393. https://doi.org/10.2134/jeq2016.01.0023

Galland G, Harrould-Kolieb E, Herr D (2012) The ocean and climate change policy. Clim Policy 12(6):764–771. https://doi.org/10.1080/14693062.2012.692207

Gans J, Wolinsky M, Dunbar J (2005) Computational improvements reveal great bacterial diversity and high metal toxicity in soil. Science 309(5739):1387–1390. https://doi.org/10.1126/science.1112665

Gao QM, Zhu SF, Kachroo P, Kachroo A (2015) Signal regulators of systemic acquired resistance. Front Plant Sci 6:228. https://doi.org/10.3389/fpls.2015.00228

Garcia J, Kao-Kniffin J (2018) Microbial group dynamics in plant rhizospheres and their implications on nutrient cycling. Front Microbiol 9:1516. https://doi.org/10.3389/fmicb.2018.01516

Garrett KA, Dendy SP, Frank EE, Rouse MN, Travers SE (2006) Climate change effects on plant disease: genomes to ecosystems. Annu Rev Phytopathol 44:489–509. https://doi.org/10.1146/annurev.phyto.44.070505.143420

Gaudet DA, Chen THH (1988) Effect of freezing resistance and low-temperature stress on development of cottony snow mold (*Coprinus psychromorbidus*) in winter wheat. Can J Bot 66(8):1610–1615. https://doi.org/10.1139/b88-219

Gautam HR, Bhardwaj ML, Kumar R (2013) Climate change and its impact on plant diseases. Curr Sci 105(12):1685–1691

Gebrehiwot K (2017) Plant species responses to climate change: a review. Climate Change 3(9):6–19

Gill US, Lee S, Mysore KS (2015) Host versus nonhost resistance: distinct wars with similar arsenals. Phytopathology 105(5):580–587. https://doi.org/10.1094/phyto-11-14-0298-rvw

Gilliam FS (2019) Excess nitrogen in temperate forest ecosystems decreases herbaceous layer diversity and shifts control from soil to canopy structure. Forests 10(1):66. https://doi.org/10.3390/f10010066

Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 169(1):30–39. https://doi.org/10.1016/j.micres.2013.09.009

Godschalx AL, Schaedler M, Trisel JA, Balkan MA, Ballhorn DJ (2015) Ants are less attracted to the extrafloral nectar of plants with symbiotic, nitrogen-fixing rhizobia. Ecology 96(2):348–354. https://doi.org/10.1890/14-1178.1

Gonzalez Megias A, Mueller C (2010) Root herbivores and detritivores shape above-ground multitrophic assemblage through plant-mediated effects. J Anim Ecol 79(4):923–931. https://doi.org/10.1111/j.1365-2656.2010.01681.x

Gonzalez A, Cardinale BJ, Allington GRH, Byrnes J, Endsley KA, Brown DG, Hooper DU, Isbell F, O'Connor MI, Loreau M (2016) Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. Ecology 97(8):1949–1960. https://doi.org/10.1890/15-1759.1

Gorzelak MA, Asay AK, Pickles BJ, Simard SW (2015) SPECIAL ISSUE: using ideas from behavioural ecology to understand plants inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. AoB Plants 7. https://doi.org/10.1093/aobpla/plv050

Gough L, Shaver GR, Carroll J, Royer DL, Laundre JA (2000) Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. J Ecol 88(1):54–66. https://doi.org/10.1046/j.1365-2745.2000.00426.x

Gray AJ, Mogg RJ (2001) Climate impacts on pioneer saltmarsh plants. Clim Res 18(1–2):105–112. https://doi.org/10.3354/cr018105

Guerrero-Ramirez NR, Craven D, Reich PB, Ewel JJ, Isbell F, Koricheva J, Parrotta JA, Auge H, Erickson HE, Forrester DI, Hector A, Joshi J, Montagnini F, Palmborg C, Piotto D, Potvin C, Roscher C, van Ruijven J, Tilman D, Wilsey B, Eisenhauer N (2017) Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. Nat Ecol Evol 1(11):1639–1642. https://doi.org/10.1038/s41559-017-0325-1

Guo X, Zhou XS, Hale L, Yuan MT, Feng JJ, Ning DL, Shi Z, Qin YJ, Liu FF, Wu LY, He ZL, Van Nostrand JD, Liu XD, Luo YQ, Tiedje JM, Zhou JZ (2018) Taxonomic and functional responses of soil microbial communities to annual removal of aboveground plant biomass. Front Microbiol 9:954. https://doi.org/10.3389/fmicb.2018.00954

Hansen J, Sato M, Kharecha P, Russell G, Lea DW, Siddall M (2007) Climate change and trace gases. Philos Trans A Math Phys Eng Sci 365(1856):1925–1954. https://doi.org/10.1098/rsta.2007.2052

Hassani MA, Duran P, Hacquard S (2018) Microbial interactions within the plant holobiont. Microbiome 6:58. https://doi.org/10.1186/s40168-018-0445-0

Hawkes CV, Wren IF, Herman DJ, Firestone MK (2005) Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecol Lett 8(9):976–985. https://doi.org/10.1111/j.1461-0248.2005.00802.x

Hawkins AP, Crawford KM (2018) Interactions between plants and soil microbes may alter the relative importance of intraspecific and interspecific plant competition in a changing climate. AoB Plants 10(4). https://doi.org/10.1093/aobpla/ply039

Heinen R, Biere A, Harvey JA, Bezemer TM (2018a) Effects of soil organisms on aboveground plant-insect interactions in the field: patterns, mechanisms and the role of methodology. Front Ecol Evol 6:106. https://doi.org/10.3389/fevo.2018.00106

Heinen R, van der Sluijs M, Biere A, Harvey JA, Bezemer TM (2018b) Plant community composition but not plant traits determine the outcome of soil legacy effects on plants and insects. J Ecol 106(3):1217–1229. https://doi.org/10.1111/1365-2745.12907

Helfer S (2014) Rust fungi and global change. New Phytol 201(3):770–780. https://doi.org/10.1111/nph.12570

Herman DJ, Firestone MK, Nuccio E, Hodge A (2012) Interactions between an arbuscular mycorrhizal fungus and a soil microbial community mediating litter decomposition. FEMS Microbiol Ecol 80(1):236–247. https://doi.org/10.1111/j.1574-6941.2011.01292.x

Herr C, Chapuis-Lardy L, Dassonville N, Vanderhoeven S, Meerts P (2007) Seasonal effect of the exotic invasive plant *Solidago gigantea* on soil pH and P fractions. J Plant Nutr Soil Sci 170(6):729–738. https://doi.org/10.1002/jpln.200625190

Hickman JE, Ashton IW, Howe KM, Lerdau MT (2013) The native-invasive balance: implications for nutrient cycling in ecosystems. Oecologia 173(1):319–328. https://doi.org/10.1007/s00442-013-2607-x

Hoegh-Guldberg O, Jacob D, Taylor M, Bindi M, Brown S, Camilloni I, Diedhiou A, Djalante R, Ebi KL, Engelbrecht F, Guiot J, Hijioka Y, Mehrotra S, Payne A, Seneviratne SI, Thomas A, Warren R, Zhou GY (2018) Impacts of 1.5°C global warming on natural and human systems. In: Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T (eds) Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty

Hoglind M, Bakken AK, Jorgensen M, Ostrem L (2010) Tolerance to frost and ice encasement in cultivars of timothy and perennial ryegrass during winter. Grass Forage Sci 65(4):431–445. https://doi.org/10.1111/j.1365-2494.2010.00762.x

Hou EQ, Chen CR, Luo YQ, Zhou GY, Kuang YW, Zhang YG, Heenan M, Lu XK, Wen DZ (2018) Effects of climate on soil phosphorus cycle and availability in natural terrestrial ecosystems. Glob Chang Biol 24(8):3344–3356. https://doi.org/10.1111/gcb.14093

Hsiang T, Matsumoto N, Millett SM (1999) Biology and management of typhula snow molds of turfgrass. Plant Dis 83(9):788–798. https://doi.org/10.1094/pdis.1999.83.9.788

Hutchins DA, Fu F (2017) Microorganisms and ocean global change. Nat Microbiol 2(6):17058. https://doi.org/10.1038/nmicrobiol.2017.58

Ilangumaran G, Lamont JR, Smith DL (2018) The role of the phytomicrobiome in maintaining biofuel crop production in a changing climate. In: Kashyap PL, Srivastava AK, Tiwari SP, Kumar S (eds) Microbes for climate resilient agriculture. Wiley, Hoboken, pp 1–24

Inderjit (2005) Soil microorganisms: an important determinant of allelopathic activity. Plant Soil 274(1–2):227–236. https://doi.org/10.1007/s11104-004-0159-x

IPCC (2013) Climate change 2013: the physical science basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. The International Panel on Climate Change (IPCC), Geneva

IPCC (2018) Intergovernmental Panel on Climate Change: 2018. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. The International Panel on Climate Change (IPCC), Geneva

ISAC (2006) Invasive species definition clarification and guidance. Invasive Species Advisory Committee (ISAC)

Islam W (2018) Plant disease epidemiology: disease triangle and forecasting mechanisms in highlights. Hosts Viruses 5(1):7–11. https://doi.org/10.17582/journal.hv/2018/5.1.7.11

Iqbal N, Trivellini A, Masood A, Ferrante A, Khan NA (2013) Current understanding on ethylene signaling in plants: the influence of nutrient availability. Plant Physiol Biochem 73:128–138. https://doi.org/10.1016/j.plaphy.2013.09.011

Jacoby R, Peukert M, Succurro A, Koprivova A, Kopriva S (2017) The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions. Front Plant Sci 8:1617. https://doi.org/10.3389/fpls.2017.01617

Jansson JK, Hofmockel KS (2018) The soil microbiome—from metagenomics to metaphenomics. Curr Opin Microbiol 43:162–168. https://doi.org/10.1016/j.mib.2018.01.013

Jones RAC (2016) Future scenarios for plant virus pathogens as climate change progresses. In: Kielian M, Maramorosch K, Mettenleiter TC (eds) Advances in virus research 95. Advances in virus research, vol 95, pp 87–147. https://doi.org/10.1016/bs.aivir.2016.02.004

Jwa NS, Hwang BK (2017) Convergent evolution of pathogen effectors toward reactive oxygen species signaling networks in plants. Front Plant Sci 8:1687. https://doi.org/10.3389/fpls.2017.01687

Karmakar R, Das I, Dutta D, Rakshit A (2016) Potential effects of climate change on soil properties: a review. Sci Int 4(2):51–73

Keiluweit M, Bougoure JJ, Nico PS, Pett-Ridge J, Weber PK, Kleber M (2015) Mineral protection of soil carbon counteracted by root exudates. Nat Clim Chang 5(6):588–595

Kelly M (2019) Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. Philos Trans R Soc Lond B Biol Sci 374(1768):20180176. https://doi.org/10.1098/rstb.2018.0176

Kerchev PI, Fenton B, Foyer CH, Hancock RD (2012) Plant responses to insect herbivory: interactions between photosynthesis, reactive oxygen species and hormonal signalling pathways. Plant Cell Environ 35(2):441–453. https://doi.org/10.1111/j.1365-3040.2011.02399.x

Khare E, Yadav A (2017) The role of microbial enzyme systems in plant growth promotion. Clim Chang Environ Sustain 5(2):122–145

Kos M, Tuijl MAB, de Roo J, Mulder PPJ, Bezemer TM (2015a) Plant-soil feedback effects on plant quality and performance of an aboveground herbivore interact with fertilisation. Oikos 124(5):658–667. https://doi.org/10.1111/oik.01828

Kos M, Tuijl MAB, de Roo J, Mulder PPJ, Bezemer TM (2015b) Species-specific plant-soil feedback effects on above-ground plant-insect interactions. J Ecol 103(4):904–914. https://doi.org/10.1111/1365-2745.12402

Kourtev PS, Ehrenfeld JG, Haggblom M (2002) Exotic plant species alter the microbial community structure and function in the soil. Ecology 83(11):3152–3166. https://doi.org/10.1890/0012-9658(2002)083[3152:epsatm]2.0.co;2

Kuebbing SE, Classen AT, Simberloff D (2014) Two co-occurring invasive woody shrubs alter soil properties and promote subdominant invasive species. J Appl Ecol 51(1):124–133. https://doi.org/10.1111/1365-2664.12161

Lakshmanan V, Selvaraj G, Bais HP (2014) Functional soil microbiome: belowground solutions to an aboveground problem. Plant Physiol 166(2):689–700. https://doi.org/10.1104/pp.114.245811

Lal R (2010) Managing soils and ecosystems for mitigating anthropogenic carbon emissions and advancing global food security. Bioscience 60(9):708–721. https://doi.org/10.1525/bio.2010.60.9.8

Lamichhane JR, Venturi V (2015) Synergisms between microbial pathogens in plant disease complexes: a growing trend. Front Plant Sci 6:385. https://doi.org/10.3389/fpls.2015.00385

Lareen A, Burton F, Schafer P (2016) Plant root-microbe communication in shaping root microbiomes. Plant Mol Biol 90(6):575–587. https://doi.org/10.1007/s11103-015-0417-8

Larios L, Suding KN (2015) Competition and soil resource environment alter plant—soil feedbacks for native and exotic grasses. AoB Plants 7. https://doi.org/10.1093/aobpla/plu077

Larranaga N, Ignacio Hormaza J (2016) Advances in genetic diversity analysis in fruit tree crops. In: Luttge U, Canovas FM, Matyssek R (eds) Progress in botany 77. Progress in botany, vol 77, pp 245–264. https://doi.org/10.1007/978-3-319-25688-7_8

Lebeis SL, Paredes SH, Lundberg DS, Breakfield N, Gehring J, McDonald M, Malfatti S, del Rio TG, Jones CD, Tringe SG, Dangl JL (2015) Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa. Science 349(6250):860–864. https://doi.org/10.1126/science.aaa8764

Lee DS, Fahey DW, Forster PM, Newton PJ, Wit RCN, Lim LL, Owen B, Sausen R (2009) Aviation and global climate change in the 21st century. Atmos Environ 43(22–23):3520–3537. https://doi.org/10.1016/j.atmosenv.2009.04.024

Lee HA, Lee HY, Seo E, Lee J, Kim SB, Oh S, Choi E, Choi E, Lee SE, Choi D (2017) Current understandings of plant nonhost resistance. Mol Plant Microbe Interact 30(1):5–15. https://doi.org/10.1094/mpmi-10-16-0213-cr

Lefevre C, Rekik F, Alcantara V, Wiese L (2017) Soil organic carbon: the hidden potential. Food and Agriculture Organization of the United Nations (FAO)

Legay N, Lavorel S, Baxendale C, Krainer U, Bahn M, Binet M-N, Cantarel AAM, Colace M-P, Foulquier A, Kastl E-M, Grigulis K, Mouhamadou B, Poly F, Pommier T, Schloter M, Clement J-C, Bardgett RD (2016) Influence of plant traits, soil microbial properties, and abiotic parameters on nitrogen turnover of grassland ecosystems. Ecosphere 7(11):e01448. https://doi.org/10.1002/ecs2.1448/full

Lenton TM (2012) Arctic climate tipping points. Ambio 41(1):10–22. https://doi.org/10.1007/s13280-011-0221-x

Lenton TM, Held H, Kriegler E, Hall JW, Lucht W, Rahmstorf S, Schellnhuber HJ (2008) Tipping elements in the Earth's climate system. Proc Natl Acad Sci U S A 105(6):1786–1793. https://doi.org/10.1073/pnas.0705414105

Li H-N, Xiao B, Liu W-X, Wan F-h (2014) Changes in soil biota resulting from growth of the invasive weed, *Ambrosia artemisiifolia* L. (*Compositae*), enhance its success and reduce growth of co-occurring plants. J Integr Agric 13(9):1962–1971. https://doi.org/10.1016/s2095-3119(13)60569-9

Lian T, Mu Y, Jin J, Ma Q, Cheng Y, Cai Z, Nian H (2019) Impact of intercropping on the coupling between soil microbial community structure, activity, and nutrient-use efficiencies. PeerJ 7:e6412. https://doi.org/10.7717/peerj.6412

Liao C, Peng R, Luo Y, Zhou X, Wu X, Fang C, Chen J, Li B (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytol 177(3):706–714. https://doi.org/10.1111/j.1469-8137.2007.02290.x

Libik-Konieczny M, Surowka E, Kuzniak E, Nosek M, Miszalski Z (2011) Effects of *Botrytis cinerea* and *Pseudomonas syringae* infection on the antioxidant profile of Mesembryanthemum crystallinum C-3/CAM intermediate plant. J Plant Physiol 168(10):1052–1059. https://doi.org/10.1016/j.jplph.2010.12.015

Libik-Konieczny M, Surowka E, Nosek M, Goraj S, Miszalski Z (2012) Pathogen-induced changes in malate content and NADP-dependent malic enzyme activity in C-3 or CAM performing *Mesembryanthemum crystallinum* L. plants. Acta Physiol Plant 34(4):1471–1477. https://doi.org/10.1007/s11738-012-0945-7

Libik-Konieczny M, Kuźniak E, Surówka E, Ślesak I, Nosek M, Miszalski Z (2019) Crassulacean acid metabolism and its role in plant acclimatization to abiotic stresses and defence against pathogens. In: Progress in botany. Springer, Berlin. https://doi.org/10.1007/124_2019_33

Lind MI, Spagopoulou F (2018) Evolutionary consequences of epigenetic inheritance. Heredity 121(3):205–209. https://doi.org/10.1038/s41437-018-0113-y

Llado S, Lopez-Mondejar R, Baldrian P (2017) Forest soil bacteria: diversity, involvement in ecosystem processes, and response to global change. Microbiol Mol Biol Rev 81(2). https://doi.org/10.1128/mmbr.00063-16

Lloyd DA, Ritz K, Paterson E, Kirk GJD (2016) Effects of soil type and composition of rhizodeposits on rhizosphere priming phenomena. Soil Biol Biochem 103:512–521. https://doi.org/10.1016/j.soilbio.2016.10.002

Lobell DB, Gourdji SM (2012) The influence of climate change on global crop productivity. Plant Physiol 160(4):1686–1697. https://doi.org/10.1104/pp.112.208298

Lorang J (2019) Necrotrophic exploitation and subversion of plant defense: a lifestyle or just a phase, and implications in breeding resistance. Phytopathology 109(3):332–346. https://doi.org/10.1094/phyto-09-18-0334-ia

Luttge U (2010) Ability of crassulacean acid metabolism plants to overcome interacting stresses in tropical environments. AoB Plants. https://doi.org/10.1093/aobpla/plq005

Luttge U (2012) Modularity and emergence: biology's challenge in understanding life. Plant Biol 14(6):865–871. https://doi.org/10.1111/j.1438-8677.2012.00659.x

Luttge U (2013) Whole-plant physiology: synergistic emergence rather than modularity. In: Luttge U, Beyschlag W, Francis D, Cushman J (eds) Progress in botany 74. Progress in botany, vol 74, pp 165–190. https://doi.org/10.1007/978-3-642-30967-0_6

Luttge U, Thellier M (2016) Revisiting principles of plant life—integration of whole-plant functionality under ecological and evolutionary perspective. In: Luttge U, Canovas FM, Matyssek R (eds) Progress in botany 77, Progress in botany, vol 77, pp 67–71

Ma Y, Prasad MNV, Rajkumar M, Freitas H (2011) Plant growth promoting rhizobacteria and endophytes accelerate phytoremediation of metalliferous soils. Biotechnol Adv 29(2):248–258. https://doi.org/10.1016/j.biotechadv.2010.12.001

Mahato A (2014) Climate change and its impact on agriculture. Int J Sci Res Publ 4(4):1–6

Makinen H, Kaseva J, Virkajarvi P, Kahiluoto H (2017) Shifts in soil-climate combination deserve attention. Agric For Meteorol 234:236–246. https://doi.org/10.1016/j.agrformet.2016.12.017

Mandakovic D, Rojas C, Maldonado J, Latorre M, Travisany D, Delage E, Bihouee A, Jean G, Diaz FP, Fernandez-Gomez B, Cabrera P, Gaete A, Latorre C, Gutierrez RA, Maass A, Cambiazo V, Navarrete SA, Eveillard D, Gonzalez M (2018) Structure and co-occurrence patterns in microbial communities under acute environmental stress reveal ecological factors fostering resilience. Sci Rep 8:5875. https://doi.org/10.1038/s41598-018-23931-0

Maron JL, Smith AL, Ortega YK, Pearson DE, Callaway RM (2016) Negative plant-soil feedbacks increase with plant abundance, and are unchanged by competition. Ecology 97(8):2055–2063. https://doi.org/10.1002/ecy.1431

Maron PA, Sarr A, Kaisermann A, Leveque J, Mathieu O, Guigue J, Karimi B, Bernard L, Dequiedt S, Terrat S, Chabbi A, Ranjard L (2018) High microbial diversity promotes soil ecosystem functioning. Appl Environ Microbiol 84(9):e02738. https://doi.org/10.1128/aem.02738-17

Marschner P, Timonen S (2006) Bacterial community composition and activity in rhizosphere of roots colonized by arbuscular mycorrhizal fungi. In: Mukerji KG, Manoharachary C, Singh J (eds) Microbial activity in the rhizoshere. Springer, Berlin, pp 139–154. https://doi.org/10.1007/3-540-29420-1_8

Marupakula S, Mahmood S, Jernberg J, Nallanchakravarthula S, Fahad ZA, Finlay RD (2017) Bacterial microbiomes of individual ectomycorrhizal *Pinus sylvestris* roots are shaped by soil horizon and differentially sensitive to nitrogen addition. Environ Microbiol 19(11):4736–4753. https://doi.org/10.1111/1462-2920.13939

Matsuda R, Yamano T, Murakami K, Fujiwara K (2016) Effects of spectral distribution and photosynthetic photon flux density for overnight LED light irradiation on tomato seedling growth and leaf injury. Sci Hortic 198:363–369. https://doi.org/10.1016/j.scienta.2015.11.045

Matyssek R, Luttge U (2013) Gaia: the planet holobiont. Nova Acta Leopoldina 114(391):325–344

McFall-Ngai M, Hadfield MG, Bosch TCG, Carey HV, Domazet-Loso T, Douglas AE, Dubilier N, Eberl G, Fukami T, Gilbert SF, Hentschel U, King N, Kjelleberg S, Knoll AH, Kremer N, Mazmanian SK, Metcalf JL, Nealson K, Pierce NE, Rawls JF, Reid A, Ruby EG, Rumpho M, Sanders JG, Tautz D, Wernegreen JJ (2013) Animals in a bacterial world, a new imperative for the life sciences. Proc Natl Acad Sci U S A 110(9):3229–3236. https://doi.org/10.1073/pnas.1218525110

McGill BJ, Dornelas M, Gotelli NJ, Magurran AE (2015) Fifteen forms of biodiversity trend in the Anthropocene. Trends Ecol Evol 30(2):104–113. https://doi.org/10.1016/j.tree.2014.11.006

McKee K, Rogers K, Saintilan N (2012) Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In: Middleton BA (ed) Global change and the function and distribution of wetlands. Springer, Dordrecht, pp 63–96. https://doi.org/10.1007/978-94-007-4494-3_2

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37(5):634–663. https://doi.org/10.1111/1574-6976.12028

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vazquez DP (2006) Biotic interactions and plant invasions. Ecol Lett 9(6):726–740. https://doi.org/10.1111/j.1461-0248.2006.00908.x

Mitter B, Pfaffenbichler N, Sessitsch A (2016) Plant-microbe partnerships in 2020. Microb Biotechnol 9(5):635–640. https://doi.org/10.1111/1751-7915.12382

Miura K, Tada Y (2014) Regulation of water, salinity, and cold stress responses by salicylic acid. Front Plant Sci 5:4. https://doi.org/10.3389/fpls.2014.00004

Montoya D, Rogers L, Memmott J (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem services. Trends Ecol Evol 27(12):666–672. https://doi.org/10.1016/j.tree.2012.07.004

Morel MA, Castro-Sowinski S (2013) The complex molecular signaling network in microbe–plant interaction. In: Arora NK (ed) Plant microbe symbiosis: fundamentals and advances. Springer, New Delhi, pp 169–199. https://doi.org/10.1007/978-81-322-1287-4_6

Morris JJ (2018) What is the hologenome concept of evolution? F1000 Res 7:1664. https://doi.org/10.12688/f1000research.14385.1

Mueller RC, Belnap J, Kuske CR (2015) Soil bacterial and fungal community responses to nitrogen addition across soil depth and microhabitat in an arid shrubland. Front Microbiol 6:891. https://doi.org/10.3389/fmicb.2015.00891

Nair A, Ngouajio M (2012) Soil microbial biomass, functional microbial diversity, and nematode community structure as affected by cover crops and compost in an organic vegetable production system. Appl Soil Ecol 58:45–55. https://doi.org/10.1016/j.apsoil.2012.03.008

Nannipieri P (2006) Role of stabilised enzymes in microbial ecology and enzyme extraction from soil with potential applications in soil proteomics. In: Nannipieri P, Smalla K (eds) Nucleic acids and proteins in soil. Springer, Berlin, pp 75–94. https://doi.org/10.1007/3-540-29449-x_4

Nannipieri P, Giagnoni L, Renella G, Puglisi E, Ceccanti B, Masciandaro G, Fornasier F, Moscatelli MC, Marinari S (2012) Soil enzymology: classical and molecular approaches. Biol Fertil Soils 48(7):743–762. https://doi.org/10.1007/s00374-012-0723-0

Nejat N, Mantri N (2017) Plant immune system: crosstalk between responses to biotic and abiotic stresses the missing link in understanding plant defence. Curr Issues Mol Biol 23:1–15. https://doi.org/10.21775/cimb.023.001

Newbery F, Qi AM, Fitt BDL (2016) Modelling impacts of climate change on arable crop diseases: progress, challenges and applications. Curr Opin Plant Biol 32:101–109. https://doi.org/10.1016/j.pbi.2016.07.002

Niu LJ, Liao WB (2016) Hydrogen peroxide signaling in plant development and abiotic responses: crosstalk with nitric oxide and calcium. Front Plant Sci 7:230. https://doi.org/10.3389/fpls.2016.00230

Noctor G, Mhamdi A (2017) Climate change, CO2, and defense: the metabolic, redox, and signaling perspectives. Trends Plant Sci 22(10):857–870. https://doi.org/10.1016/j.tplants.2017.07.007

Noman A, Aqeel M, Lou YG (2019) PRRs and NB-LRRs: from signal perception to activation of plant innate immunity. Int J Mol Sci 20(8):E1882. https://doi.org/10.3390/ijms20081882

Novoa A, Rodriguez R, Richardson D, Gonzalez L (2014) Soil quality: a key factor in understanding plant invasion? The case of *Carpobrotus edulis* (L.) N.E.Br. Biol Invasions 16(2):429–443. https://doi.org/10.1007/s10530-013-0531-y

Oburger E, Dell'mour M, Hann S, Wieshammer G, Puschenreiter M, Wenzel WW (2013) Evaluation of a novel tool for sampling root exudates from soil-grown plants compared to conventional techniques. Environ Exp Bot 87:235–247. https://doi.org/10.1016/j.envexpbot.2012.11.007

Okubo A, Matsusaka M, Sugiyama S (2016) Impacts of root symbiotic associations on interspecific variation in sugar exudation rates and rhizosphere microbial communities: a comparison among four plant families. Plant Soil 399(1–2):345–356. https://doi.org/10.1007/s11104-015-2703-2

Ordookhani K, Zare M (2011) Effect of *Pseudomonas*, *Azotobacter* and arbuscular mycorrhiza fungi on lycopene, antioxidant activity and total soluble solid in tomato (*Lycopersicon esculentum* F1 Hybrid, *Delba*). Adv Environ Biol 5(6):1290–1294

Ostrem L, Folkestad J, Solhaug KA, Brandsaeter LO (2018) Frost tolerance, regeneration capacity after frost exposure and high photosystem II efficiency during winter and early spring support high winter survival in *Juncus* spp. Weed Res 58(1):25–34. https://doi.org/10.1111/wre.12277

Ourry M, Lebreton L, Chaminade V, Guillerm-Erckelboudt A-Y, Herve M, Linglin J, Marnet N, Ourry A, Paty C, Poinsot D, Cortesero A-M, Mougel C (2018) Influence of belowground herbivory on the dynamics of root and rhizosphere microbial communities. Front Ecol Evol 6. https://doi.org/10.3389/fevo.2018.00091

Pachauri RK, Allen MR, Barros VR, Broome J, Cramer W, Christ R, Church JA, Clarke L, Dahe Q, Dasgupta P, Dubash NK, Edenhofer O, Elgizouli I, Field CB, Forster P, Friedlingstein P, Fuglestvedt J, Gomez-Echeverri L, Hallegatte S, Hegerl G, Howden M, Jiang K, Jimenez Cisneroz B, Kattsov V, Lee H, Mach KJ, Marotzke J, Mastrandrea MD, Meyer L, Minx J, Mulugetta Y, O'Brien K, Oppenheimer M, Pereira JJ, Pichs-Madruga R, Plattner GK, Portner HO, Power SB, Preston B, Ravindranath NH, Reisinger A, Riahi K, Rusticucci M, Scholes R, Seyboth K, Sokona Y, Stavins R, Stocker TF, Tschakert P, van Vuuren D, van Ypserle JP (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. The International Panel on Climate Change (IPCC)

Page AP, Yergeau E, Greer CW (2015) Salix purpurea stimulates the expression of specific bacterial xenobiotic degradation genes in a soil contaminated with hydrocarbons. PLoS One 10(7):e0132062. https://doi.org/10.1371/journal.pone.0132062

Pandey P, Irulappan V, Bagavathiannan MV, Senthil-Kumar M (2017) Impact of combined abiotic and biotic stresses on plant growth and avenues for crop improvement by exploiting physio-morphological traits. Front Plant Sci 8:537. https://doi.org/10.3389/fpls.2017.00537

Panke-Buisse K, Poole AC, Goodrich JK, Ley RE, Kao-Kniffin J (2015) Selection on soil microbiomes reveals reproducible impacts on plant function. ISME J 9(4):980–989. https://doi.org/10.1038/ismej.2014.196

Parmesan C, Hanley ME (2015) Plants and climate change: complexities and surprises. Ann Bot 116(6):849–864. https://doi.org/10.1093/aob/mcv169

Pathak R, Singh SK, Tak A, Gehlot P (2018) Impact of climate change on host, pathogen and plant disease adaptation regime: a review. Biosci Biotechnol Res Asia 15(3):529–540

Payne RJ, Dise NB, Field CD, Dore AJ, Caporn SJM, Stevens CJ (2017) Nitrogen deposition and plant biodiversity: past, present, and future. Front Ecol Environ 15(8):431–436. https://doi.org/10.1002/fee.1528

Peiffer JA, Spor A, Koren O, Jin Z, Tringe SG, Dangl JL, Buckler ES, Ley RE (2013) Diversity and heritability of the maize rhizosphere microbiome under field conditions. Proc Natl Acad Sci U S A 110(16):6548–6553. https://doi.org/10.1073/pnas.1302837110

Peyraud R, Dubiella U, Barbacci A, Genin S, Raffaele S, Roby D (2017) Advances on plant-pathogen interactions from molecular toward systems biology perspectives. Plant J 90(4):720–737. https://doi.org/10.1111/tpj.13429

Philippot L, Spor A, Henault C, Bru D, Bizouard F, Jones CM, Sarr A, Maron P-A (2013) Loss in microbial diversity affects nitrogen cycling in soil. ISME J 7:1609. https://doi.org/10.1038/ismej.2013.34. https://www.nature.com/articles/ismej201334#supplementary-information

Pozo MJ, Lopez-Raez JA, Azcon-Aguilar C, Garcia-Garrido JM (2015) Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses. New Phytol 205(4):1431–1436. https://doi.org/10.1111/nph.13252

Prasad M, Srinivasan R, Chaudhary M, Choudhary M, Jat LK (2019) Chapter seven—plant growth promoting *Rhizobacteria* (PGPR) for sustainable agriculture: perspectives and challenges. In: Singh AK, Kumar A, Singh PK (eds) PGPR amelioration in sustainable agriculture. Woodhead Publishing, pp 129–157. https://doi.org/10.1016/B978-0-12-815879-1.00007-0

Prasch CM, Sonnewald U (2015) Signaling events in plants: stress factors in combination change the picture. Environ Exp Bot 114:4–14. https://doi.org/10.1016/j.envexpbot.2014.06.020

Purahong W, Wubet T, Lentendu G, Schloter M, Pecyna MJ, Kapturska D, Hofrichter M, Krueger D, Buscot F (2016) Life in leaf litter: novel insights into community dynamics of bacteria and fungi during litter decomposition. Mol Ecol 25(16):4059–4074. https://doi.org/10.1111/mec.13739

Qin Z, Xie J-F, Quan G-M, Zhang J-E, Mao D-J, DiTommaso A (2014) Impacts of the invasive annual herb *Ambrosia artemisiifolia* L. on soil microbial carbon source utilization and enzymatic activities. Eur J Soil Biol 60:58–66. https://doi.org/10.1016/j.ejsobi.2013.11.007

Quatrini R, Johnson DB (2018) Microbiomes in extremely acidic environments: functionalities and interactions that allow survival and growth of prokaryotes at low pH. Curr Opin Microbiol 43:139–147. https://doi.org/10.1016/j.mib.2018.01.011

Quiza L, St-Arnaud M, Yergeau E (2015) Harnessing phytomicrobiome signaling for rhizosphere microbiome engineering. Front Plant Sci 6:507. https://doi.org/10.3389/fpls.2015.00507

Raizada P, Raghubanshi AS, Singh JS (2008) Impact of invasive alien plant species on soil processes: a review. Proc Natl Acad Sci India B Biol Sci 78:288–298

Ramirez F, Coll M, Navarro J, Bustamante J, Green AJ (2018) Spatial congruence between multiple stressors in the Mediterranean Sea may reduce its resilience to climate impacts. Sci Rep 8:14871. https://doi.org/10.1038/s41598-018-33237-w

Rapacz M, Ergon A, Hoglind M, Jorgensen M, Jurczyk B, Ostrem L, Rognli OA, Tronsmo AM (2014) Overwintering of herbaceous plants in a changing climate. Still more questions than answers. Plant Sci 225:34–44. https://doi.org/10.1016/j.plantsci.2014.05.009

Ratnayake RMCS (2014) Address on “Why plant species become invasive?—characters related to successful biological invasion”. In: Proceedings of the national symposium on invasive alien species (IAS), pp 22–41

Ravichandran KR, Thangavelu M (2017) Role and influence of soil microbial communities on plant invasion. Ecol Quest 27:9–23. https://doi.org/10.12775/eq.2017.024

Reidinger S, Eschen R, Gange AC, Finch P, Bezemer TM (2012) Arbuscular mycorrhizal colonization, plant chemistry, and aboveground herbivory on *Senecio jacobaea*. Acta Oecol 38:8–16. https://doi.org/10.1016/j.actao.2011.08.003

Rengel Z (2011) Soil pH, soil health and climate change. In: Singh BP, Cowie AL, Chan KY (eds) Soil health and climate change 29, Soil biology, vol 29, pp 69–85. https://doi.org/10.1007/978-3-642-20256-8_4

Requena N, Perez-Solis E, Azcon-Aguilar C, Jeffries P, Barea JM (2001) Management of indigenous plant-microbe symbioses aids restoration of desertified ecosystems. Appl Environ Microbiol 67(2):495–498. https://doi.org/10.1128/aem.67.2.495-498.2001

Rodriguez PA, Rothballer M, Chowdhury SP, Nussbaumer T, Gutjahr C, Falter-Braun P (2019) Systems biology of plant-microbiome interactions. Mol Plant 12(6):804–821. https://doi.org/10.1016/j.molp.2019.05.006

Rohde K (1992) Latitudinal gradients in species-diversity—the search for the primary cause. Oikos 65(3):514–527. https://doi.org/10.2307/3545569

Roos J, Hopkins R, Kvarnheden A, Dixelius C (2011) The impact of global warming on plant diseases and insect vectors in Sweden. Eur J Plant Pathol 129(1):9–19. https://doi.org/10.1007/s10658-010-9692-z

Rosenberg E, Zilber-Rosenberg I (2018) The hologenome concept of evolution after 10 years. Microbiome 6:78. https://doi.org/10.1186/s40168-018-0457-9

Rosenblueth M, Martinez-Romero E (2006) Bacterial endophytes and their interactions with hosts. Mol Plant Microbe Interact 19(8):827–837. https://doi.org/10.1094/mpmi-19-0827

Rousk J, Brookes PC, Baath E (2009) Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. Appl Environ Microbiol 75(6):1589–1596. https://doi.org/10.1128/aem.02775-08

Rout ME, Callaway RM (2012) Interactions between exotic invasive plants and soil microbes in the rhizosphere suggest that 'everything is not everywhere'. Ann Bot 110(2):213–222. https://doi.org/10.1093/aob/mcs061

Rout ME, Southworth D (2013) The root microbiome influences scales from molecules to ecosystems: the unseen majority. Am J Bot 100(9):1689–1691. https://doi.org/10.3732/ajb.1300291

Ruan YL (2014) Sucrose metabolism: gateway to diverse carbon use and sugar signaling. Annu Rev Plant Biol 65:33–67. https://doi.org/10.1146/annurev-arplant-050213-040251

Rumpel C, Creme A, Ngo PT, Velasquez G, Mora ML, Chabbi A (2015) The impact of grassland management on biogeochemical cycles involving carbon, nitrogen and phosphorus. J Soil Sci Plant Nutr 15(2):353–371

Ruppel S, Franken P, Witzel K (2013) Properties of the halophyte microbiome and their implications for plant salt tolerance. Funct Plant Biol 40(8–9):940–951. https://doi.org/10.1071/fp12355

Rustad L, Campbell J, Dukes JS, Huntington T, Fallon Lambert K, Mohan J, Rodenhouse N (2012) Changing climate, changing forests: the impacts of climate change on forests of the northeastern United States and eastern Canada. US FOREST SERVICE 11 CAMPUS BLVD SUITE 200 NEWTOWN SQUARE PA 19073

Ryalls JMW, Moore BD, Riegler M, Johnson SN (2016) Above-below ground herbivore interactions in mixed plant communities are influenced by altered precipitation patterns. Front Plant Sci 7:345. https://doi.org/10.3389/fpls.2016.00345

Saijo Y, Loo EP, Yasuda S (2018) Pattern recognition receptors and signaling in plant-microbe interactions. Plant J 93(4):592–613. https://doi.org/10.1111/tpj.13808

Santoyo G, Moreno-Hagelsieb G, Orozco-Mosqueda MD, Glick BR (2016) Plant growth-promoting bacterial endophytes. Microbiol Res 183:92–99. https://doi.org/10.1016/j.micres.2015.11.008

Santoyo G, Hernandez-Pacheco C, Hernandez-Salmeron J, Hernandez-Leon R (2017) The role of abiotic factors modulating the plant-microbe-soil interactions: toward sustainable agriculture. A review. Span J Agric Res 15(1):e03R01. https://doi.org/10.5424/sjar/2017151-9990

Sardans J, Penuelas J (2015) Potassium: a neglected nutrient in global change. Glob Ecol Biogeogr 24(3):261–275. https://doi.org/10.1111/geb.12259

Sardans J, Janssens IA, Alonso R, Veresoglou SD, Rillig MC, Sanders TGM, Carnicer J, Filella I, Farre-Armengol G, Penuelas J (2015) Foliar elemental composition of European forest tree species associated with evolutionary traits and present environmental and competitive conditions. Glob Ecol Biogeogr 24(2):240–255. https://doi.org/10.1111/geb.12253

Sax DF, Gaines SD (2003) Species diversity: from global decreases to local increases. Trends Ecol Evol 18(11):561–566. https://doi.org/10.1016/s0169-5347(03)00224-6

Scharlemann JPW, Tanner EVJ, Hiederer R, Kapos V (2014) Global soil carbon: understanding and managing the largest terrestrial carbon pool. Carbon Manag 5(1):81–91. https://doi.org/10.4155/cmt.13.77

Schimel JP, Schaeffer SM (2012) Microbial control over carbon cycling in soil. Front Microbiol 3:348. https://doi.org/10.3389/fmicb.2012.00348

Schloss PD, Handelsman J (2006) Toward a census of bacteria in soil. PLoS Comput Biol 2(7):786–793. https://doi.org/10.1371/journal.pcbi.0020092

Scotland RW, Wortley AH (2003) How many species of seed plants are there? Taxon 52(1):101–104. https://doi.org/10.2307/3647306

Selvakumar G, Krishnamoorthy R, Kim K, Sa T-M (2016) Genetic diversity and association characters of bacteria isolated from arbuscular mycorrhizal fungal spore walls. PLoS One 11(8):e0160356. https://doi.org/10.1371/journal.pone.0160356

Sham A, Moustafa K, Al-Ameri S, Al-Azzawi A, Iratni R, AbuQamar S (2015) Identification of Arabidopsis candidate genes in response to biotic and abiotic stresses using comparative microarrays. PLoS One 10(5):e0125666. https://doi.org/10.1371/journal.pone.0125666

Sharma SB, Sayyed RZ, Trivedi MH, Gobi TA (2013) Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. SpringerPlus 2(1):587. https://doi.org/10.1186/2193-1801-2-587

Shaw RG, Etterson JR (2012) Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. New Phytol 195(4):752–765. https://doi.org/10.1111/j.1469-8137.2012.04230.x

Short FT, Kosten S, Morgan PA, Malone S, Moore GE (2016) Impacts of climate change on submerged and emergent wetland plants. Aquat Bot 135:3–17. https://doi.org/10.1016/j.aquabot.2016.06.006

Si C, Liu X, Wang C, Wang L, Dai Z, Qi S, Du D (2013) Different degrees of plant invasion significantly affect the richness of the soil fungal community. PLoS One 8(12):e85490. https://doi.org/10.1371/journal.pone.0085490

Sielaff AC, Upton RN, Hofmockel KS, Xu X, Polley HW, Wilsey BJ (2018) Microbial community structure and functions differ between native and novel (exotic-dominated) grassland ecosystems in an 8-year experiment. Plant Soil 432(1–2):359–372. https://doi.org/10.1007/s11104-018-3796-1

Simkin SM, Allen EB, Bowman WD, Clark CM, Belnap J, Brooks ML, Cade BS, Collins SL, Geiser LH, Gilliam FS, Jovan SE, Pardo LH, Schulz BK, Stevens CJ, Suding KN, Throop HL, Waller DM (2016) Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. Proc Natl Acad Sci U S A 113(15):4086–4091. https://doi.org/10.1073/pnas.1515241113

Simon J, Schmidt S (2017) Editorial: plant competition in a changing world. Front Plant Sci 8:651. https://doi.org/10.3389/fpls.2017.00651

Singh RP, Hodson DP, Jin Y, Lagudah ES, Ayliffe MA, Bhavani S, Rouse MN, Pretorius ZA, Szabo LJ, Huerta-Espino J, Basnet BR, Lan C, Hovmoller MS (2015) Emergence and spread of new races of wheat stem rust fungus: continued threat to food security and prospects of genetic control. Phytopathology 105(7):872–884. https://doi.org/10.1094/phyto-01-15-0030-fi

Smith NG, Dukes JS (2017) Short-term acclimation to warmer temperatures accelerates leaf carbon exchange processes across plant types. Glob Chang Biol 23(11):4840–4853. https://doi.org/10.1111/gcb.13735

Smith SA, Tank DC, Boulanger LA, Bascom-Slack CA, Eisenman K, Kingery D, Babbs B, Fenn K, Greene JS, Hann BD, Keehner J, Kelley-Swift EG, Kembaiyan V, Lee SJ, Li PY, Light

DY, Lin EH, Ma C, Moore E, Schorn MA, Vekhter D, Nunez PV, Strobel GA, Donoghue MJ, Strobel SA (2008) Bioactive endophytes warrant intensified exploration and conservation. PLoS One 3(8):e3052. https://doi.org/10.1371/journal.pone.0003052

Smith P, Cotrufo ME, Rumpel C, Paustian K, Kuikman PJ, Elliott JA, McDowell R, Griffiths RI, Asakawa S, Bustamante M, House JI, Sobocka J, Harper R, Pan G, West PC, Gerber JS, Clark JM, Adhya T, Scholes RJ, Scholes MC (2015) Biogeochemical cycles and biodiversity as key drivers of ecosystem services provided by soils. Soil 1(2):665–685. https://doi.org/10.5194/soil-1-665-2015

Smith DL, Gravel V, Yergeau E (2017) Signaling in the phytomicrobiome. Front Plant Sci 8:611. https://doi.org/10.3389/fpls.2017.00611

Smithwick EAH, Naithani KJ, Balser TC, Romme WH, Turner MG (2012) Post-fire spatial patterns of soil nitrogen mineralization and microbial abundance. PLoS One 7(11):e50597. https://doi.org/10.1371/journal.pone.0050597

Sorte CJB, Ibanez I, Blumenthal DM, Molinari NA, Miller LP, Grosholz ED, Diez JM, D'Antonio CM, Olden JD, Jones SJ, Dukes JS (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecol Lett 16(2):261–270. https://doi.org/10.1111/ele.12017

Souza GM, Luttge U (2015) Stability as a phenomenon emergent from plasticity–complexity–diversity in eco-physiology. In: Luttge U, Beyschlag W (eds) Progress in botany 76, vol 76. Springer, pp 211–239

Souza GM, Bertolli SC, Luettge U (2016) Hierarchy and information in a system approach to plant biology: explaining the irreducibility in plant ecophysiology. In: Luttge U, Canovas FM, Matyssek R (eds) Progress in botany 77. Progress in botany, vol 77, pp 167–186. https://doi.org/10.1007/978-3-319-25688-7_5

Steinweg JM, Jagadamma S, Frerichs J, Mayes MA (2013) Activation energy of extracellular enzymes in soils from different biomes. PLoS One 8(3):e59943. https://doi.org/10.1371/journal.pone.0059943

Suding KN, Harpole WS, Fukami T, Kulmatiski A, MacDougall AS, Stein C, van der Putten WH (2013) Consequences of plant-soil feedbacks in invasion. J Ecol 101(2):298–308. https://doi.org/10.1111/1365-2745.12057

Sun DC (2018) Pull in and push out: mechanisms of horizontal gene transfer in bacteria. Front Microbiol 9:2154. https://doi.org/10.3389/fmicb.2018.02154

Talaat NB, Shawky BT (2017) Microbe-mediated induced abiotic stress tolerance responses in plants. In: Singh DP, Singh HB, Prabha R (eds) Plant-microbe interactions in agro-ecological perspectives, vol 2. Microbial interactions and agro-ecological impacts. Springer, Singapore, pp 101–133. https://doi.org/10.1007/978-981-10-6593-4_5

Theis KR, Dheilly NM, Klassen JL, Brucker RM, Baines JF, Bosch TCG, Cryan JF, Gilbert SF, Goodnight CJ, Lloyd EA, Sapp J, Vandenkoornhuyse P, Zilber-Rosenberg I, Rosenberg E, Bordenstein SR (2016) Getting the hologenome concept right: an eco-evolutionary framework for hosts and their microbiomes. mSystems 1(2):e00028-16. https://doi.org/10.1128/mSystems.00028-16

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176(2):256–273. https://doi.org/10.1111/j.1469-8137.2007.02207.x

Thuiller W, Lavorel S, Araujo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. Proc Natl Acad Sci U S A 102(23):8245–8250. https://doi.org/10.1073/pnas.0409902102

Trębicki P, Dáder B, Vassiliadis S, Fereres A (2017) Insect–plant–pathogen interactions as shaped by future climate: effects on biology, distribution, and implications for agriculture. Insect Sci 24(6):975–989. https://doi.org/10.1111/1744-7917.12531

Trinder CJ, Brooker RW, Robinson D (2013) Plant ecology's guilty little secret: understanding the dynamics of plant competition. Funct Ecol 27(4):918–929. https://doi.org/10.1111/1365-2435.12078

Tripathi BM, Stegen JC, Kim M, Dong K, Adams JM, Lee YK (2018) Soil pH mediates the balance between stochastic and deterministic assembly of bacteria. ISME J 12(4):1072–1083. https://doi.org/10.1038/s41396-018-0082-4

Trnka M, Hlavinka P, Semeradova D, Dubrovsky M, Zalud Z, Mozny M (2007) Agricultural drought and spring barley yields in the Czech Republic. Plant Soil Environ 53(7):306–316. https://doi.org/10.17221/2210-pse

Turner BL, Condron LM (2013) Pedogenesis, nutrient dynamics, and ecosystem development: the legacy of TW Walker and JK Syers. Plant Soil 367(1–2):1–10. https://doi.org/10.1007/s11104-013-1750-9

Turrini A, Avio L, Giovannetti M, Agnolucci M (2018) Functional complementarity of arbuscular mycorrhizal fungi and associated microbiota: the challenge of translational research. Front Plant Sci 9:1407. https://doi.org/10.3389/fpls.2018.01407

Unterseher M, Persoh D, Schnittler M (2013) Leaf-inhabiting endophytic fungi of European Beech (*Fagus sylvatica* L.) co-occur in leaf litter but are rare on decaying wood of the same host. Fungal Divers 60(1):43–54. https://doi.org/10.1007/s13225-013-0222-0

Utobo EB, Tewari L (2015) Soil enzymes as bioindicators of soil ecosystem status. Appl Ecol Environ Res 13(1):147–169

van der Putten WH (2012) Climate change, aboveground-belowground interactions, and species' range shifts. Annu Rev Ecol Evol Syst 43:365–383. https://doi.org/10.1146/annurev-ecolsys-110411-160423

van der Putten WH, Klironomos JN, Wardle DA (2007a) Microbial ecology of biological invasions. ISME J 1(1):28–37. https://doi.org/10.1038/ismej.2007.9

van der Putten WH, Kowalchuk GA, Brinkman EP, Doodeman GTA, van der Kaaij RM, Kamp AFD, Menting FBJ, Veenendaal EM (2007b) Soil feedback of exotic savanna grass relates to pathogen absence and mycorrhizal selectivity. Ecology 88(4):978–988. https://doi.org/10.1890/06-1051

van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philos Trans R Soc Lond B Biol Sci 365(1549):2025–2034. https://doi.org/10.1098/rstb.2010.0037

van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, Suding KN, Van de Voorde TFJ, Wardle DA (2013) Plant-soil feedbacks: the past, the present and future challenges. J Ecol 101(2):265–276. https://doi.org/10.1111/1365-2745.12054

van Kleunen M, Rockle M, Stift M (2015) Admixture between native and invasive populations may increase invasiveness of *Mimulus guttatus*. Proc R Soc B Biol Sci 282(1815). https://doi.org/10.1098/rspb.2015.1487

Vandenkoornhuyse P, Quaiser A, Duhamel M, Le Van A, Dufresne A (2015) The importance of the microbiome of the plant holobiont. New Phytol 206(4):1196–1206. https://doi.org/10.1111/nph.13312

Vannier N, Mony C, Bittebiere A-K, Vandenkoornhuyse P (2015) Epigenetic mechanisms and microbiota as a toolbox for plant phenotypic adjustment to environment. Front Plant Sci 6:1159. https://doi.org/10.3389/fpls.2015.01159

Varma S, Winslow M (2004) Healing wounds: how the international centers of the CGIAR help rebuild agriculture in countries affected by conflicts and natural disasters. Consultative Group on International Agricultural Research (CGIAR), Washington, DC

Velasquez AC, Castroverde CDM, He SY (2018) Plant-pathogen warfare under changing climate conditions. Curr Biol 28(10):R619–R634. https://doi.org/10.1016/j.cub.2018.03.054

Venturi V, Keel C (2016) Signaling in the rhizosphere. Trends Plant Sci 21(3):187–198. https://doi.org/10.1016/j.tplants.2016.01.005

Verma P, Yadav AN, Kumar V, Singh DP, Saxena AK (2017) Beneficial plant-microbes interactions: biodiversity of microbes from diverse extreme environments and its impact for crop improvement. In: Singh DP, Singh HB, Prabha R (eds) Plant-microbe interactions in agro-ecological perspectives, vol. 2. Microbial interactions and agro-ecological impacts. Springer, Singapore, pp 543–580. https://doi.org/10.1007/978-981-10-6593-4_22

Vila M, Weiner J (2004) Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. Oikos 105(2):229–238. https://doi.org/10.1111/j.0030-1299.2004.12682.x

Vile D, Pervent M, Belluau M, Vasseur F, Bresson J, Muller B, Granier C, Simonneau T (2012) Arabidopsis growth under prolonged high temperature and water deficit: independent or interactive effects? Plant Cell Environ 35(4):702–718. https://doi.org/10.1111/j.1365-3040.2011.02445.x

Voroney RP (2007) The soil habitat. In: Paul EA (ed) Soil microbiology, ecology and biochemistry, 3rd edn. Academic, London, pp 25–49

Wallenstein MD (2017) Managing and manipulating the rhizosphere microbiome for plant health: a systems approach. Rhizosphere 3(Part 2):230–232. https://doi.org/10.1016/j.rhisph.2017.04.004

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879):389–395. https://doi.org/10.1038/416389a

Wang M, Chen J-K, Li B (2007) Characterization of bacterial community structure and diversity in rhizosphere soils of three plants in rapidly changing salt marshes using 16S rDNA. Pedosphere 17(5):545–556. https://doi.org/10.1016/s1002-0160(07)60065-4

Wang CY, Xiao HG, Liu J, Wang L, Du DL (2015) Insights into ecological effects of invasive plants on soil nitrogen cycles. Am J Plant Sci 6(1):34–46. https://doi.org/10.4236/ajps.2015.61005

Wang Y, Ji HF, Gao CQ (2016) Differential responses of soil bacterial taxa to long-term P, N, and organic manure application. J Soils Sediments 16(3):1046–1058. https://doi.org/10.1007/s11368-015-1320-2

Wang R, Zhang H, Sun L, Qi G, Chen S, Zhao X (2017) Microbial community composition is related to soil biological and chemical properties and bacterial wilt outbreak. Sci Rep 7:343. https://doi.org/10.1038/s41598-017-00472-6

Wardle DA (2002) Communities and ecosystems. Linking the aboveground and belowground components. Monogr Popul Biol 34(i–vii):1–392

Wardle DA, Yeates GW, Barker GM, Bonner KI (2006) The influence of plant litter diversity on decomposer abundance and diversity. Soil Biol Biochem 38(5):1052–1062. https://doi.org/10.1016/j.soilbio.2005.09.003

Weidenhamer JD, Callaway RM (2010) Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. J Chem Ecol 36(1):59–69. https://doi.org/10.1007/s10886-009-9735-0

Werner C, Zumkier U, Beyschlag W, Maguas C (2010) High competitiveness of a resource demanding invasive acacia under low resource supply. Plant Ecol 206(1):83–96. https://doi.org/10.1007/s11258-009-9625-0

Williams A, Petriacq P, Beetling DJ, Cotton TEA, Ton J (2018) Impacts of atmospheric CO_2 and soil nutritional value on plant responses to rhizosphere colonization by soil bacteria. Front Plant Sci 9:1493. https://doi.org/10.3389/fpls.2018.01493

Willis CG, Davis CC (2014) Reply to Angelo: climate change and species loss in Thoreau's woods (Concord, Massachusetts, USA). Phytoneuron 59:1–4

Willis CG, Ruhfel B, Primack RB, Miller-Rushing AJ, Davis CC (2009) Reply to McDonald et al.: climate change, not deer herbivory, has shaped species decline in Concord, Massachusetts. Proc Natl Acad Sci U S A 106(10):E29–E29. https://doi.org/10.1073/pnas.0900170106

Willis CG, Ruhfel BR, Primack RB, Miller-Rushing AJ, Losos JB, Davis CC (2010) Favorable climate change response explains non-native species' success in Thoreau's woods. PLoS One 5(1):8878. https://doi.org/10.1371/journal.pone.0008878

Wilson H, Johnson BR, Bohannan B, Pfeifer-Meister L, Mueller R, Bridgham SD (2016) Experimental warming decreases arbuscular mycorrhizal fungal colonization in prairie plants along a Mediterranean climate gradient. PeerJ 4:e2083. https://doi.org/10.7717/peerj.2083

Winkler DE (2019) Contemporary human impacts on alpine ecosystems: the direct and indirect effects of human-induced climate change and land use. https://doi.org/10.1016/b978-0-12-409548-9.11879-2

Wolfe BE, Klironomos JN (2005) Breaking new ground: soil communities and exotic plant invasion. Bioscience 55(6):477–487. https://doi.org/10.1641/0006-3568(2005)055[0477:bngsca]2.0.co;2

Wroblewski T, Caldwell KS, Piskurewicz U, Cavanaugh KA, Xu HQ, Kozik A, Ochoa O, McHale LK, Lahre K, Jelenska J, Castillo JA, Blumenthal D, Vinatzer BA, Greenberg JT, Michelmore RW (2009) Comparative large-scale analysis of interactions between several crop species and the effector repertoires from multiple pathovars of *Pseudomonas* and *Ralstonia*. Plant Physiol 150(4):1733–1749. https://doi.org/10.1104/pp.109.140251

Wu EJ, Yang LN, Zhu W, Chen XM, Shang LP, Zhan JS (2016) Diverse mechanisms shape the evolution of virulence factors in the potato late blight pathogen *Phytophthora* infestans sampled from China. Sci Rep 6:26182. https://doi.org/10.1038/srep26182

Yanez-Lopez R, Torres-Pacheco I, Guevara-Gonzalez R, Hernandez-Zul M, Quijano-Carranza J, Rico-García E (2012) The effect of climate change on plant diseases. Afr J Biotechnol 11(10):2417–2428

Yang Q, Carrillo J, Jin H, Shang L, Hovick SM, Nijjer S, Gabler CA, Li B, Siemann E (2013) Plant-soil biota interactions of an invasive species in its native and introduced ranges: implications for invasion success. Soil Biol Biochem 65:78–85. https://doi.org/10.1016/j.soilbio.2013.05.004

Yang J, Pedlar JH, McKenney DW, Weersink A (2015) The development of universal response functions to facilitate climate-smart regeneration of black spruce and white pine in Ontario, Canada. Environ Res Lett 339:34–43. https://doi.org/10.1016/j.foreco.2014.12.001

Yergeau E, Sanschagrin S, Maynard C, St-Arnaud M, Greer CW (2014) Microbial expression profiles in the rhizosphere of willows depend on soil contamination. ISME J 8(2):344–358. https://doi.org/10.1038/ismej.2013.163

Ying-Ning H, Dony Chacko M, Chieh-Chen H (2017) Plant-microbe ecology: interactions of plants and symbiotic microbial communities. In: Zubaida Y (ed) Plant ecology—traditional approaches to recent trends. IntechOpen. https://doi.org/10.5772/intechopen.69088

Yu H, Deng Y, He Z, Van Nostrand JD, Wang S, Jin D, Wang A, Wu L, Wang D, Tai X, Zhou J (2018) Elevated CO_2 and warming altered grassland microbial communities in soil top-layers. Front Microbiol 9:1790. https://doi.org/10.3389/fmicb.2018.01790

Zachow C, Muller H, Tilcher R, Berg G (2014) Differences between the rhizosphere microbiome of *Beta vulgaris* ssp *maritima*-ancestor of all beet crops-and modern sugar beets. Front Microbiol 5:415. https://doi.org/10.3389/fmicb.2014.00415

Zeilinger S, Gupta VK, Dahms TES, Silva RN, Singh HB, Upadhyay RS, Gomes EV, Tsui CKM, Nayak SC, van der Meer JR (2016) Friends or foes? Emerging insights from fungal interactions with plants. FEMS Microbiol Rev 40(2):182–207. https://doi.org/10.1093/femsre/fuv045

Zengler K, Zaramela LS (2018) The social network of microorganisms—how auxotrophies shape complex communities. Nat Rev Microbiol 16(6):383–390. https://doi.org/10.1038/s41579-018-0004-5

Zhang H, Sonnewald U (2017) Differences and commonalities of plant responses to single and combined stresses. Plant J 90(5):839–855. https://doi.org/10.1111/tpj.13557

Zhang G, Muglia LJ, Chakraborty R, Akey JM, Williams SM (2013) Signatures of natural selection on genetic variants affecting complex human traits. Appl Transl Genom 2:78–94

Zhang C, Jiang J, Ma J, Zhang X, Yang Q, Ouyang Q, Lei X (2015) Evaluating soil reinforcement by plant roots using artificial neural networks. Soil Use Manag 31(3):408–416. https://doi.org/10.1111/sum.12196

Zhang B, Wang C, Wei ZH, Sun HZ, Xu GZ, Liu JX, Liu HY (2016) The effects of dietary phosphorus on the growth performance and phosphorus excretion of dairy heifers. Asian Australas J Anim Sci 29(7):960–964. https://doi.org/10.5713/ajas.15.0548

Zhang R, Vivanco JM, Shen Q (2017) The unseen rhizosphere root-soil-microbe interactions for crop production. Curr Opin Microbiol 37:8–14. https://doi.org/10.1016/j.mib.2017.03.008

Zhang P, Neher DA, Li B, Wu J (2018) The impacts of above- and below-ground plant input on soil microbiota: invasive *Spartina alterniflora* versus *native phragmites australis*. Ecosystems 21(3):469–481. https://doi.org/10.1007/s10021-017-0162-8

Zhou Y, Van Leeuwen SK, Pieterse CMJ, Bakker PAHM, Van Wees SCM (2019) Effect of atmospheric CO_2 on plant defense against leaf and root pathogens of *Arabidopsis*. Eur J Plant Pathol 154(1):31–42. https://doi.org/10.1007/s10658-019-01706-1

Ziska LH, Blumenthal DM, Runion GB, Hunt ER, Diaz-Soltero H (2011) Invasive species and climate change: an agronomic perspective. Clim Chang 105(1–2):13–42. https://doi.org/10.1007/s10584-010-9879-5

zu Castell W, Luttge U, Matyssek R (2019) Gaia—a holobiont-like system emerging from interaction. In: Wegner LH, Lüttge U (eds) Emergence and modularity in life sciences. Springer International Publishing, Cham, pp 255–279. https://doi.org/10.1007/978-3-030-06128-9_12

Chapter 2
Loss of Agro-Biodiversity and Productivity Due to Climate Change in Continent Asia: A Review

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Abstract The population of the world is growing day by day, and according to the estimation by the year 2050 the population will exceed nine billion. The food demand will increase and agricultural activities need modification to satisfy the hunger and nutrition requirements of this up-surging population. The demand for productive agricultural land will be increased. The environmentally sustainable system needs to be introduced to maintain the level of production and the quality of food. The increasing greenhouse gases are the cause of climate change, due to industrialization. The agricultural activities are particularly affected by the environmental issues, including climatic alterations, increasing scarcity of water resource. The movement of populations from rural to urban areas will increase the burden on resources. That is the reason the agricultural practices needed to be renewed by undertaking the ecological, economic, and social aspects of agriculture sector. Moreover, the food and nutrition requirements in the increasing population of developing and resource-scarce countries, especially in Asia and Africa is a challenge. These countries are already poor and resource scarce, and the phenomenon of climate change is adding further challenges for the agriculture practice of small-scale farmers. This review presents the science-based evidence of climate change effect on crops. So the sustainable modifications in agricultural activities should be made by keeping in view these effects. The concept of sustainable practices is distributed in four categories such as agrarian farming, health and nutrition valve, sustainability of ecosystems, and prosperity of the populations and associated factors. The formulation and implementation of policies along with initiatives to mitigate and adapt to the climatic variations. The strategy of agro-biodiversity can be effective to overcome these problems associated with increasing population and climate change. The agro-biodiversity can reduce the challenges of global food security.

Keywords Agro-biodiversity · Climate change · Crop production · Livestock · Food scarcity

2.1 Introduction

2.1.1 Agro-Biodiversity: Trends and Varieties

Variability and changeability of wildlife, vegetation, and microbial species are used directly or tortuously for the production of food in agricultural activities, comprising harvesting of edible and other crops, livestock, forestry, and fisheries. The agro-biodiversity encompasses the variety of innate assets (diversities, strains) and the type of species used in the production of food for humans, animal fodder, medicines, and other resources. The species, which are not used for directly as food purposes but they play a vital role in the growth of other species such as microbial species, arthropods, and predator species. These non-harvested species are part of environment and significant for the diversity of agro-ecosystem (FAO 1999a, b). Agro-biodiversity is associated with agricultural biodiversity and the hereditary resource for the food and agronomy, it contains the following:

- Agro-biodiversity includes harvestable crops that are used for foodstuff and other purposes like breeding of livestock, and for all species of fishes. The wild species within the agricultural land, rangeland and forest species, aquatic biodiversity, goods from trees and plants, species hunted for food purposes.
- The species which help in the growth and production of harvestable species are non-harvested species. It includes pollinators, micro-biota, insects, honey bees, butterflies, etc. All species which are present in environment and which support the production of biodiversity are part of agro-biodiversity (FAO 2004).

2.1.2 Productivity of Crops

2.1.2.1 100 Years of Agricultural Change: Trends and Figures Related to Agro-Biodiversity

The threat posed by locally varied food production systems may include skilled men and women farmers, culture and local knowledge regarding older systems. As a result, extensive decline in agro-diversity was taking place. Therefore, other wild and native species disappear along the harvested crops and species (Rizwan et al. 2017a, b). Today, most of the world population is getting food only from 5 animal and 12 plant species; this may constitute 75% of total world food requirement. About 2.5–3 million species are used for food purposes, while humans use approximately 200 species for different purposes. More than 60% of Recommended Daily Intake (RDI) for calories and protein is obtained only from three sources, i.e., rice, maize, and wheat. Approximately 35% food necessities of humans are dependent on animals. About 12% of the world's inhabitants are dependent on animal species for different products. In order to increase the yield, farmers use GMO plants and seeds which is ultimately the reason for 75% extinction of original genetic species since 1990. Therefore, about 30% livestock species are becoming extinct. Many crop varieties and animals are lost from fields. The 17 main fish species of the world produced more than their sustainable limits to fulfill the food requirements. The genetic diversity of agro-biodiversity is affected due to loss of forests and wetlands and pollution of water bodies (FAO 1999b). The acceleration of decline in agro-biodiversity throughout the twentieth century can be due to expanding population and exploitation of resources to fulfill the need of population.

2.1.2.2 The Decrease in Cultivated Land and Green Revolution Agriculture

The rigorous production of livestock, aquaculture, and industrial fisheries, use of genetically modified organisms, and varieties and breeding of animals are the major reasons for the decline of agro-biodiversity. Moreover, limited number of domestic animal breeds and aquatic species have reared due to demand, and the prevalence of monocultures with cultivation of few crop varieties compact the agro-diversity in the ecology (Farid et al. 2020).

2.1.2.3 Food System and Marketing Globalization

The agro-biodiversity is declined due to perception and preferences of producers and customers, and this competition is increasing day by day. The policies are being developed for industries to secure patents for the cultivation of widespread and fewer varieties of GM products. This system will eventually create more competition in the global market, more uniform and reduced diversity of species.

2.1.2.4 Reduced Incorporation of Livestock in Arable Production

The livestock feed is limited and it has no diversity, similarly fisheries is nurtured to conserve and develop aquatic biodiversity. The major reason for the genetic eradication of agro-diversity is the replacement of local varieties by exotic or improved varieties and species, as reported by almost all countries. Recurrently, genetic eradication takes place when old varieties in fields are substituted by newer varieties. The previous gene varieties are not found in modern varieties due to the use of commercial varieties. Nowadays, genetic erosion is a serious problem in many countries according to FAO (1996).

2.1.3 Varieties of Crops and Their Production

2.1.3.1 South Asia

The diversity of South Asian region with regard to flora and fauna, climate, agroecology, and ethnicity is evident. The number of cultivated plant species at Hindustani (Indian subcontinent) Diversity Centre reaches up to 166 (Zeven and de Wet 1982). They possess extensive variability among wild plants. More than 300 species of such wild relatives of crops have reported in India alone (Arora and Nayar 1984). The conversion of sustenance production system to commercial agriculture is responsible for the change in agricultural landscape in this area (Farid et al. 2019). Crops produced by old-style farming are mainly used for domestic feeding and sold in market if produced in surplus. The cultivation of traditional cash crops like jute, sugarcane, and tobacco, etc. has reduced with the passage of time; most of the farmers now turn to commercial production and edible crops including rice, wheat, fruits, and vegetables because they are the best to generate income. The availability and traditional choices on numerous kinds of cereals is the reason for diverse food consumption pattern. In India, about 1.1 billion inhabitants are dependent on agrarian sector. India still has numerous native genetic diversities including trees of bamboo and rattan (Rana and Handel 1992). The hotspot of native species in India is Western Ghats, Deccan Plateau, Central India, North-Western Himalayas, and North-Eastern hilly region. Nepal is also an agrarian country, 80% population is dependent upon agricultural sector, and 90% agriculture is performed by sowing seeds (Joshi 2000).

2.1.3.2 Southeast Asia

Southeast Asia is a center containing seven biodiversity hotspots, including Indonesia, Philippines, and Malaysia known for their vast diversity. Traditional, wild and few landraces are the backbone of agriculture in this region. Cambodia's agriculture includes only typical varieties of rice, maize, sesame, and vegetables holding 80% of area. Biodiversity reduces massively due to carelessness of human intervention like urbanization, industrialization, and exploitation of resources that leads to deterioration of stability in agriculture and agro-biodiversity in countries like Laos that also affects plantations of maize, cassava, tea, teak, and rubber leading to deforestation. Vietnam leads in rice production holding 80% of area fulfilling 90% of food requirement cementing its second position. Maize, sweet potato, cassava, legumes, soybean, fruits, and vegetables are tried for alternate crops of rice through facilitation of government of Thailand in terms of income and subsidies.

2.1.3.3 East Asia

In East Asia, mostly rice, wheat, corn, soybeans, sorghum, barley, millet, peanuts, pulses, sugar beets, potatoes, cotton, oilseeds, forages, root crops, vegetables, and fruits are grown. East Asia is the center for crop diversity in the world. About 300 edible crops are grown in this area, and they are famous in the globe including soybean, rice, wheat, citrus, oat, barley, buckwheat, Chinese cabbage, and tea. East Asia is also famous for production of rice over 7000 years. East Asia is rich in eco-geographical diversities and ancient agronomy practices. Approximately 200 hundred crops of 600 species are grown in china. Extensive and intensive farming practices for food requirements and economic development are the reason for biodiversity damage. About 70% of plants are imported for cultivation purposes, which can damage native species. The variability of wheat seeds in china decreased about 90% from 1949 to 1970. Fifteen million hectares of land in china are used to grow hybrid rice. Similarly, it is reported in Japan that genetic diversity has declined.

2.2 Impact of Climate Change on Crops

Asian agriculture culture is accountable for two-third of agricultural Gross Domestic Product (GDP) globally. There have been many researches explaining the effect of climate change on crop productivity in particular places in Asia, but no research has so far studied crops through the whole continent (Mendelsohn 2014). The vast continent of Asia is distributed into regions of South and Southeast Asia (Pakistan, Viet Nam, India, Indonesia, Myanmar, Cambodia, Bangladesh, Thailand, Malaysia, and Philippines) and East Asia (China, North and South Korea, Japan, and Taiwan).

Agriculture in Southeast and South Asia is extremely susceptible to weather-related hazards, mainly storm surges, tropical cyclones, droughts, and floods that harm life, crop production, and property. In January 1991, the Philippine weather bureau "Philippine Atmospheric, Geophysical and Astronomical Services Administration (PAGASA)" reported that after the beginning of an ENSO-related drought, maize and rice crops faced a loss of 753 million dollars (Escafio and Buendia 1994). Seasonal monsoons are the foremost climate feature. The surface waters of Indonesia and Malaysia are the main part of the ENSO procedures. Changes in these leading climate features have significant effects on agriculture in this region. Climate change also increases sea level, causing flooding of low coastline areas which maintain great populations and widespread agricultural production (for instance, Bangladesh). A drop in production of rice due to the effects of climate and rise in sea level, along with quickly growing population, would impede food security.

Because of climatic variations, the biotic stress is enhanced in both plants and animals. Due to climate change, precursors associated with growth and development of plants is also altered. Due to environmental changes, pollination of plants is affected, more disease-causing agents can arise, and they can become more resistant. Various components of the global food system is threatened due to the changes in climate patterns. Extreme weather events can disrupt the entire global food system (Brown et al. 2013).

There is clear proof for an estimated rise in global temperature and changes in precipitation patterns in the course of the twentieth century. The most forthcoming variations in current era is the rise in the temperature of globe because of amplified level of GHGs including CO_2, CH_4, O_3, N_2O, and CFCs. Due to the increasing amounts of these greenhouse gases, there are projections about climate change showing warning about future variations in climate and indirect or direct impact on agricultural sector (Farid et al. 2018a). The amount of CO_2 rise in atmosphere and the projected changes in climate because of global warming are expected to disturb the agrarian yield in the future because of fluctuations in transpiration factor and plant development rate (Mendelsohn 2014).

The growth of crops is distributed in two long-term seasons. The summer or kharif crop-growing season (June to September) overlaps with South-West monsoon. The main kharif crops include soybean, maize, rice, cotton, sugarcane, bajra, jute, etc. Depending on the period of crops, kharif crops can be reaped during the winter (December to February) or autumn (October to November) months. The South-West monsoon is dangerous for the kharif crop that accounts for approximately 51% of grain yield and around 65% of oilseed crops. The internal monsoon precipitation inconsistency in India is the reason for massive flood and droughts causing a decrease in the Indian food crops yield and economy. Sowing and growth of the winter (rabi) crop begins after the rains in summer and remains over the coming spring or primary summer. Precipitation at the end of the monsoon season offers soil moisture and frequent water availability for irrigation of rabi crop (October to November). The summer rainy season as a result is in charge for both crop productions in India. The main rabi crops include gram, potato, onion, mustard, barley, wheat, etc. (Farid et al. 2018b).

In various tropical and sub-tropical areas, possible yields are predicted to decline due to maximum anticipated rises in heat. The effects of increased carbon dioxide must be measured in the framework of alterations in the air temperature, mainly nighttime temperature. Because of the rise in carbon dioxide and numerous trace fumes and fluctuations in humidity accessibility and its effect on vegetation v/s reproduction, requirement of more farming means (for instance, fertilizers) and the distribution and persistence of pest, therefore evolve a new balance between pests and crops. Ultimately, there will be significant change on land use because of ice melting, temporal and spatial precipitation changes, accessibility of irrigation, occurrence, and concentration of inter- and intra-seasonal floods and droughts, soil organic matter conversions, soil erosion, alteration in pest profiles, deterioration of arable areas due to expansion of sea, and accessibility of energy. In Asia, the overall 8% decline was measured due to climatic variations including the wheat crop (12%), maize (7%), sorghum (3%), and millet (9%). According to projections, this situation will be more severe by 2050.

2.2.1 Factors Involved in Decreasing Crop Productivity

Approximately 50% of crop production is endorsed to the impact of climatic influences. The following are some atmospheric variables that effect the crop production.

1. Temperature
2. Precipitation
3. Atmospheric gases (CO_2, CH_4, O_3, CFCs, and N_2O)
4. Solar radiation
5. Atmospheric humidity
6. Wind velocity

2.2.1.1 Temperature Variations

There is a major increase in the number of warm days approximately in all areas of the region. Warm nights have increased in rate nearly in each part of the region which is noteworthy. Cold nights and cool days have decreased in rate approximately all over the region. The increase in the quantity of warm days and nights and the decrease in the quantity of cool nights and days are realistically undeviating throughout the years (1961–1998) which have a major impact on the production of crops in the continent Asia. The number of warm nights and hot days has risen by the ratio of around 2–3 while the number of cold nights and cool days has declined nearly half of the total.

2.2.1.2 Water Deficiency

By 2030 only 60% of water demand will reach by existing resource at the current rate while 40% of population will be without access to water it needs. In the region of South Asia, water is needed for 1.6 billion people. The urbanization is creating pressure on water demand while in the rural areas the ground water is withdrawn for domestice purposes thus causing the depletion and deficiency of ground water table. The number of farmers complaining that their agriculture production is decreasing only by water deficiency that causes great loss to farmer every year in Pakistan and India. In India, 22 out of 32 cities daily face water crisis. In Nepal, people wait for hours and struggle for miles to obtain drinking water. The problem of water in South Asian region is scarcity amid abundance. Transboundary rivers that include Ganges, Indus, and Brahmaputra have great history. The rivers are now under pressure due to industrial sector, development of cities, increase in population, and environmental pollution (Surie 2015). Water contamination affects the Yellow River in China and the River Ganga in India by the domestic issues. Sino-Indian conflict regarding the fresh water is also rising. Due to water crises in Asia, water diversion projects are initiated such as China's South-to-North Water Diversion Project. Indians are drinking contaminated water containing harmful chemicals present in water, and half of the million population has water-borne diseases. Water crises in Asia are intensifying and sustainable water supply is decreased, which is giving rise to water wars. The construction of dams and diversion of water are the reasons for conflicts in Asian countries (Challaney 2017).

2.2.1.3 Rising CO_2

The concentration of CO_2 in atmosphere is rising day by day either because of anthropogenic activities or natural phenomenon that is becoming a reason for climatic variability. According to a report of Intergovernmental Panel on Climate Change (IPCC) 2007, the amount of carbon dioxide in the air has raised almost 22% since 1960. Enhanced economic and other anthropogenic activities are eliminating the globally available natural resources for sinking of carbon dioxide due to which CO_2 in the atmosphere is rising by the average of 1.3–3.3% annually as observed from 1990s to onwards 2006 (Canadell et al. 2007). The heat waves leaving the earth's surface are absorbed by the increased concentration of atmospheric CO_2 as a result of which earth's temperature increases and long-term changes in climatic condition occur. Rise of carbon dioxide concentration in the atmosphere and hence climatic variability has prominent impacts on human health and environment (Patz and Kovats 2002).

A significant change in the response of plants has been observed because of increased atmospheric carbon dioxide. The whole plant mechanism is affected due to increased CO_2 in the air because atmospheric CO_2 is the exclusive source of carbon availability to plants for the process of photosynthesis. Plants need a sufficient amount of carbon to carry out the process of photosynthesis. Increased concentration of CO_2 in the atmosphere is serving efficiently in this regard because around 95% of plants are not able to grow efficiently due to unavailability of sufficient supply of carbon. However, the plant growth with the supply of carbon is dependent on temperature (Long 1991). Because of the supply of sufficient carbon to the plants, atmospheric carbon dioxide increases, hence resulting in increased temperature which can potentially affect plant growth (Ziska et al. 2008).

2.2.1.4 Emission Trends

Plants face biotic and abiotic stress conditions because of variability in climatic conditions. They face stress factors such as high temperature and high light due to variation in the surroundings and results in the release of different volatile organic compounds (VOCs). When the temperature varies in the surrounding (in long-term climate change), plants undergo biotic and abiotic stress and they not only release carbon, oxygen, and water vapors but also a massive concentration of VOCs in the atmosphere (Habiba et al. 2015; Ehsan et al. 2014). These emissions include different derivatives of fatty acids, amino acids, and their derived metabolites, terpenes, phenylpropanoids, etc. The emissions of such volatile organic compounds are normally coupled with a series of biotic and abiotic stress in plants. The release of such compounds from plants is dependent on different factors such as plants type or species, phase of development of plant, and surrounding conditions such as climate, emission trends in the atmosphere, etc. The prevailing environmental conditions widely influence biotic and abiotic stress factors in plants, and emissions of volatile compounds from plants are also dependent on environmental parameters. For example, an increase in the release of volatile substances, such as (Duhl et al. 2008) a range of terpene compounds and some isoprene (Sharkey and Yeh 2001) and monoterpenes (Loreto et al. 1996), has been observed in herbaceous and woody plant species (Schuh et al. 1997) because of climatic variability (Holopainen and Gershenzon 2010).

2.2.2 Most Affected Crops

The emission of greenhouse gases is enhanced due to rapid increase in anthropogenic activities and development interest. The rapid increase in emission increases the temperature of the earth, and agriculture is the most vulnerable sector affected by these emission trends. This increase in temperature day by day affects the yield of crops and enhances pests and weeds growth (Nelson et al. 2009). Not only the crop yield is reduced because of climate change but also survival of some wild plant species such as potato, peanuts, and cowpea is vulnerable due to altering climatic conditions (Jarvis et al. 2008). In recent years, different crops are taken under observation and tested for seeing the impacts of global heat stress on agricultural crops due to varying climatic conditions (Farid et al. 2017a). Different species of maize, soya bean, rice and wheat are taken for applying statistical models and testing land use types to simulate the changing trends in crops growth, yield and nutrient value due to climate change (Teixeira et al. 2013). And the results have shown that agricultural production is affected worldwide due to global warming, and global warming poses threat to food security globally (Fischer et al. 2005; Schmidhuber and Tubiello 2007; Ainsworth and Ort 2010).

2.3 Impact of Climate Change on Livestock

Livestock is important for global food requirements. In developing Asia, total protein from livestock was 68.9 g/capita in 2002 (Steinfeld et al. 2006a, b). Climate change impacts on livestock in Asia are in a number of ways and mostly neglected. Many factors influence and alter livestock very speedily in emerging nations, especially in Asia and Africa. The manufacture of livestock products will raise constantly in the coming years around the globe due to population and urbanization expansion (Delgado et al. 1999; Thornton et al. 2009). The significant impacts of alterations in livestock would be harmful for lives of poor people and of those who depend on livestock. The changes in this system are inclined by alteration in natural variants in resources and also by changes in demand (Thornton et al. 2009). Major variations have been detected in many other continents due to climate change, particularly global warming, and substantial impacts on physical and biological structure have been witnessed (Rosenzweig et al. 2008). Livestock depend on agricultural practice. Regular weather determines plant development, growth rate, water requirement, and yield so even a small deviation in climate can be harmful for plants (Keeling et al. 1995). In south East Asia, the production of livestock is high alongwith their access to ocean enhanced their imports to rest of the world. Thus, climate change has direct and indirect impacts on livestock and can affect the imports to the world (Steinfeld et al. 2006a, b).

2.3.1 Direct Impacts of Climate Change on Livestock

2.3.1.1 Feeds Quality and Quantity

In South Asia, the quality and quantity of feed of livestock is at risk in consequences of climatic variations. In Asia, climatic variation is causing reduction in meat quality and calories content is reducing, which is harmful for the growth of children (Nelson et al. 2009). The food insecurity is rising due to high carbon in soil and atmosphere in Central and South Asia and china and requires carbon sequestration. The reduction in soil organic carbon reduces the yield of these regions (Lal 2004). Water availability is expected to reduce in Brahmaputra and Indus Basin and will raise the issue of food security approximately for 60 million people due to low crop and livestock production (Immerzeel et al. 2010).

2.3.1.2 Heat Stress

According to Sirohi and Michaelowa (2007), due to heat stress animal breeding, fertility, and low intake of food can be affected as thermal comfort temperature is 5–15 °C. In developing countries, intensification and temperate breeding could be more vulnerable for livestock (Parsons et al. 2001; Mader and Davis 2004; King et al. 2006).

2.3.1.3 Water Availability

Water demand for livestock is rising with an increase in atmospheric temperature. Major contributors to world livestock production, i.e., China, Brazil, India, and Pakistan are under the severe danger of shift in atmospheric temperature (Farid et al. 2017b). An increase in temperature will significantly affect livestock in Asia (Rust and Rust 2013; Rosegrant et al. 2010). Climate change also leads to various infections and vector-borne diseases in crops and livestock (Medlock and Leach 2015; Nardone et al. 2010).

2.3.1.4 Diseases and Infections

Harvell et al. (2002) and Baylis and Githeko (2006) describe about vector and non-vector diseases of livestock in developing countries. As a result of ozone layer depletion, mammalian cellular immunity can be inhibited and genetic variations in animals and disease outbreak can occur. Climatic variations can increase the number of brown-ear ticks, *Rhipicephalus appendiculatus,* the main cause for East Coast Fever, a sickness that disturbs feeding of livestock. The development of disease depends on many factors such as species and age. (Thornton et al. 2009; Tabachnick 2010; Irado et al. 2010).

2.3.1.5 Biodiversity

Loss of biodiversity due to various factors has been observed in developing countries such as feline species population decreased by 7–10% (FAO 2007). In India, rice production is at risk due to climate change (Ehrenfeld 2005). Studies have shown that a 2.5 °C increase in temperature will lead to loss of biodiversity. Especially 20–30% endemic plant species would be more vulnerable. All species cannot adapt to changing environment and climate change; this would damage biodiversity in the coming years on a large scale (Pereira et al. 2010; Bellard et al. 2012). As a result of rising population and food demand, changes in agricultural systems will occur. New technologies introduced for enhanced economy to save labor cost and more production, intensifications of agriculture practices, and livestock production can be affected due to climate change (Baltenweck et al. 2003; Steinfeld et al. 2006a, b).

2.3.2 Indirect Impacts of Climate Change

The direct influence of climate change will affect the health of humans ultimately. Transmission and outbreak of diseases, mortality, and morbidity rate can enhance due to favorable conditions in developing countries under climate change conditions. More vulnerable are poor people due to low economy. Due to the spread of diseases such as AIDs\HIV, labor issues can arise which also have impacts on economy (Thornton et al. 2009; Patz et al. 2005).

2.4 Impact of Climate Change on Fisheries

In marine ecosystem, composition, distribution, and richness of species vary leading to rising ocean temperatures (Perry et al. 2005; Pörtner and Peck 2010). In result of temperature variations on various stages of ecosystem, physical alterations at molecular, cellular and at entire ecosystem level will depend on species-specific reactions. Climate change, CO_2, acidification, nutrients, oxygen level, and temperature are main factors of biological changes (Portner 2001, 2002; Pörtner and Peck 2010). The increase in temperature creates a cloud of extra deviations, such as increase in sea level, amplified ocean stratification, reduced sea-ice degree, and changes in arrays of ocean movement, rain, and freshwater contribution (Keeling et al. 2010). All fish are exothermic and cannot regulate their temperature through physiological changes and their body temperature is identical to environment (Moyle and Cech 2004). Poles and tropical ecosystems are more vulnerable. Coral reefs are also at risk as they are sensitive to temperature. Climate change will cause fluctuations in whole marine and terrestrial ecosystem and will also affect services (Doney et al. 2011). South Asia is severely affected by climate change and the increase in food insecurity is due to population rise, natural resource degradation, heat waves, and change in rainfall pattern across Himalaya. Fisheries are affected in abundance due to climate change, and poverty and hunger are on the rise in this region (Sivakumar and Stefanski 2010). Northeast Asia is the biggest hotspot of fish production, consumption, and trade in the world. Industrialization leads to GHG emissions and warming in this region. Mostly small fishes are yield, i.e., pelagic fish which is very sensitive to climatic variations. Production of fisheries biomass is affected by climate change thus leading to economic and social issues in Asia (Kim 2010; Barange et al. 2014; Ficke et al. 2007). According to Jackson and Mandrak (2002), global warming will lead to introduction of warmth water species in Asia which will affect native species of marine ecosystem (Ficke et al. 2007). So there is need for better management of fisheries in Asia at various levels for better ecosystem, economy, and service (Pomeroy et al. 2001).

2.5 Economic Loss Due to Climate Change

Climate change has adverse effects on global food production by affecting the quality and quantity of food. Agriculture, livestock, and fish sector are greatly affected by the changing in weather for the last few years. It also reduces our capacity to maintain an adequate supply of food for all living organisms (Sen 1982). It is very difficult to estimate net impact of these environmental changes on agriculture sector and food production which creates the issue of food security. It is not only determined by the climate factor but also by the ability of people to afford, access, and use food (Battisti and Naylor 2009).

2.5.1 Fluctuation in Prices of Staple Foods

Climatic variations will be the reason for great economic pressure on food availability and its prices. According to International Model for Policy Analysis of Agricultural Commodities and Trade by International Food Policy Research Institute, the cost of the three mostly used edible crops in the world, i.e., wheat, maize, and rice will be increased by 31–106% by 2050. Most important factors that define the exact values of these crops within the range are mitigation, income growth, and population growth (Nelson et al. 2010). Mostly analysis in numerous countries shows higher prices of food that enhance food insecurity and poverty in both urban and rural areas (Ivanic and Martin 2008). People that are net consumers are also affected by inflation of prices. The benefits of greater income may help out some smallholder farmers to adjust with the expensive food but landless laborers working on these farms will face this more badly (Singh et al. 1986). Higher prices also reduce nutrient intake and increase malnourishment rate among people. Magnitude of effect will vary depending upon the income status and wealth across the country. In low-income countries, review on price elasticities reveals that price increase is also linked to the national economy. The impact of expensive food and higher rates of crops increases food insecurity which depends on the structure of economy and the capability of agrarians to adapt to unstable economic and ecological conditions (Morton 2007).

2.5.2 GDP and Economic Growth

Gross domestic product (GDP) is also affected by fluctuation in food prices (Schmidhuber and Tubiello 2007). It is very difficult to project growth trajectories, even by excluding the environmental variables. A recent research work on the association between temperature and macroeconomic productivity within countries reveals that labor productivity, labor supply, and crop production are largely affected due to extreme heat. The author finds that lower earning issues and temperature-related issues will rise by 75% in the developed nations by 2100. Due to the increase in the intensity of climate change and low economic growth scenario, almost 43% of all countries will be at risk and also be poorer by the end of this century than they are now (Burke et al. 2015). This will clearly show that there is a chance of increasing economic losses due to unmitigated climate change situation, which also greatly weakened the purchasing power of consumers to obtain basic facilities of life in the developing world. Even, if we are successful in improving the crop yield and increasing the production of food worldwide, resource-scarce countries are still struggling for access to food on the global market because there is a huge difference between where food is produced and where food is needed. An increase in food production in developed countries will not improve the drought and low attitude agriculture situation of poorer countries. These threats will increase with the demographic reality that a large part of world's anticipated population of almost 2.5–3.0 billion will be expected to occur in cities in the coming decades for the developing countries.

2.6 Effects on Food Security and Nutrition

Climate change has adverse effects on food production, crops yield, and food insecurity. The demand dynamics of market and supply of food are not only the factors that create food scarcity in an area (Hodges et al. 2011). Utilization of food and resources, cooking nutritious and safe food, protecting food stocks against pests and spoilage allowed to retain the nutrients in food for consuption. (Parfitt et al. 2010). Safe growth, healthy food, and then protection are very difficult in those situations where safe water and sanitation system are absent, and crops will face harsh climate issues like increased rainfall and prolonged drought (Rose 2015). This will also lead to increased exposure of parasites, mycotoxins, viruses, and pathogenic bacteria that destroys the harvested crops too. These infectious crops cause diarrheal diseases in children which have intense influence on child development and its nutritional status (Ngure et al. 2014). An environmental survey of 171 countries in the context of health represents their whole nation from 70 countries from all over the world between 1986 and 2007 reveals that the level of growth restricting in children under 5 years is highly associated with access to poor sanitation and water quality (Fink et al. 2011).

2.6.1 Fluctuation in Prices

Trends like levels of income, prices, production, and disease will define the future predictions of food accessibility and consumption in the upcoming time. Prices will also fluctuate greatly by the increase of temporal and spatial variability in a food production pattern due to climate change. The projections and final estimation of the future food scarcity rate in the world are very difficult when we are considering all the determinants for that, with respect to food access and volatility. But all the economic and biophysical models reveal that upcoming world will experience more fluctuations in food pricing due to harsh climatic conditions (Lobell et al. 2009).

2.6.2 Nutrient Quality of Food

Environmental changes also have a serious impact on the production and nutritional value of crops. Climate change reduces the nutrients from vegetables and legumes, also reduces the yield of crops day by day. Water scarcity and the increase in temperature have a large impact on the nutrient quality of food. Greater concentration of carbon dioxide affects the process of photosynthesis in plants which allows plant to transform sunlight into food. It also has influence on the nutrient content of sea food and food chain. It changes the nutritional composition of phytoplankton communities by reducing long-chain polyunsaturated fatty acid content (Bermudez et al. 2015). Thermal pollution also limits the uptake of iron and minerals and alters the micronutrient composition in fishes (Chavez et al. 2011). Like plants, carbon dioxide combined with climate changes leads to substantial uncertainties regarding the availability of food and nutrition (Myers et al. 2017).

In Asia, most of the countries are developing and agriculture is their most important sector of economy. GHG emissions and atmospheric concentrations will continue to increase for some decades; therefore, mitigation measures are not sufficient to control food scarcity issues. Climate functions and predicted changes in temperature will also disturb the food production and agro-ecological conditions. Thus, farmers need to adjust their practices and modify their technologies to meet the food requirement of future generations. Adapting to new climate scenarios is not feasible all the time because weather forecasts are not always trustable (Caldeira et al. 2004). Sometimes better seed varieties will not endure weather conditions and cause more food scarcity. To better prepare the vulnerable regions, scientists and economists have to make models according to the high-risk regions and crops present there, and also socioeconomic impacts that affect those models and their prediction, along with all uncertainties (Rosegrant et al. 2010).

2.7 Future Projections of Climate Change

The state of climate in future can be derived from different models which are projecting statistical analysis of weather and climatic patterns. According to the second report of assessment of IPCC, the warmer span of season increased the colder one, and hence there is occurrence of prolonged summers and short winters as well as variability in precipitation rate, etc. According to different reports and assessments, there is a complexity in different weather and climatic patterns just like heat stress in warm areas and variable rainfall pattern as well as variability of cooling days, etc. (Meehl et al. 2000). The data from different projection reports suggested that East Asia will face warmer climatic patterns in the twenty-first century, and the area of continent will experience high precipitation and temperature rate then oceanic area according to different spatial indications. It is projected that regular temperature changes for East Asia for the 30-year periods of 2020s, 2050s, and 2080s simulated 1.2, 2.5, and 4.1 °C increase, and precipitation changes are 0.4, 2.2, and 5.0% increase, respectively (Min et al. 2004). Climatic changes in stream flow sinks directly impact supply of freshwater, irrigation, etc. according to different assessments; the glaciation in the future is complex in the extent of water availability and majorly in Central Asia (Sorg et al. 2012). The study reveals that water for food security situation will intricate and might get daunting if no action is taken. The agricultural sector globally and in Asia has pressure on needs due to increasing population; it also increases the use of water and land resources. The greenhouse gas emissions from agricultural sector have a diverse negative impact (Hanjra and Qureshi 2010; Bellard et al. 2012). The carbon level in atmosphere is variably altering and atmospheric chemistry is crucially changing. The warming in continent Asia is not equally distributed overall, and agricultural sector is majorly affected sector along with various corresponding factors. The losses due to climate change in Asia are more in terms of crop yield and cause a severe issue of food security (Rosegrant et al. 2010). Since 1980, crop productivity is reduced in Southeast Asia. Immediate response is required to cope with these climatic variations, and agricultural production needs to be increased.

2.8 Conclusion

Our planet is facing climatic alterations and problems like water shortage, change in rainfall pattern, high temperature issues, and drought conditions. All major staple crops of the Asian continent such as rice, cereals, vegetables, grains, and spices are climatically sensitive. Due to rising temperature and changing of rainfall pattern, water scarcity increases which result in low productivity of crops and ultimately food shortage. Developing countries are facing food insecurity, crucial hindrance to their economic and social development. The decrease in crop yield is the cause of fluctuation in food prices, and it will be the reason for high food prices in the future and food security. The nutrition valve of crops is reduced. Agro-biodiversity provides income and food to farmers in this area. Native genetic diversity is declining in the continent. Due to climate change, GM species are mostly used nowadays, which is the reason for the decline in biodiversity. The species which can adapt adverse ecological conditions need to be introduced. The actions are need to be taken for the conservation of agro-biodiversity on international level. Asian Productivity Organization (APO) is working for Green Revolution and working to store genetics of agro-biodiversity. To increase the production, more climate-resistive species are being introduced which can provide more yield and more nutritional valve by genetic resources. But more research and policy need to be developed and implemented in this production of new species.

References

Ainsworth EA, Ort DR (2010) How do we improve crop production in a warming world? Plant Physiol 154:526–530

Arora RK, Nayar ER (1984) Wild relatives of crop plants in India. NBPGR. SciMong 7:90

Baltenweck I, Staal SJ, Ibrahim MNM, Manyong V, Williams TO, Jabbar M, Holmann F, Patil BR, Herrero M, Thornton PK, de Wolff T (2003) SLP project on transregional analysis of crop–livestock systems. Level 1 report: broad dimensions of crop–livestock intensification and interaction across three continents. ILRI, Nairobi

Barange M, Merino G, Blanchard JL, Scholtens J, Harle J, Allison EH et al (2014) Impacts of climate change on marine ecosystem production in societies dependent on fisheries. Nat Clim Chang 4(3):211

Battisti DS, Naylor RL (2009) Historical warnings of future food insecurity with unprecedented seasonal heat. Science 323(5911):240–244

Baylis M, Githeko AK (2006) The effects of climate change on infectious diseases of animals. Report for the Foresight Project on Detection of Infectious Diseases, Department of Trade and Industry, UK Government, p 35

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15(4):365–377

Bermudez R, Feng Y, Roleda MY, Tatters AO, Hutchins DA, Larsen T, Winder M (2015) Long-term conditioning to elevated pCO_2 and warming influences the fatty and amino acid composition of the diatom *Cylindrotheca fusiformis*. PLoS One 10(5):e0123945

Burke M, Hsiang SM, Miguel E (2015) Global non-linear effect of temperature on economic production. Nature 527(7577):235

Caldeira K, Granger Morgan M, Baldocchi D, Brewer PG, Chen CTA, Nabuurs GJ, Nakicenovic N, Robertson GP (2004) A portfolio of carbon management options. In: Field C, Raupach M (eds) Towards CO_2 stabilization: issues, strategies, and consequences, a SCOPE report (scientific committee on problems in the environment). Island Press, Washington, DC, pp 103–129

Canadell JG, Le Quéré C, Raupach MR, Field CB, Buitenhuis ET, Ciais P, Marland G (2007) Contributions to accelerating atmospheric CO2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proc Natl Acad Sci 104(47):18866–18870

Chavez FP, Messié M, Pennington JT (2011) Marine primary production in relation to climate variability and change. Ann Rev Mar Sci 3:227–260

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, English CA, Polovina J (2011) Climate change impacts on marine ecosystems. Ann Rev Mar Sci 4:11–37

Duhl TR, Helmig D, Guenther A (2008) Sesquiterpene emissions from vegetation: a review. Biogeosciences 5(3):761–777

Ehrenfeld D (2005) The environmental limits to globalization. Conserv Biol 19(2):318–326

Ehsan S, Ali S, Noureen S, Mahmood K, Farid M, Ishaque W, Shakoor MB, Rizwan M (2014) Citric acid assisted phytoremediation of cadmium by Brassica napus L. Ecotoxicol Environ Saf 106:164–172

FAO (1996) Global plan of action for the conservation and sustainable utilisation of plant genetic resources for food and agriculture. Leipzig, June 1996

FAO (1999a) Agricultural biodiversity, multifunctional character of agriculture and land conference, background paper 1. Maastricht

FAO (1999b) Women: users, preservers and managers of agrobiodiversity. www.fao.org/FOCUS/E/Women/Biodiv-e.htm. Accessed 23 Sept 2018

FAO (2004) The State of Food Insecurity in the World, monitoring progress towards the World Food Summit and Millennium Development Goals. ISBN 92-5-105178-X

FAO (2007) CGRFA (Commission on Genetic Resources for Food and Agriculture). The State of the World's Animal Genetic Resources for Food and Agriculture, p 523

Farid M, Ali S, Rizwan M, Ali Q, Abbas F, Bukhari SAH, Saeed R, Wu L (2017a) Citric acid assisted phytoextraction of chromium by sunflower; morpho-physiological and biochemical alterations in plants. Ecotoxicol Environ Saf 145:90–102

Farid M, Ali S, Rizwan M, Saeed R, Tauqeer HM, Sallah-Ud-Din R, Azam A, Raza N (2017b) Microwave irradiation and citric acid assisted seed germination and phytoextraction of nickel (Ni) by Brassica napus L.: morpho-physiological and biochemical alterations under Ni stress. Environ Sci Pollut Res 24(26):21050–21064

Farid M, Ali S, Zubair M, Saeed R, Rizwan M, Sallah-Ud-Din R, Azam A, Ashraf R, Ashraf W (2018a) Glutamic acid assisted phyto-management of silver-contaminated soils through sunflower; physiological and biochemical response. Environ Sci Pollut Res 25(25):25390–25400

Farid M, Ali S, Rizwan M, Ali Q, Saeed R, Nasir T, Abbasi GH, Rehmani MIA, Ata-Ul-Karim ST, Bukhari SAH, Ahmad T (2018b) Phyto-management of chromium contaminated soils through sunflower under exogenously applied 5-aminolevulinic acid. Ecotoxicol Environ Saf 151:255–265

Farid M, Ali S, Saeed R, Rizwan M, Bukhari SAH, Abbasi GH, Hussain A, Ali B, Zamir MSI, Ahmad I (2019) Combined application of citric acid and 5-aminolevulinic acid improved biomass, photosynthesis and gas exchange attributes of sunflower (L.) grown on chromium contaminated soil. Int J Phytoremediation 21(8):760–767

Farid M, Ali S, Rizwan M, Yasmeen T, Arif MS, Riaz M, Saqib M, Zia ur Rehman M, Ayub MA (2020) Combined effects of citric acid and 5-aminolevulinic acid in mitigating chromium toxicity in sunflower (Helianthus annuus l.) grown in cr spiked soil. Pak J Agri Sci (Accepted: online)

Ficke AD, Myrick CA, Hansen LJ (2007) Potential impacts of global climate change on freshwater fisheries. Rev Fish Biol Fish 17(4):581–613

Fink G, Günther I, Hill K (2011) The effect of water and sanitation on child health: evidence from the demographic and health surveys 1986–2007. Int J Epidemiol 40(5):1196–1204

Fischer G, Shah M, Tubiello FN, van Velhuizen H (2005) Socio-economic and climate change impacts on agriculture: an integrated assessment, 1990–2080. Philos Trans R Soc B 29:2067–2083

Habiba U, Ali S, Farid M, Shakoor MB, Rizwan M, Ibrahim M, Abbasi GH, Hayat T, Ali B (2015) EDTA enhanced plant growth, antioxidant defense system, and phytoextraction of copper by Brassica napus L. Environ Sci Pollut Res 22(2):1534–1544

Hanjra MA, Qureshi ME (2010) Global water crisis and future food security in an era of climate change. Food Policy 35(5):365–377

Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD (2002) Ecology—climate warming and disease risks for terrestrial and marine biota. Science 296:2158–2162

Hodges RJ, Buzby JC, Bennett B (2011) Postharvest losses and waste in developed and less developed countries: opportunities to improve resource use. J Agric Sci 149(S1):37–45

Holopainen JK, Gershenzon J (2010) Multiple stress factors and the emission of plant VOCs. Trends Plant Sci 15(3):176–184

Immerzeel WW, Van Beek LP, Bierkens MF (2010) Climate change will affect the Asian water towers. Science 328(5984):1382–1385

Irado MC, Clarke R, Jaykus LA, McQuatters-Gollop A, Frank JM (2010) Climate change and food safety: a review. Food Res Int 43(7):1745–1765

Ivanic M, Martin W (2008) Implications of higher global food prices for poverty in low-income countries. The World Bank, Washington, DC

Jackson DA, Mandrak NE (2002) Changing fish biodiversity: predicting the loss of cyprinid biodiversity due to global climate change. In: McGinn NA (ed) American fisheries society symposium 32: fisheries in a changing climate. American Fisheries Society, Bethesda, pp 89–98

Jarvis A, Lane A, Hijmans RJ (2008) The effect of climate change on crop wild relatives. Agric Ecosyst Environ 126(1–2):13–23

Joshi KD (2000) Strengthening the farmers' seed system in Nepal. Biotechnol Dev Monit 42:15–17

Keeling CD, Whorf TP, Wahlen MM, Van der Plicht J (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. Nature 375:666–670

Keeling RF, Kortzinger A, Gruber N (2010) Ocean deoxygenation in a warming world. Annu Rev Mar Sci 2:199–229

Kim S (2010) Fisheries development in northeastern Asia in conjunction with changes in climate and social systems. Mar Policy 34(4):803–809

King JM, Parsons DJ, Turnpenny JR, Nyangaga J, Bakari P, Wathes CM (2006) Modelling energy metabolism of Friesians in Kenya smallholdings shows how heat stress and energy deficit constrain milk yield and cow replacement rate. Ani Sci 82:705–716

Lal R (2004) Soil carbon sequestration impacts on global climate change and food security. Science 304(5677):1623–1627

Lobell DB, Cassman KG, FieldC B (2009) Crop yield gaps: their importance, magnitudes, and causes. Annu Rev Environ Resour 34:179–204

Long SP (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO2 concentrations: has its importance been underestimated? Plant Cell Environ 14(8):729–739

Loreto F, Ciccioli P, Cecinato A, Brancaleoni E, Frattoni M, Tricoli D (1996) Influence of environmental factors and air composition on the emission of [alpha]-pinene from *Quercus ilex* leaves. Plant Physiol 110(1):267–275

Mader TL, Davis MS (2004) Effect of management strategies on reducing heat stress of feedlot cattle: feed and water intake. J Anim Sci 82:3077–3087

Medlock JM, Leach SA (2015) Effect of climate change on vector-borne disease risk in the UK. Lancet Infect Dis 15(6):721–730

Meehl GA, Zwiers F, Evans J, Knutson T, Mearns L, Whetton P (2000) Trends in extreme weather and climate events: issues related to modeling extremes in projections of future climate change. Bull Am Meteorol Soc 81(3):427–436

Mendelsohn R (2014) The impact of climate change on agriculture in Asia. J Integr Agric 13(4):660–665

Min SK, Park EH, Kwon WT (2004) Future projections of East Asian climate change from multi-AOGCM ensembles of IPCC SRES scenario simulations. J Meteorol Soc Jpn Ser II 82(4):1187–1211

Morton JF (2007) The impact of climate change on smallholder and subsistence agriculture. Proc Natl Acad Sci 104(50):19680–19685

Moyle PB, Cech JJ (2004) Fishes: an introduction to ichthyology, 5th edn. Prentice Hall, Englewood Cliffs

Myers SS, Smith MR, Guth S, Golden CD, Vaitla B, Mueller ND, Huybers P (2017) Climate change and global food systems: potential impacts on food security and undernutrition. Annu Rev Public Health 38:259–277

Nardone A, Ronchi B, Lacetera N, Ranieri MS, Bernabucci U (2010) Effects of climate changes on animal production and sustainability of livestock systems. Livest Sci 130(1–3):57–69

Nelson GC, Rosegrant MW, Koo J, Robertson R, Sulser T, Zhu T et al (2009) Climate change: impact on agriculture and costs of adaptation, vol 21. International Food Policy Research Institute, Washington, DC

Nelson GC, Rosegrant MW, Palazzo A, Gray I, Ingersoll C, Robertson R, Msangi S (2010) Food security, farming, and climate change to 2050: scenarios, results, policy options, vol 172. International Food Policy Research Institute, Washington, DC

Ngure FM, Reid BM, Humphrey JH, MbuyaM N, Pelto G, Stoltzfus RJ (2014) Water, sanitation, and hygiene (WASH), environmental enteropathy, nutrition, and early child development: making the links. Ann N Y Acad Sci 1308(1):118–128

Parfitt J, Barthel M, Macnaughton S (2010) Food waste within food supply chains: quantification and potential for change to 2050. Philos Trans R Soc Lond B Biol Sci 365(1554):3065–3081

Parsons DJ, Armstrong AC, Turnpenny JR, Matthews AM, Cooper K, Clark JA (2001) Integrated models of livestock systems for climate change studies Grazing systems. Glob Chang Biol 7:93–112

Patz JA, Kovats RS (2002) Hotspots in climate change and human health. BMJ 325(7372):1094–1098

Patz JA, Campbell-Lendrum D, Holloway T, Foley JA (2005) Impact of regional climate change on human health. Nature 438:310–317

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JP, Fernandez-Manjarrés JF et al (2010) Scenarios for global biodiversity in the 21st century. Science 330(6010):1496–1501

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

Pomeroy RS, Katon BM, Harkes I (2001) Conditions affecting the success of fisheries co-management: lessons from Asia. Mar Policy 25(3):197–208

Portner HO (2001) Climate change and temperature dependent biogeography: oxygen limitation of thermal tolerance in animals. Naturwissenschaften 88:137–146

Portner HO (2002) Climate change and temperature dependent biogeography: systemic to molecular hierarchies of thermal tolerance in animals. Comp Biochem Physiol A 132:739–761

Pörtner HO, Peck MA (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J Fish Biol 77(8):1745–1779

Rana RS, Handel KPS (1992) In: Khoshoo TN, Sharma M (eds) Sustainable management of resources—crops plant germplasm in sustainable management of natural resources. National Academy of Science, Malhotra Publishing House, New Delhi, pp 159–197

Rizwan M, Ali S, Hussain A, Ali Q, Shakoor MB, Zia-ur-Rehman M, Farid M, Asma M (2017a) Effect of zinc-lysine on growth, yield and cadmium uptake in wheat (Triticum aestivum L.) and health risk assessment. Chemosphere 187:35–42

Rizwan M, Ali S, Qayyum MF, Ok YS, Adrees M, Ibrahim M, Zia-ur-Rehman M, Farid M, Abbas F (2017b) Effect of metal and metal oxide nanoparticles on growth and physiology of globally important food crops: a critical review. J Hazard Mater 322:2–16

Rosegrant MW, Yohe G, Ewing M, Valmonte-Santos R (2010) Climate change and Asian agriculture. Asian J Agric Dev 7(1):41

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G et al (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453(7193):353

Rust JM, Rust T (2013) Climate change and livestock production: a review with emphasis on Africa. South Afr J Anim Sci 43(3):255–267

Schmidhuber J, Tubiello FN (2007) Global food security under climate change. Proc Natl Acad Sci 104(50):19703–19708

Schuh G, Heiden AC, Hoffmann T, Kahl J, Rockel Z, Rudolph J, Wildt J (1997) Emissions of volatile organic compounds from sunflower and beech: dependence on temperature and light intensity. J Atmos Chem 27(3):291–318

Sen A (1982) Poverty and famines: an essay on entitlement and deprivation. Oxford University Press, New Delhi

Sharkey TD, Yeh S (2001) Isoprene emission from plants. Annu Rev Plant Biol 52(1):407–436

Singh I, Squire L, Strauss J (1986) A survey of agricultural household models: recent findings and policy implications. World Bank Econ Rev 1(1):149–179

Sirohi S, Michaelowa A (2007) Sufferer and cause: Indian livestock and climate change. Clim Chang 85:285–298

Sivakumar MV, Stefanski R (2010) Climate change in South Asia. In: Climate change and food security in South Asia. Springer, Dordrecht, pp 13–30

Sorg A, Bolch T, Stoffel M, Solomina O, Beniston M (2012) Climate change impacts on glaciers and runoff in Tien Shan (Central Asia). Nat Clim Chang 2(10):725

Steinfeld H, Gerber P, Wassenaar T, Castel V, Rosales M, de Haan C (2006a) Livestock's long shadow: environmental issues and options. FAO, Rome

Steinfeld H, Wassenaar T, Jutzi S (2006b) Livestock production systems in developing countries: status, drivers, trends. Rev Sci Tech 25(2):505–516

Tabachnick WJ (2010) Challenges in predicting climate and environmental effects on vector-borne disease episystems in a changing world. J Exp Biol 213(6):946–954

Teixeira EI, Fischer G, van Velthuizen H, Walter C, Ewert F (2013) Global hot-spots of heat stress on agricultural crops due to climate change. Agric For Meteorol 170:206–215

Thornton PK, van de Steeg J, Notenbaert A, Herrero M (2009) The impacts of climate change on livestock and livestock systems in developing countries: a review of what we know and what we need to know. Agric Syst 101(3):113–127

Zeven AC, de Wet JMJ (1982) Dictionary of cultivated plants and their regions of diversity. Pudoc, Wageningen

Ziska LH, Epstein PR, Schlesinger WH (2008) Rising CO2, climate change, and public health: exploring the links to plant biology. Environ Health Perspect 117(2):155–158

Chapter 3
Stress Implications and Crop Productivity

Syed Uzma Jalil and Mohammad Israil Ansari

Contents

Abstract Stress conditions are severe problems and limit the crop productivity of modern cultivars. Abiotic stresses like low and high temperature, drought, water, salinity, heavy metals, and pesticides have a negative impact on agro-economic conditions and threaten food security worldwide. Plant yield affected by stresses is due to less availability of water or disorder in nutrient uptake. This may cause deficiency symptoms or ion toxicity leading to alteration in physiological and biochemical processes such as degeneration of chloroplast, disruption in photosynthesis, degradation of chlorophyll and macromolecules, disintegration of mitochondria and nuclei, and deterioration and leakiness of the membrane, which causes oxidative damage in the cells. Stresses also induced premature senescence in plants that also has a detrimental effect on crop yield. Plants have intricate responses for tolerance against abiotic stresses by regulating several metabolic processes. Therefore, it is required to study the strategies that are essential for the investigation of the mechanism involved in regulating stress tolerance in plants and lessening the implications

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of stresses on plants to increase crop production. This chapter emphasizes the effect of different stress conditions on plant productivity.

Keywords Stress · Productivity · Senescence · Oxidative damage · Deficiency

3.1 Introduction

Plants are affected by several stress environments, and abiotic stress is the main reason of restraining the crop productivity globally (Bray et al. 2000; Wang et al. 2003). The impact of abiotic factors on the plant is influenced by its extent or intensity. The plant entails a limited amount of abiotic factors for their optimal growth. Slight change from such optimum environmental situations that are insufficient in the environment is deliberated as abiotic stress and unfavorably influences plant productivity (Bray et al. 2000). They are chronic features of nearly all the world's climatic regions since several critical environmental risks and threats are mobilized by global climate change and population growth (Gleick 1995, 1998, 2000).

Anomalous environmental conditions generate abiotic stresses that are the primary restrictive factors for limiting crop production (Padgham 2009; Grayson 2013). Abiotic stresses comprise of heat, cold, drought, alkaline conditions and salinity, waterlogging, light intensity, and nutrient deficiency (Bailey-Serres and Voesenek 2008; Ansari and Silva da 2012). Drought has influenced 64%, salt stress 6%, hypoxia 13%, soil alkalinity 15%, mineral starvation 9%, and chilling 57% of land all over the globe (Mittler 2006; Riadh et al. 2010; Dresselhaus and Hückelhoven 2018).

Atmosphere fluctuation and limits are as of now contrarily undermining production of major crops in tropical districts and without adjustment; this is relied upon to exacerbate as temperatures increment and become more extreme. The number of outrageous atmosphere-related debacles, including high temperature, floods, and drought, has multiplied since the mid-1990s, with these events happening each year amid the time of 1990–2016 (FAO 2009). These harm agricultural productivity adding to shortages in nourishment accessibility. Inside-season changes may not enlist as extraordinary atmosphere occasions (drought, floods, or tempests) yet are parts of atmosphere fluctuation that influence the development of crops and the accessibility of field for domesticated animals, with possibly huge ramifications for sustenance security and nourishment (Hussain et al. 2018). Of every hazard—floods, drought, and hurricanes influence nourishment generation the most. Drought, specifically, causes in excess of 80% the harm and losses in agribusiness, particularly for the animals and crop production subsectors (FAO 2009).

Plants adapt with the rapid alteration and affliction of ecological conditions as a result of their natural metabolic mechanisms (Simontacchi et al. 2015). Deviations in the abiotic conditions can place the plant metabolism available for homeostasis (Foyer and Noctor 2005) and make the need for the plant to harbor few metabolic and genetic mechanisms in the cell (Apel and Hirt 2004). Plants retain a variety of defense mechanisms to combat abiotic stress conditions (Gill and Tuteja 2010; Yolcu et al. 2016; Jalil and Ansari 2018). These mechanisms involve in the metabolic reprogramming in cellular system to enable biophysicochemical processes of the external conditions (Mickelbart et al. 2015).

It is an undeniable fact that atmosphere climate variability and extremes environmental conditions influence agricultural productivity, as far as changes in yields (the amount of agricultural production harvested per unit of land area, trimming zones territory planted or gathered, or cropping intensity).

3.2 Effect of Environmental Stress on Plants

3.2.1 Lessening the Physiological Process of Plant

Plants required abiotic environment for their physiological and developmental mechanism. An unfavorable abiotic environment is an intricate set of stress conditions that limit plant productivity (Fig. 3.1). Plants detect and counter to stress conditions in various methods that support their nourishment (Jiang et al. 2016). Plants not only recognize the previous exposure to stresses but also the mechanisms involved in defense, and again when the same stress exposes, they can adapt consequently (Hilker et al. 2016). The highly noticeable consequence of unfavorable environments is initially seen at the cell levels that from that point onward, physiological side effects are noticeable. Water stress antagonistically influences physiological eminence of plants comprising the photosystem (Xu and Zhou 2006). Prolonged exposure of water stress affects morphological and physiological characters of plants (Osakabe et al. 2014; Xu et al. 2016). Hence, plants can sagaciously progress distinctive mechanisms to limit utilization of optimum aquatic assets and regulate their development before the exposure with environmental stress (Osakabe et al. 2013). Experience of adverse light intensities reduces the physiological process and unfavorably impacts on plant development. Abundance of light prompts photooxidation that enhances the fabrication of reactive oxygen species (ROS) to influence enzymes and other biomolecules (Li et al. 2009; Koini et al. 2009; Pareek et al. 2010).

3.2.2 Biochemical Changes Under Stress Conditions

Several abiotic factors influence plant growth and limit crop productivity; diverse intensities of acidic environments unfavorably affect soil nutrients that cause a nutrient deficiency in plant and disrupt normal physiological ability for plant development (Rorison 1986; Bromham et al. 2013; Emamverdian et al. 2015). Prolonged

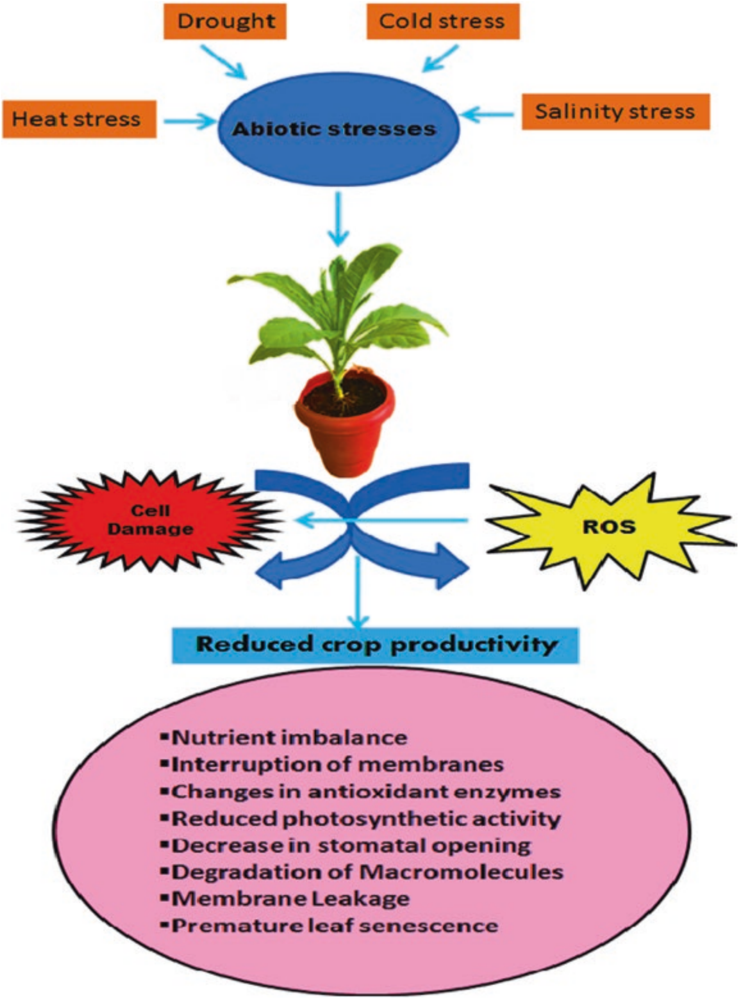

Fig. 3.1 Effect of abiotic stresses on crop productivity. Abiotic stress conditions cause the generation of reactive oxygen species, which act with the biological molecules that degraded during adverse environmental conditions that reduced the membrane fluidity and caused peroxidation, membrane leakage, and finally cell damage, which negatively affect the crop productivity

experience to salt stress causes toxicity in the cell along with interruption of osmotic balance. The consequence of ionic trailed with osmotic stresses results to altered plant growth (Munns and Tester 2008). Forbearance to salinity stress needed to regulate ionic and osmotic balance in the cells. For resistance toward salinity, plants protect delicate plant tissues from extreme salinity area or via emanating ions from roots or cytoplasm (Silva et al. 2010). During freezing conditions, some plants developed a mechanism to cope with cold temperatures by elevating their defense response by the process of cold acclimation (Thomashow 2010). After sensing the stress, plants show a quick and compelling reaction to initiate an intricate stress-specific signaling by synthesizing plant hormone (Tiwari et al. 2011). Generation of ROS is mainly caused by adverse environment conditions. The generation and eradication of free radicals are at balance in normal conditions, while under abiotic stresses, it disrupts this equilibrium by increasing the production of ROS that are lethal for the organism as they adversely impact on the biomolecules. The ROS production occurs in various compartments of plant cell. Singlet oxygen and hydrogen peroxide are generated in mitochondria because of the over-reduction of the electron transport chain. Chloroplasts are the foremost site for the generation of superoxide and hydrogen peroxide (Davletova et al. 2005), due to higher oxygen pressure and reduced molecular oxygen than in other organelles in the electron transport chain within PSI. They degraded the macromolecules such as proteins, fatty acids, carbohydrates, and nucleic acids that lead to cell death and finally reduced the crop productivity (Foyer and Noctor 2005) as shown in Fig. 3.1.

3.3 Implications of Stress on Plant Productivity

3.3.1 Drought Stress

The underlying impact of drought stress is the reduced seed germination and disabled seedling formation. Different investigations have detailed the adverse effects of drought stress on plants (Kaya et al. 2006; Zeid and Shedeed 2006; Farooq et al. 2009; Hussain et al. 2018). Plant development is fundamentally proficient by cell division, augmentation, and separation. Water-deficit condition impedes cell extension that restricts development and due to which decreased physiological parameters were accounted in vital crops such as pea, horse feed, and rice (Fahad et al. 2017). Drought stress confines the procedure of cell development principally because of reduced turgor pressure (Taiz and Zeiger 2006; Fahad et al. 2017) that affects in debilitated cell prolongation predominantly due to the deprived water stream through xylem to the adjacent cells (Fahad et al. 2017). The extension of the leaves ordinarily relies on absorption, decreased turgor pressure, and moderate photosynthesis rate during water-deficit situations which for the most part reduced the leaf extension. Fresh and dry weights are additionally seriously decreased during drought stress (Zhao et al. 2006). Phenotypic parameters were fundamentally diminished during drought stress in *Zea mays* (Khan et al. 2015). Additionally, the biomass aggregation in *Zea mays* was essentially diminished during drought stress imposed at different development phases (Kamara et al. 2003).

Yield is fundamentally the perplexing coordination of the distinctive physiological procedures. The greater parts of these physiological procedures are adversely influenced through the water-deficit conditions (Hussain et al. 2018). The negative effects of drought stress on the yield fundamentally rely on the seriousness of the pressure and the plant development. Noteworthy, decreased productivity has been accounted in foremost crops because of drought conditions that were prompted at the pre-anthesis stage and diminished the period of grain development in oats (Estrada-Campuzano et al. 2008). The exposure of plants to water-deficit condition disquiet at the blooming stage can affect the total sterility in pearl (Yadav et al. 2004).

Drought stress which incited decrease in the yield may be because of different factors, for example, diminished photosynthetic rate, irritated acclimatize parceling, or reduced leaf expansion (Fahad et al. 2017). The experience of *Zea mays* to water-deficit environments on the tasseling phase brought about huge yield damage (Anjum et al. 2011). Thus, a critical decrease in the boll's establishment and termination of delivered boll was observed during water-deficit condition that influenced the yield of cotton (Pettigrew 2004). A noteworthy decrease in the yields of barley was likewise seen in drought stress for the most part due to reduced quantity of ripe tillers and grains (Samarah 2005; Samarah et al. 2006). Moreover, the contact of pigeon pea to water-deficit conditions at the blooming phase leads to over half in the decrease in the grain yield (Nam et al. 2001).

3.3.2 High-Temperature Stress

Under the tropical atmospheres, extreme radiations and heat stress are other significant constraining factors to plant growth. Heat stress can influence blistering of the shoots, leaves alongside visual indications of leaves senescence, development restraint, and depigmentation of plant parts (Fahad et al. 2017). Extreme temperature may lessen seed germination and negatively affect crops (Fahad et al. 2016a, b). Heat stress diminished spikes and florets per plant in rice (Prasad et al. 2006), and seed development in sorghum (Fahad et al. 2016a, b) was likewise adversely influenced under comparative environments. During heat stress, flower infertility has been connected to lessened anther dehiscence, meager flaking of pollen, reduced pollen grains development, and diminished elongation of pollen tubes (Fahad et al. 2015, 2016a, b). A critical decrease in the development was seen in *Z. mays* and *Saccharum officinarum* during high temperature (Ashraf and Hafeez 2004; Wahid and Close 2007). There was a huge decrease in the biomass aggregation and precocious foliar senescence in sugarcane in high temperature (Ebrahim et al. 1998).

In temperate regions, the heat stress stuns amid the regenerative stage may result to generous decrease in the productivity of significant crops. The quality of the grains and oilseed crops is likewise adversely influenced by high temperatures; it decreases the biochemical properties generously (Fahad et al. 2017). It has been observed huge decrease in the biomass and quantity of wheat grain in heat stress (Ferris et al. 1998). High temperature diminished rice yield by lessening the execution of various rice development and qualities. The biomass of rice cultivar is almost steady in a tranquil situation (Mohammed and Tarpley 2010); conversely, during raised evening temperature, a decline in single-grain weight brought about critical decrease in rice productivity (Fahad et al. 2016a). High temperature affected significant decreases in the production of beans and shelled nut (Vara Parasad et al. 1999;

Rainey and Griffiths 2005). A noteworthy impact of the high-temperature stress is normally seen in tomato as it impacts meiosis, treatment, and development at last causing a perceptible decrease in productivity (Camejo et al. 2005).

3.3.3 Salinity Stress

Salinity has come to be a foremost problem restraining the developmental mechanism of several plants. It has been accounted that 7% of the total global land is adversely influenced by salinity stress (Munns 2002). Impacts of salinity stress harm on plants are associated with different morphological, physiological, and biochemical processes (Ashraf 1993). For instance, plant roots can adversely be influenced by increased amount of sodium and chlorine ions. The overaccumulation of sodium and chlorine ions in plants leads to ion toxicity and furthermore diminishes the retention of other ions prompting development restraint and metabolic disruption during salinity stress. Furthermore, salt stress earnestly decreases the capacity of plants taking up water bringing about drought condition (Al-Karaki 1997; Okcu et al. 2005; Bybordi et al. 2010a, b; Woodrow et al. 2016). Those negative impacts specifically or in a roundabout way cause generation of reactive oxygen species (ROS) that results to oxidative harm in plants during high-salinity condition (Liu et al. 2007). It is notable that salinity stress contrarily influences every single vegetative phase of plants, particularly for seed germination (Cuartero et al. 2006). Earlier studies have demonstrated that excessive salinity fundamentally decreased the germination rate and shoot and root length of various plants (Barbagallo et al. 2010).

Salt stress becomes a serious threat to worldwide, which results to gigantic decrease in the crop productivity. However, it assessed that salinity influenced roughly 6% of land area worldwide, which establishes over 800 million hectares of dry land (FAO 2009). Out of 230 million hectares of irrigated area influenced by various environmental stresses, 45 million hectares are influenced by salt stress globally (Ashraf 2010). As indicated by another gauge, an 831 × 106 hectare area has been affected by salinity, worldwide (Beltran and Manzur 2005). About half of the cultivable land will be inclined to harms by salinity stress by year 2050 (Manchanda and Garg 2008). Saboora et al. (2006) expressed that the salt stress is debasing approximately 10% of land area per annum globally. The issue of salt stress is more severe in water-deficit regions particularly the regions with low rainfall and high transpiration rate and hotness (Neto et al. 2006). The issue of salt stress condition is uplifting all over the globe because of utilization of low-quality water bringing about aggregation of some dissolvable salts in the plant roots. The issue is further expanding by deprived soil management rehearses (Pitman and Lauchli 2002).

3.3.4 Stress-Induced Senescence

Generally, crops are accessible to adverse environmental conditions and are certainly affected by different abiotic and biotic stresses during a growth period that causes reduction in production of economically significant crops (Bray et al. 2000). Leaf senescence can be induced by several external and endogenous factors, including stresses that involve protein degradation, damage and degradation of nucleic acids, disruption of cellular structure, and finally death of the cells, that enhance the synthesis of free radicals. Reactive oxygen species (ROS) are the natural by-product of cellular plant metabolism, which are produced due to leakage of electrons from the electron transport activities of subcellular sites of plants. It is clear that adverse environment conditions can induce a precocious leaf senescence that limits the assimilation, ultimately increasing the maturation process of the complete plant (Jalil et al. 2017) that negatively affected the crop productivity (Ansari et al. 2014). Leaf senescence has an imperative effect on agro-economy, influencing productivity of crops and shelf life of leafy vegetables and ornamental plants (Quirino et al. 2000; Gepstein 2004). There are huge differences in instant plant responses to stresses and the senescence process at gene regulation level; thus, the various stress conditions convey to increase the execution program similar to leaf senescence process (Guo and Gan 2014). Stress conditions activated many signaling pathways for promoting leaf senescence (Jalil et al. 2017), but the regulation of this pathway is not clear; however, they involved certain phytohormones such as ethylene, abscisic acid, salicylic acid, and jasmonic acid that also synthesized in stress conditions (Robert-Seilaniantz et al. 2011; Peleg et al. 2011). The regulation of these signaling pathways is essential for crop productivity.

It is generally seen that plants develop a protective mechanism due to abiotic stress, where the plants inhibit shoot growth and divert the essential cellular activities. Another characteristic to cope with stress conditions is to induce the process of leaf senescence, which is termed as stress-induced senescence. The senescence process has much similarity to abiotic stresses in relation to the plant responses such as defected plant morphology, biochemical and physiological properties, and gene expression pattern. Thus, environmental stress conditions and senescence process negatively impact global crop productivity. However, the predicted climate changes in future pose a serious threat to the agro-economic condition of the world. The result of abiotic stress-induced senescence is limitation of the yield of the crops. Accordingly, research and development are required for the same. Abiotic stress conditions such as heat, drought, water lodging, cold, and salinity are the main reason of reduction of optimal growth and yield of crops. Various mechanisms involved the plants to tolerate against different stress conditions. By understanding the intricate mechanisms in the development of stress-induced senescence, many strategies can be developed for the enhancement of crops that have the capability to resist against the stress-induced senescence (Gepstein and Glick 2013).

3.4 Defense Mechanism of Plants Against Environmental Stress

Plants smartly sense and defend against the changing environmental conditions. Their approaches and responses to adverse environmental conditions comprise collaborative metabolic cross-talk inside various biosynthetic pathways (Yin et al. 2019). Root pattern is delicate in intuiting stress signals and responding consequently in the root zones (Khan et al. 2016). It is an intricate mechanism that includes changes at hereditary, cell, metabolic, and physiological dimensions (Atkinson and Urwin 2012). The prime influence of abiotic stresses is generated water-deficit conditions inside cells pursued by the advancement of biochemical, atomic, and phenotypic activity against stresses (Ansari and Lin 2011; Xu and Zhou 2006; Almoguera et al. 1995). Tolerance to stresses is a vital phenomenon including different stages of plant development. Abiotic stress reactions may diminish or expand the powerlessness of plants toward biotic anxieties caused by bugs or pathogens (Rizhsky et al. 2004). This turns out to be progressively critical in record to agrarian harvests in light of the fact that, in different rural frameworks, most yields develop in ominous natural condition, which are limited to the hereditary capability of plants for development and advancement (Bray et al. 2000).

Plants involve intricate responses at cellular, molecular, physiological, and metabolic levels for tolerance against abiotic stresses by mediating osmotic regulation, antioxidant metabolism, and stress signaling and hormone metabolism. Researchers are interested to work on the complete profiling of metabolites, proteins, and genes by using proteomic, transcriptomic, metabolomics, and genomic approaches of different plant species involved in stress tolerance (Wang et al. 2019; Rastogi et al. 2019). However, due to lack of information on these approaches, it is important to work on the combined approach, which is essential for the determination of the key pathways and mechanisms involved in controlling abiotic stress tolerance.

In addition, in spite of the significant progress in the understanding of stress responses by plants, there is still no clarity about transmembrane ion transport, sensor, and receptor in the signaling transduction. Genetic engineering has been proved to be an efficient approach to the development of abiotic stress-tolerant plants, and this approach will become more influential as more applicant genes related with abiotic stress tolerance are identified and extensively utilized (Rastogi et al. 2019; Ansari and Lin 2010). In the recent years, nano-biotechnology is also receiving attraction for involving the encouraging position to alleviate the limitation related with abiotic stresses to achieve an improved agricultural production globally (Jalil and Ansari 2019). Application of nanoparticles shows improved antioxidant potential of plants to cope with adverse environmental conditions via scavenging the ROS and enhancing antioxidant activity of plants (Jalil et al. 2018).

3.5 Conclusions

Environmental stresses restrict the growth and production of crops and come to be a severe threat for the agronomists. Plants are exposed to different abiotic stress conditions and able to deal with several changes during temperature, humidity, light intensity, and other abiotic factors. When these abiotic influences exceeded from optimum limit, plants are exposed to stress; this can result in reduced reproduction, declined growth rate, and even programmed cell death. Changes in environmental stress can also conceivably influence biological diversity, alterations in ecological traits, and functioning of ecosystem. Abiotic stress also negatively affects the crop productivity, the extent of which changes in every year. The concurrent events of rapidly increasing temperatures, cold, and drought are the utmost prominent phenomena that intimidate plants, which have not adapted and are not capable to promptly acclimatize to these stress conditions. Plants involved various complex responses to cope with adverse environmental conditions via regulating antioxidant metabolism, stress signaling, hormone metabolism, and many other processes of plants. However, the information of these approaches for completely combating with abiotic stress is still lacking; thus, it is required to research on the combined approaches that are vital for the determination of the pathways and mechanism involved in regulating stress tolerance in plants, which helps to increase the productivity of field crops.

References

Al-Karaki G (1997) Barley response to salt stress at varied levels of phosphorus. J Plant Nutr 20:1635–1643

Almoguera C, Coca MA, Jordano J (1995) Differential accumulation of sunflower tetraubiquitin mRNAs during zygotic embryogenesis and developmental regulation of their heat-shock response. Plant Physiol 107:765–773

Anjum SA, Wang LC, Farooq M, Hussain M, Xue LL, Zou CM (2011) Brassinolide application improves the drought tolerance in maize through modulation of enzymatic antioxidants and leaf gas exchange. J Agron Crop Sci 197:177–185

Ansari MI, Lin TP (2010) Molecular analysis of dehydration in plants. Int Res J Plant Sci 1(2):21–25

Ansari MI, Lin TP (2011) *Arabidopsis thaliana* thylakoid lumen 18.3 protein gene is up-regulated during dehydration. J Physiol Pathophysiol 2(2):18–24

Ansari MI, Silva da JAT (2012) Molecular analysis of TLP18.3gene in response to the abiotic stress in *Arabidopsis thaliana*. Plant Stress 6:22–24

Ansari MI, Hasan S, Jalil SU (2014) Leaf senescence and GABA shunt. Bioinformation 10:730–732

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399

Ashraf M (1993) Effect of sodium chloride on water relations and some organic osmotica in arid zone plant species *Melilotus indica* (L.) All. Tropenlandwirt 94:95–102

Ashraf M (2010) Registration of 'S-24' spring wheat with improved salt tolerance. J Plant Registr 4:34–37

Ashraf M, Hafeez M (2004) Thermo tolerance of pearl millet and maize at early growth stages: growth and nutrient relations. Biol Plant 48:81–86

Atkinson NJ, Urwin PE (2012) The interaction of plant biotic and abiotic stresses: from genes to the field. J Exp Bot 63:3523–3543

Bailey-Serres J, Voesenek LA (2008) Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol 59:313–339

Barbagallo A, Nicola AD, Missikoff M (2010) The influence of salt stress on seed germination, growth and yield of canola cultivars. Notulae Bot Horti Agrobotanici Cluj-Napoca 38:128–133

Beltran JM, Manzur CL (2005) Overview of salinity problems in the world and FAO strategies to address the problem. In: Proceedings of the international salinity forum, Riverside, 25–27 Apr 2005, pp 311–313

Bray AB, Bailey-Serres J, Weretilnyk E (2000) Responses to abiotic stress. In: Buchanan BB, Gruissem W, Jones RL (eds) Biochemistry and molecular biology of plants. American Society of Plant Physiol, Rockville, pp 1158–1203

Bromham L, Saslis-Lagoudakis CH, Bennett TH, Flowers TJ (2013) Soil alkalinity and salt tolerance: adapting to multiple stresses. Biol Lett 9:20130642

Bybordi A, Tabatabaei SJ, Ahmedov A (2010a) Effect of salinity on the growth and peroxidase and IAA oxidase activities in canola. J Food Agric Environ 8:109–112

Bybordi A, Tabatabaei SJ, Ahmedov A (2010b) Effects of salinity on fatty acid composition of canola (*Brassica napus* L.). J Food Agric Environ 8:113–115

Camejo D, Rodriguez P, Morales MA, Dell'amico JM, Torrecillas A, Alarcon JJ (2005) High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. J Plant Physiol 162:281–289

Cuartero J, Bolarín MC, Asíns MJ, Moreno V (2006) Increasing salt tolerance in the tomato. J Exp Bot 57:1045–1058

Davletova S, Rizhsky L, Liang H, Shengqiang Z, Oliver DJ, Coutu J et al (2005) Cytosolic ascorbate peroxidase 1 is a central component of the reactive oxygen gene network of arabidopsis. Plant Cell 17:268–281

Dresselhaus T, Hückelhoven R (2018) Biotic and abiotic stress responses in crop plants. Agronomy 8:267

Ebrahim MK, Zingsheim O, El-Shourbagy MN, Moore PH, Komor E (1998) Growth and sugar storage in sugarcane grown at temperature below and above optimum. J Plant Physiol 153:593–602

Emamverdian A, Ding Y, Mokhberdoran F, Xie Y (2015) Heavy metal stress and some mechanisms of plant defense response. Sci World J 2015:75–81

Estrada-Campuzano G, Miralles DJ, Slafer GA (2008) Genotypic variability and response to water stress of pre- and post-anthesis phases in triticale. Eur J Agron 28:171–177

Fahad S, Hussain S, Saud S, Tanveer M, Bajwa AA, Hassan S et al (2015) A biochar application protects rice pollen from high-temperature stress. Plant Physiol Biochem 96:281–287

Fahad S, Hussain S, Saud S, Hassan S, Tanveer M, Ihsan MZ et al (2016a) A combined application of biochar and phosphorus alleviates heat-induced adversities on physiological, agronomical and quality attributes of rice. Plant Physiol Biochem 103:191–198

Fahad S, Hussain S, Saud S, Khan F, Hassan S, Amanullah et al (2016b) Exogenously applied plant growth regulators affect heat-stressed rice pollens. J Agron Crop Sci 202:139–150

Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, Sadia S, Nasim W, Adkins S, Saud S, Ihsan MZ, Alharby H, Wu C, Wang D, Huang J (2017) Crop production under drought and heat stress: plant responses and management options. Front Plant Sci 8

FAO (2009) FAO land and plant nutrition management service. http://www.fao.org/ag/agl/agll/spush

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA (2009) Plant drought stress: effects, mechanisms and management. Agron Sustain Dev 29(1):185–212

Ferris R, Ellis RH, Wheeler TR, Hadley P (1998) Effect of high temperature stress at anthesis on grain yield and biomass of field grown crops of wheat. Ann Bot 82:631–639

Foyer CH, Noctor G (2005) Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant Cell Environ 28:1056–1071

Gepstein S (2004) Leaf senescence—not just a ‘wear and tear’ phenomenon. Genome Biol 5:212

Gepstein S, Glick BR (2013) Strategies to ameliorate abiotic stress-induced plant senescence. Plant Mol Biol 82:623–633

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 48:909–930

Gleick PH (1995) Water, war, and peace in the Middle East. Environment 36:7–41

Gleick PH (1998) Water in crisis: paths to sustainable water use. Ecol Appl 8:571–579

Gleick PH (2000) The World’s water 2000-2001. The Biennial report on freshwater resources. Island Press, Washington, DC, p 245

Grayson M (2013) Agriculture and drought. Nature 501:S1

Guo Y, Gan SS (2014) Translational researches on leaf senescence for enhancing plant productivity and quality. J Exp Bot 65:3901–3913

Hilker M, Schwachtje J, Baier M, Balazadeh S, Bäurle I, Geiselhardt S et al (2016) Priming and memory of stress responses in organisms lacking a nervous system. Biol Rev Camb Philos Soc 91:1118–1133

Hussain HA, Hussain S, Khaliq A, Ashraf U, Anjum SA, Men S, Wang L (2018) Chilling and drought stresses in crop plants: implications, cross talk, and potential management opportunities. Front Plant Sci 9:393

Jalil SU, Ansari MI (2018) Plant microbiome and its functional mechanism in response to environmental stress. Int J Green Pharm 12(1):S81–S92

Jalil SU, Ansari MI (2019) Nanoparticles and abiotic stress tolerance in plants: synthesis, action and signalling mechanisms. In: Khan MIR, Sudhakar P, Ferrante RA, Khan N (eds) Plant signaling molecules—role and regulation under stressful environments, 1st edn. Elsevier, pp 549–561

Jalil SU, Ahmad I, Ansari MI (2017) Functional loss of GABA transaminase (GABA-T) expressed early leaf senescence under various stress conditions in *Arabidopsis thaliana*. Curr Plant Biol 9–10:11–22

Jalil SU, Zahera M, Khan MS, Ansari MI (2018) Biochemical synthesis of gold nanoparticles from leaf protein of *Nicotiana tabacum* L. cv. xanthi and their physiological, developmental and ROS scavenging responses on tobacco plant under stress conditions. IET Nanobiotechnol 13:23–29

Jiang QY, Zhuo F, Long SH, Zhao HD, Yang DJ, Ye ZH et al (2016) Can arbuscular mycorrhizal fungi reduce cd uptake and alleviate cd toxicity of *Lonicera japonica* grown in cd-added soils? Sci Rep 6:21805

Kamara AY, Menkir A, Badu-Apraku B, Ibikunle O (2003) The influence of drought stress on growth, yield and yield components of selected maize genotypes. J Agric Sci 141:43–50

Kaya MD, Okcub G, Ataka M, Cikilic Y, Kolsaricia O (2006) Seed treatments to overcome salt and drought stress during germination in sunflower (*Helianthus annuus* L.). Eur J Agron 24:291–295

Khan MB, Hussain M, Raza A, Farooq S, Jabran K (2015) Seed priming with $CaCl_2$ and ridge planting for improved drought resistance in maize. Turk J Agric For 39:193–203

Khan MA, Gemenet DC, Villordon A (2016) Root system architecture and abiotic stress tolerance: current knowledge in root and tuber crops. Front Plant Sci 7:1584

Koini MA, Alvey L, Allen T, Tilley CA, Harberd NP, Whitelam GC et al (2009) High temperature-mediated adaptations in plant architecture requires the bHLH transcription factor PIF4. Curr Biol 19:408–413

Li Z, Wakao S, Fischer BB, Niyogi KK (2009) Sensing and responding to excess light. Annu Rev Plant Biol 60:239–260

Liu K, Xu S, Xuan W, Ling T, Cao Z, Huang B, Sun Y, Fang L, Liu Z, Zhao N (2007) Carbon monoxide counteracts the inhibition of seed germination and alleviates oxidative damage caused by salt stress in *Oryza sativa*. Plant Sci 172:544–555

Manchanda G, Garg N (2008) Salinity and its effects on the functional biology of legumes. Acta Physiol Plant 30:595–618

Mickelbart MV, Hasegawa PM, Bailey-Serres J (2015) Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. Nat Rev Genet 16:237–251

Mittler R (2006) Abiotic stress, the field environment and stress combination. Trends Plant Sci 11:15–19

Mohammed AR, Tarpley L (2010) Effects of high night temperature and spikelet position on yield-related parameters of rice (*Oryza sativa* L.) plants. Eur J Agron 33:117–123

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25:239–250

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681

Nam NH, Chauhan YS, Johansen C (2001) Effect of timing of drought stress on growth and grain yield of extra-short-duration pigeon pea lines. J Agric Sci 136:179–189

Neto AAD, Prisco JT, Encas-Filho J, Abreu CEB, Filho EG (2006) Effect of salt stress on antioxidative enzymes and lipid peroxidation in leaves and roots of salt tolerant and salt-sensitive maize genotypes. Environ Exp Bot 56:87–94

Okcu G, Kaya MD, Atak M (2005) Effects of salt and drought stresses on germination and seedling growth of pea (*Pisum sativum* L.). Turk J Agric For 29:237–242

Osakabe Y, Arinaga N, Umezawa T, Katsura S, Nagamachi K, Tanaka H et al (2013) Osmotic stress responses and plant growth controlled by potassium transporters in *Arabidopsis*. Plant Cell 25:609–624

Osakabe Y, Osakabe K, Shinozaki K, Tran LS (2014) Response of plants to water stress. Front Plant Sci 5:86–91

Padgham J (2009) Agricultural development under a changing climate: opportunities and challenges for adaptation. Agriculture and Rural Development and Environmental Departments, The World Bank, Washington, DC, pp 30–45

Pareek A, Sopory SK, Bohnert HK, Govindjee (2010) Abiotic stress adaptation in plants: physiological, molecular and genomic foundation. Springer, Dordrecht, p 526

Peleg Z, Reguera M, Tumimbang E, Walia H, Blumwald E (2011) Cytokinin-mediated source/sink modifications improve drought tolerance and increase grain yield in rice under water-stress. Plant Biotechnol J 9:747–758

Pettigrew WT (2004) Physiological consequences of moisture deficit stress in cotton. Crop Sci 44:1265–1272

Pitman MG, Lauchli A (2002) Global impact of salinity and agricultural ecosystems. In: Lauchli A, Luttge U (eds) Salinity: environment plants molecules. Kluwer, Dordrecht, pp 3–20

Prasad PVV, Boote KJ, Allen LH (2006) Adverse high temperature on pollen viability, seed-set, seed yield and harvest index of grain-sorghum (*Sorghum bicolor* (L.) Moench) are more severe at elevated carbon dioxide due to higher tissue temperature. Agric For Meteorol 139:237–251

Quirino BF, Noh YS, Himelblau E, Amasino RM (2000) Molecular aspects of leaf senescence. Trends Plant Sci 5:278–282

Rainey K, Griffiths P (2005) Evaluation of *Phaseolus acutifolius* A. Gray plant introductions under high temperatures in a controlled environment. Genet Resour Crop Evol 52:117–120

Rastogi S, Shah S, Kumar R, Vashisth D, Akhtar MQ, Kumar A et al (2019) Ocimum metabolomics in response to abiotic stresses: cold, flood, drought and salinity. PLoS One 14(2):e0210903

Riadh K, Wided M, Hans-Werner K, Chedly A (2010) Responses of halophytes to environmental stresses with special emphasis to salinity. Adv Bot Res 53:117–145

Rizhsky L, Liang H, Shuman J, Shulaev V, Davletova S, Mittler R et al (2004) When defense pathways collide. The response of *Arabidopsis* to a combination of drought and heat stress. Plant Physiol 134:1683–1696

Robert-Seilaniantz A, Grant M, Jones JDG (2011) Hormone crosstalk in plant disease and defense: more than just Jasmonate–Salicylate antagonism. Annu Rev Phytopathol 49:317–343

Rorison IH (1986) The response of plants to acid soils. Experientia 42:357–362

Saboora A, Kiarostami K, Behroozbayati F, Hashemi SH (2006) Salinity (NaCl) tolerance of wheat genotypes at germination and early seedling growth. Pak J Biol Sci 9:2009–2021

Samarah NH (2005) Effects of drought stress on growth and yield of barley. Agron Sustain Dev 25(1):145–149. Available from https://www.researchgate.net/publication/41713983_Samarah_NH_Effects_of_drought_stress_on_growth_and_yield_of_barley_Agron_Sustain_Dev_25_145-149. Accessed 13 Feb 2020

Samarah NH, Mullen RE, Cianzio SR, Scott P (2006) Dehydrin-like proteins in soybean seeds in response to drought stress during seed filling. Crop Sci 46:2141–2150

Silva EN, Ribeiro RV, Ferreira-Silva SL, Viégas RA, Silveira JA (2010) Comparative effects of salinity and water stress on photosynthesis, water relations and growth of *Jatropha curcas* plants. J Arid Environ 74:1130–1137

Simontacchi M, Galatro A, Ramos-Artuso F, Santa-María GE (2015) Plant survival in a changing environment: the role of nitric oxide in plant responses to abiotic stress. Front Plant Sci 6:977

Taiz L, Zeiger E (2006) Plant physiology, 4th edn. Sinauer Associates Inc Publishers, Sunderland

Thomashow MF (2010) Molecular basis of plant cold acclimation: insights gained from studying the CBF cold response pathway. Plant Physiol 154:571–577

Tiwari S, Singh P, Tiwari R, Meena KK, Yandigeri M, Singh DP et al (2011) Salt-tolerant rhizobacteria-mediated induced tolerance in wheat (*Triticum aestivum*) and chemical diversity in rhizosphere enhance plant growth. Biol Fertil Soils 47:907–916

Vara Parasad PV, Craufurd PQ, Summerfield RJ (1999) Fruit number in relation to pollen production and viability in groundnut exposed to short episodes of heat stress. Ann Bot 84:381–386

Wahid A, Close TJ (2007) Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. Biol Plant 51:104–109

Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218:1–4

Wang C, Gao G, Cao S, Xie Q, Qi H (2019) Isolation, and functional validation of the CmLOX08 promoter associated with signalling molecule and abiotic stress responses in oriental melon, *Cucumis melo* var. makuwa Makino. BMC Plant Biol 19:75

Woodrow P, Ciarmiello LF, Annunziata MG, Pacifico S et al (2016) Durum wheat seedling responses to simultaneous high light and salinity involve a fine reconfiguration of amino acids and carbohydrate metabolism. Physiol Plant 159:290–312

Xu ZZ, Zhou GS (2006) Combined effects of water stress and high temperature on photosynthesis, nitrogen metabolism and lipid peroxidation of a perennial grass *Leymus chinensis*. Planta 224:1080–1090

Xu Z, Jiang Y, Jia B, Zhou G (2016) Elevated-CO_2 response of stomata and its dependence on environmental factors. Front Plant Sci 7:657

Yadav RS, Hash CT, Bidinger FR, Devos KM, Howarth CJ (2004) Genomic regions associated with grain yield and aspects of post flowering drought tolerance in pearl millet across environments and tester background. Euphytica 136:265–277

Yin H, Li M, Li D, Khan SA, Hepworth SR, Wang SM (2019) Transcriptome analysis reveals regulatory framework for salt and osmotic tolerance in a succulent xerophyte. BMC Plant Biol 2219:88. https://doi.org/10.1186/s12870-019-1686-1

Yolcu S, Ozdemir F, Güler A, Bor M (2016) Histone acetylation influences the transcriptional activation of POX in *Beta vulgaris* L. and *Beta maritima* L. under salt stress. Plant Physiol Biochem 100:37–46

Zeid IM, Shedeed ZA (2006) Response of alfalfa to putrescine treatment under drought stress. Biol Plant 50:635–640

Zhao T-J, Sun S, Yang L, Liu J-M, Liu Q, Yan Y-B, Zhou H-M (2006) Regulating the drought-responsive Element (DRE)-mediated signaling pathway by synergic functions of transactive and trans-inactive DRE binding factors in Brassica napus. J Biol Chem 281(16):10752–10759

Chapter 4
Impact of Climate Change on Postharvest Physiology of Edible Plant Products

Sajid Ali, Shaghef Ejaz, Muhammad Akbar Anjum, Aamir Nawaz, and Shakeel Ahmad

Contents

Abstract Climate change has shown a significant impact on preharvest physiology affecting subsequent postharvest quality and storage potential of various edible plant products. Our edible plant-based products such as grains, fruits, vegetables, and seeds are derived from different systems of agriculture. Climate change-induced alterations in precipitation, temperature, carbon dioxide, solar radiation, ozone, and UV radiations directly influence agricultural produces during preharvest production stage. It is important to understand the impact of climatic-based alterations on

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the postharvest storage and quality of the said edible products. It is a well-established fact that different environmental factors during preharvest stages substantially influence and modify postharvest physiology and related quality attributes of different edible plant products during storage. Due to altered climatic conditions during preharvest stage, the harvested products have different levels of secondary metabolites, nutraceutical compounds, mycotoxins, nutrients status, ethylene biosynthesis, respiration rate, and postharvest shelf- or storage-life potential. Moreover, climate change, by affecting the food quality, is indirectly affecting the markets and industries related to harvested produce. The changing global climate pattern also influences various plant pest and pathogen infestation especially along with the increase in mycotoxin contamination, ultimately making the plant-based edible produce unsuitable for human consumption. Due to climate-induced alterations, proper cold supply chain should be maintained to slow down different metabolic changes as well as to reduce food poisoning pathogens of the harvested edible produce. So, the basic understanding of climate change on the said aspects is very imperative for global food security. The current chapter covers a comprehensive overview regarding the impacts of climate change on physiology and quality of edible plant-based products during postharvest life.

Keywords Climate change · Edible products · Food quality · Physiological changes · Postharvest physiology · Sustainable production

Abbreviations

1-MCP	1-Methylcyclopropene
ADP	Adenosine triphosphate
AMP	Adenosine monophosphate
ATP	Adenosine triphosphate
CAT	Catalase
CCO	Cytochrome C oxidase
CHT	Chitinase
CO_2	Carbon dioxide
DI	Deficit irrigation
O_3	Ozone
PAL	Phenylalanine lyase
POD	Peroxidase
PPO	Polyphenol oxidase
RDI	Regulated deficit irrigation
SOD	Superoxide dismutase
UV	Ultraviolet

4.1 Introduction

Climate change is emerging as a key factor that has started to significantly affect everyday life of humans. The Intergovernmental Panel on Climate Change has reported that mean air temperature may rise between 1.4 and 5.8 °C at the end of the twentieth century (Moretti et al. 2010) and there are still certain unstudied climatic components that, if found to be positively correlating with temperature rise, may aggravate the situation. However, Kalnay and Cai (2003) predicted the increasing rate of 0.088 °C per decade for the twentieth century which is a relatively less severe situation. Whichever climate-predicting model is correct, it is more likely that the rise in temperature will induce more adverse environmental conditions like drought, flooding, and heat waves. These circumstances will not only directly create hurdles for daily human life but also will exponentially increase their effects by disturbing different biological systems, such as production of food, that are essential for the very existence of human beings. It is a well-established fact that adverse climate conditions are stressful for normal growth and production of agricultural plants especially edible plants, but there is a need to realize that these adverse conditions leave their mark that lasts even after the crop is harvested. For example, drought is of great concern in agriculture whereby it not only reduces the yield potential of a crop but also decreases the postharvest life of fruits by accelerating the ripening process of fruits (Henson 2008). Change in climate also affects phenology in many fruit species. Many phenological time series trends have shown their association with warming temperatures (Menzel et al. 2006; Rosenzweig et al. 2008).

4.2 Climate Change and Postharvest Quality of Edible Produces

The impact of climate change has substantially increased during the past few decades, and it is still increasing with the passage of time. The increased climate-induced changes will have certain negative effects on the edible plant products. Climate change-induced lack of irrigation water (drought), increased temperature, and decreased crop production are expected to cause reduction in the produce quality (De-Pinto et al. 2012). It will also lead to favored growth and subsequent infections of toxigenic fungus along with increased population of insect pests in the stored edible products (Schmidhuber and Tubiello 2007). An increased CO_2 level may negatively affect postharvest fresh produce and grain quality. Elevated CO_2 led to reduced concentration of glucose and raffinose in kidney bean seeds (Thomas et al. 2009). Increased temperature during production period caused substantial reduction in accumulation of starch in wheat grains (Barnabás et al. 2008). In the same way, elevated CO_2 led to decrease in Ca, N, S, and Mg in flour of different wheat cultivars (Högy and Fangmeier 2008). The changes in different fatty acids in response to elevated temperature also varies. Oleic acid percentage increases, whereas linoleic acid level shows reduction in the oil of soybean seeds (Thomas et al. 2003). Besides grains and seeds, elevated temperature as well as concentration of ozone and CO_2 also significantly affect postharvest quality of fruits and vegetables. High atmospheric ozone enhances ascorbic acid content and reduces the production of esters in strawberries. Moreover, elevated CO_2 accumulation has direct influence on incidence of common scab, tuber malformation, and changes in reducing sugar contents of potato during postharvest storage (Högy and Fangmeier 2009). Similarly, exposure of tomato fruits to ozone increased lutein, total carotenoids, and lycopene concentrations (Moretti et al. 2010). So besides various grains and seeds, climate change-induced alterations in atmospheric temperature, CO_2, and ozone may also alter the postharvest quality of different fresh fruits and vegetables.

4.3 Preharvest Climatic Factors Affecting Postharvest Quality of Edible Plant's Products

Environmental conditions during growth, such as extremely high or low temperature, wind, carbon dioxide, rain, and hail, not only determine yield but also the quality of that commodity during storage. The quality of an edible portion of a plant at harvest stage almost entirely defines its behavior during postharvest phase. In fruits, the fruit location within the canopy and its exposure to sunlight or shade can affect the development of various bioactive compounds and, thus, determines its postharvest quality during supply chain or storage. Even fruits harvested at the same time from the same tree have differences in their physiological responses owing to complex interrelationships between environmental drivers acting on a horticultural commodity. Higher temperatures have been shown to be directly related to flowering. In apple, for example, the flowering date reaches 4.6 days earlier if the mean air temperature increases 1 °C (Chmielewski et al. 2004).

4.3.1 Carbon Dioxide

Nitrogen, oxygen, argon, and carbon dioxide (CO_2) are the most abundant gases in the atmosphere with a concentration of 78.1%, 20.9%, 0.93%, and 0.031%, respectively (Lide 2009). The role of nitrogen and oxygen in global warming is entirely negligible as these gases are transparent to radiation. However, CO_2 has a significant role in increasing the average air temperature of Earth as CO_2 absorbs infrared radiation and thus traps heat. Therefore, increasing the CO_2 levels will translate into more global warming (Lloyd and Farquhar 2008). Besides involving in increasing temperature and thus indirectly affecting postharvest physiology of horticultural crops, CO_2 has shown direct effects on quality of horticultural food products. For example, 50% higher concentration of CO_2 in the atmosphere increased malformation in potato tubers which showed poor quality for processing as was reflected by browning and acryl amide formation during processing (Högy and Fangmeier 2009). Moreover, higher CO_2 concentration increased the common scab susceptibility, glucose, and fructose and reduced sugar concentrations. Similarly, the loss of nutritional components like protein, potassium, and calcium and visual quality was also observed. Bindi et al. (2001) also observed that increased CO_2 concentration in the atmosphere led to increase in dry weight, tartaric acid, and sugar contents during ripening stage of grapes.

4.3.2 Temperature

The growth of different plants bearing edible produce is significantly affected by different temperature regimes (Moretti et al. 2010). It has also been noted that maintained quality and extended storage potential of grains are linked with moisture contents and prevailing temperature. The temperature and moisture should be controlled to extend the storage potential of grains (Suleiman et al. 2013). Under current climate change scenario, temperature has significantly increased (Moses et al. 2015). Extended drought and increased temperature during preharvest certainly affect quality of grains during postharvest storage (Controy et al. 1994). Moreover, increased temperature also affects nutritional, physicochemical, and toxicological characteristics of grains during storage (Jang et al. 2009). Elevated temperature resulted in negative changes of insoluble amylose content during storage in wheat grains (Rehman and Shah 1999; Ndindeng et al. 2014). Heat stress after flowering significantly influenced the grain nutritional quality attributes such as proteins, carotenoids, and antioxidant activity of durum wheat flour after harvest (Leonardis et al. 2015). High-temperature-induced tip burn damage to lettuce would have risk of soft rot during storage. In the same way, cabbage and lettuce damaged due to sunscald and high-temperature stress are highly prone to postharvest decay during storage (Moretti et al. 2010). Heat stress-induced reduction in volume-to-surface ratio of tomatoes increased weight loss under postharvest storage (Gruda 2005; Toivonen and Hodges 2011). Similarly, high-temperature-induced heat stress significantly increased membrane permeability of the affected fruits and vegetables (Moretti et al. 2010). Climate change-induced increased temperature also decreases palatability of the grains during storage due to reduced proteins and increased concentration of free fatty acid contents (Moses et al. 2015). In addition, increased rainfall due to climate change at harvest stage increased the damp conditions for the grains which in combination with elevated temperature resulted in deterioration of grain spoilage during storage (Moses et al. 2015). Increased moisture causes increased multiplication of mold and insect eventually leading to enhanced risk of mycotoxin contaminations in processed products (Stathers et al. 2013). High temperature in the form of heat treatments may also enhance biochemical reaction rates catalyzed by different antioxidant enzymes. The higher induction of the enzymatic antioxidants in relation to certain treatments would reduce membrane permeability, oxidative stress, and lipid peroxidation eventually leading to conserved quality and extended storage life of the treated fresh produce (Ali et al. 2019).

The difference between temperature at which a crop is grown and at which it is stored may alter fruit quality and subsequently its postharvest life. For example, the few regions of Australia where pineapple is grown have large differences in day and night temperatures. Night temperature may fall ˂21 °C, and this causes internal browning of the fruit tissue during postharvest phase of fruit development (Smith and Glennie 1987). California-grown Valencia orange can be stored up to 8 weeks at a temperature range from 3 to 9 °C (Thompson 2003). However, if the same cultivar is cultivated in Florida, then it can be successfully stored for 12 weeks at 0 °C. Generally, oranges that are cultivated in tropical zone have more sugar content and soluble solids than those grown in subtropical regions. However, comparing the oranges of these two regions, tropical-cultivated oranges are less orange in color and are harder to peel. Both of these factors seem to be linked with low diurnal temperature variation that occurs in the tropics rather than to the actual temperature difference between the tropics and subtropics. Similarly, fruits of apple cultivar Cox's Orange Pippin grown in the United Kingdom are susceptible to chilling injury if these are stored below 3 °C, while the fruits of apple cultivated in New Zealand can be successfully stored at 0 °C (Thompson 2003).

Cool or warm growing conditions trigger different physiological disorders after harvest and also affect sugar and acid content of fruits. In Braeburn apples, the growing conditions were found to be triggering scald, browning disorder, and internal cavities during storage. Therefore, if apples were harvested after a cool growing season, it was suggested to store the fruits in air at 0 °C to mitigate the risks of these disorders. On the other hand, after a warm season, harvested apples are recommended to be stored in controlled atmospheres to better retain their texture and acidity (Lau 1998). In another study, apples and avocados when exposed to high temperature during growth showed different behavior during storage after harvest. In such circumstances, avocados showed chilling injury and had water core disorder if fruits have been subjected to higher temperatures while on the tree. Similarly, scald in apples is related to the times a fruit is exposed to low temperature in a growing season (Ferguson et al. 1999). Oosthuyse (1998) found that if during harvest mangoes are exposed to cool, humid, or wet conditions, it leads to the development of lenticel damage during postharvest stage. On the contrary, if harvest day is marked by dry and hot conditions, it discourages the development of lenticel damage. Watercore susceptibility in apples is a problematic physiological disorder. Yamada and Kobayashi (1999) studied how watercore development is affected by preharvest fruit temperatures (10, 15, or 25 °C) as reflected by ethylene production, fruit pulp firmness, and membrane integrity in two apple cultivars. Lower temperature induced significantly more watercore occurrence after 2–3 weeks of treatment, whereas temperature of 25 °C completely inhibited the watercore occurrence.

An extensive study on grapes' earlier maturity was conducted by Webb et al. (2011). They used data from 44 vineyards blocks; short-term data was 17 years in length and long term from 25 to 115 years long. A tendency of earlier maturity in grapes was evident in almost all vineyards. Over the recent period (1993–2009), the average advance was 1.7 days per year. The trend to earlier maturity was associated with warming temperature trends for all of the blocks assessed in the study. Besides early maturity, warmer temperature causes fluctuation in biochemical composition of fruits such as in grapes. Increasing the temperature has been found to be linked with the increase in sugar levels and decrease in titratable acidity in grape fruits (Coombe 1987). Higher temperature only increases malate concentration in grapes, whereas tartrate was not affected by the increase in temperature.

It has been reported that the stress factors and growing conditions of environment do not substantially affect product quality at harvest, but these negatively and significantly influence shelf- and storage-life of the edible fresh produce (Farneti et al. 2013; Bisbis et al. 2018). High temperature during development also substantially influences water relations, photosynthesis, and membrane stability along with certain hormones and primary as well as secondary metabolites. Higher concentration of certain polyamines in relation to high-temperature stress during preharvest growth stages significantly influences postharvest quality and storage potential of edible produce (Malik and Singh 2006). Temperature is also very critical in determining the harvest index. The higher range of prevailing temperature during preharvest stages will lead to early crop maturity. The maturity of a large number of varieties in the narrow harvest window may probably lead to glut produce and lower quality because the crops may mature early without developing characters of quality imperative for their postharvest performance (Moretti et al. 2010). It has been observed that cauliflower, celery, lettuce, and kiwi fruit matured earlier under high-temperature conditions compared to the crops grown during lower-temperature regimes (Hall et al. 1996; Wurr et al. 1996). High spring temperatures reduce the number of days and increase the rate of growth/day in peach fruits between full blossom and reference date (the date growers use to determine the fruit size for fruit thinning). Therefore, it can be hypothesized that excessive high spring temperatures pose a hurdle to fruit trees in supplying resources rapidly enough to support their maximum potential fruit growth rates. Cumulative preharvest hours below 10 °C induce adaptive changes in apple fruit. Increasing the chilling hours before harvesting increases apple fruit firmness, soluble solid content, starch index, and ethylene production (Diamantidis et al. 2002). These adaptive changes are considered to be increasing fruit tolerance to cold storage. Cool nighttime temperature in apple fruits causes more redder color and an early onset of ethylene production and development of abscission zone compared to fruits exposed to warm nighttime temperature (Blankenship 1987). However, firmness, soluble solid content and fruit maturity, diameter, and length remain unaffected by nighttime temperature.

Temperature variation at any stage from bud break to fruit maturation has lasting effects on fruit quality during ripening. Fujisawa and Kobayashi (2010) observed that, in apples grown in Japan, temperature has profound effect on the timings of bud break and their subsequent flowering during spring season. Similarly, in South Africa, winter and early spring temperature and rainfall determine the full bloom dates of apple (Grab and Craparo 2011). Besides, prebloom temperature variation and post-bloom temperatures noticeably affected the visual and nutritional fruit quality during ripening. In another similar series of experiments, apple plants were provided with controlled conditions of temperatures (experiment 1, 16, 20, and 24 °C; experiment 2, 16 and 22 °C) for 6 weeks immediately after bloom. This was followed by fixing the temperature in experiment 1 at 20 °C and adjusting the temperature to 22 °C from week 6 to 14 and 22 °C from week 14 to 22 in experiment 2. Temperature manipulation during post-bloom stage markedly modified the rate of fruit ripening and ethylene production, flesh firmness, starch content, skin color, and red blush, but these variations did not respond to the same degree. The temperature of 22 °C during post-bloom phase led to fruits that were significantly greener and firmer, high in starch content, and contain redder blush at 16 than at 24 °C given from week 14 to 22. Higher temperature either during post-bloom phase or at fruit maturation period both reduced acid content in fruit during ripening.

Researchers have investigated whether increasing temperature alters fruit quality traits such as taste, texture, and firmness. Fruit softening is one of the most consumer-sensitive attributes of fruit quality and is also the most delicate attribute that may get affected by water, temperature, humidity, nutrition, and soil characteristics. Several studies have proposed that if the numbers of heating days are increased, then the fruit softening may be affected mostly following the increasing path. So far very few studies are available that have focused on the effects of climate change on consumer-related attributes of foods such as taste, flavor, and texture of fresh fruits and vegetables. One such study utilized the data records up to 40 years and found that taste and texture of apple fruits are significantly changing with recent global warming (Sugiura et al. 2013). Acid levels, fruit firmness, and development of watercore decreased, and, in some cases, total soluble solid content increased at maturity, whereas maturity was measured by phenological, morphological, and chemical indices. These changes were attributed to higher temperatures and earlier blooming during the maturation period.

Environmental conditions may also affect the pathogen infestation directly. Many pathogens thrive in soil or survive on plant debris in the field, from where winds and rain may disperse them to potential hosts. *Botrytis cinerea* thrives well under high temperatures and causes infection in tomato flowers because warm weather causes an increase in development and senescence of flowers making them vulnerable (Eden et al. 1996).

4.3.3 Solar Radiation

Solar radiation is composed of various wavelengths. The most important wavelengths for plant growth and development are red, blue, and somewhat UV wavelengths. The extent to which a fruit is directly exposed to solar radiation while still in development stage alters the quality attributes especially bioactive compounds of an edible produce. In grapes, flavonols including glycosides of quercetin, kaempferol, and myricetin may increase up to tenfold concentration in sunlight-exposed cluster compared to shaded clusters. Ultraviolet barriers have been used to shade the clusters from direct sunlight that led to a significant decrease in levels of glycosides of quercetin, kaempferol, and myricetin and total flavonols. On the other hand, interestingly, temperature showed little to no effect on flavonol concentrations (Spayd et al. 2002). Moreover, low-light conditions led to reduced dry matter, declined protein concentration, and increased chalky percentage in rice kernels (Liu et al. 2014).

It has also been reported that long and intensive sunlight exposure and high temperature before commercial harvest had a significant impact on edible produce quality and bruise susceptibility (Hussein et al. 2018). Sun-exposed sides of avocado fruits had higher firmness and potential susceptibility to bruising (Woolf and Ferguson 2000). The exposure of apples to high-light intensity may lead to thick wax clumps leading to cushioning and subsequent reduced bruise susceptibility (Tahir et al. 2009). The reduced bruise susceptibility may help to transport the product to distant markets with limited damage of the produce during postharvest handling. High-light intensity causes increased transpirational losses from the fruits (Mowatt 1997). The higher loss of water through transpiration will eventually result in loss of turgor (wilted produce eventually will have limited marketability) and increased weight loss during postharvest storage. At the same time, it is also possible that reduced turgor of the commodity may have lower bruise susceptibility (Hussein et al. 2018). So, light intensity in combination with temperature can also greatly influence quality of the produce at harvest and during postharvest. Preharvest O_3 stress led to necrosis, leaf chlorosis, and altered sugars and starch composition in tubers, roots, fruit, and vegetables. However, it improved shelf-life potential of cucumbers and broccoli during postharvest (Moretti et al. 2010).

Modification of sunlight quality for agricultural crop production can also be achieved by using photoselective shade nets which absorb specific spectral bands. Red and yellow photoselective nets have been tested to produce high-quality horticultural commodities such as peppers. These nets yield higher quantities of good-quality products with more aroma volatiles. Red and yellow peppers grown by using black photoselective nets have higher levels of β-carotene, lower total phenolics, and deep red and orange color after storage (Selahle et al. 2015). Peppers grown under pearl net showed reduced weight loss and increased fruit firmness, ascorbic acid levels, and antioxidant activity. Moreover, after storage, organoleptic evaluation suggested that red pepper fruits from plants grown under pearl nets are better in consumer-related quality attributes. Sensory evaluation or organoleptic analysis is considered as part of an authentic approach of analyzing and estimating the differences in color, flavor, and texture of fruits at postharvest stage. These tests give a very good estimate from consumer point of view. Corollaro et al. (2015) constituted a panel of trained sensory panel to sort out the difference between Fuji apples produced under black, red, white, yellow, and blue photoselective nets. The greatest differences were observed between fruits from yellow and red photoselective nets. Apples grown under red photoselective nets were higher in yellow color perception, sweeter in taste, and relatively firmer, whereas lower in green color perception. The reason for this could be that the spectrum band of transmitted light affects cell proliferation and fruit ripening process and, therefore, modifies the sensory perception of color, taste, and texture (Corollaro et al. 2015).

The parts of a same plant respond differently if they are exposed to solar radiation or shade. The fruits facing sun and the fruits on the opposite side (in shade) have different quality at harvest stage and also during postharvest phase. If fruits of two of the most economically important fruit plants, citrus and mango are fully exposed to the sun, these had thinner peel, less weight, low juice content, low acidity, and high total soluble solid content (Sites and Reitz 1949, 1950a, b). Similarly, studies have shown that even a single fruit exhibits different postharvest quality characteristics on shaded side compared to sunlight-exposed side. Woolf et al. (2000) observed the same phenomenon whereby delayed ripening, as shown by late emergence of ethylene peak, by the avocadoes that had been exposed to the sun was noted compared with the nonexposed fruits. Moreover, sun-facing and shaded sides of the same fruit showed that sunlight exposure leads to higher firmness. The side of the fruit that had been exposed to the sun was generally firmer than the nonexposed side, and the average firmness was higher than that of shade fruits. Citrus fruits grown in shade are less prone to low-temperature injury during postharvest storage at chilling temperature (Ferguson et al. 1999; Thompson 2003).

Proline is an important osmolyte that accumulates in plant cells during stressful conditions and helps cells to survive against stress. Edible agricultural fruits also accumulate proline in response to stressful conditions. Rosales et al. (2007) observed accumulation of proline in exocarp of fruits of cherry tomato plant grown under higher temperature and solar radiation. These researchers noticed the increase in the activities of proline synthesis enzymes (1-pyrroline-5-carboxylate synthetase and ornithine-amino transferase) and in the activities of proline degrading enzyme proline dehydrogenase. Under stressful conditions, the synthesis and degradation of proline point toward a strategy that a plant adapts to mitigate stress by reducing reactive oxygen species and forming H^+ ions.

4.3.4 Water

Water is the most important limiting factor in agriculture crop production and precipitation, and its frequency is the uncontrolled form of water that is showing its effects in recently changing weather patterns. Rain is associated with unpredictable climatic drivers that affect plant growth and development in a specific region. These drivers include change in temperature, humidity, flood, and winds; non-climatic factors associated with rain are pest and pathogen whose outbreak has the ability to destroy the standing crops or leave a lasting impact on edible commodities. All these factors have been found to alter the maturation period of perennial horticultural crops. For example, Grab and Craparo (2011) discovered the relationship between rainfall and earliness in blooming time in apple and pear in South Africa.

Too much water, either through rain or irrigation, causes leafy vegetables like lettuce to become more brittle. Similarly, carrot roots split due to heavy irrigation after 90 days followed by drilling. However, if heavy irrigation is preceded by minimal irrigation for the first 120 days, it prevents splitting and improved skin color with a small decrease in yield (McGarry 1993). In carrots, preharvest drought stress decreases membrane integrity in roots that may increase dehydration during postharvest storage (Shibairo et al. 1998). Water stress was also applied to mangoes by Vega Pina et al. (2000) for 30 or 45 days before flowering, and then fruits were stored at 13 °C after harvest. The researchers found that fruits of the plants stressed for 45 days have higher peel redness, firmness, titratable acidity, and severity of internal pulp darkening. Scarcity of water to fruit plants during growth may positively or negatively influence the taste and aroma of fruits during postharvest storage. Precipitation also positively or negatively affects the edible produce. One of the rain-associated problems in banana is that if fully mature bananas are harvested just after rainfall, then it exponentially increases the chances of fruit splitting, microbial infestation, and rotting during postharvest handling (Thompson and Burden 1995).

Present predictions of the climate change indicate increased intensity and frequency of drought periods in the world. The drought stress in many edible products leads to reduced production and higher losses of crops during preharvest as well as during postharvest stage (García-Galiano et al. 2015; Romero-Trigueros et al. 2017). The inferences of drought on quality of crops are contradictory. According to Sehgal et al. (2018), drought negatively affects quality of different food crops. In contrast, Dwivedi et al. (1996) found that drought stress decreased behenic fatty acid concentration, while increasing the oleic and stearic acid contents in peanuts. Drought stress reduced total oil content and increased linolenic acid and oleic acid of maize seeds (Ali et al. 2012). Also, significant reduction in tocopherols, phenolics, and flavonoids was observed in maize seed oil (Ali et al. 2010, 2012). Water deficiency reduced flavor in basil (Bekhradi et al. 2015), whereas it increased it in pomegranate (Peña et al. 2013; Peña-Estévez et al. 2015) during storage. At the same time, it has also been observed that low water supply during preharvest period led to extended shelf life due to inhibited weight loss in tomato (Conesa et al. 2014a, b). In contrast, drought stress during preharvest production stage increased water loss, and carrots were highly susceptible to chilling-related injury (Table 4.1) (Toivonen and Hodges 2011). At the same time, it has also been reported that drought in the form of regulated deficit irrigation positively increases quality at harvest and during postharvest (Romero-Trigueros et al. 2017). Regulated deficit irrigation (RDI) improved the quality of grapefruits at harvest and under postharvest conditions (Romero-Trigueros et al. 2017). RDI at 75% evapotranspiration rate enhanced acidity, firmness, and soluble solids along with lower weight loss and oxidative damage in blueberries during storage (Lobos et al. 2016). RDI-20-60 (20 and 60% compared with control, respectively) resulted in significantly higher yield and anticipated quality of Japanese plums (Table 4.1) (Samperio et al. 2015). RDI reduced side skin cracking and splitting of ostiole ends that led to enhanced postharvest life of figs (Kong et al. 2013). The 70% evapotranspiration rate increased yield and enhanced quality, mineral nutrients, and antioxidant activities in date palm (Alikhani-Koupaei et al. 2018). DI before harvest substantially increased yield, sensory quality, nutrient composition, and consumer acceptance of nectarine fruits (Lopez et al. 2016). In the same way, 110% ETc in combination with 1.25 μL L^{-1} 1-MCP maintained overall quality during storage under postharvest conditions

Table 4.1 Effect of drought (deficit irrigation) on postharvest quality of edible plant products

Commodity	Inferences	References
Blueberries	Regulated deficit irrigation (50% ETa) showed increased fruit firmness, SSC, and lower total acidity, while moderate irrigation (75% Eta) produced similar-quality fruit as in control (100% ETs)	Lobos et al. (2016)
Date palm	Deficit irrigation (70% ETc at 100 mm evaporation interval) did not affect yield and quality of the produce but increased POD and PPO activities	Alikhani-Koupaei et al. (2018)
Figs	Regulated deficit irrigation at 55% ETc significantly reduced "skin side cracking" and "ostiole-end splitting" with increased marketability	Kong et al. (2013)
Grapefruit	Deficit irrigation enhanced ripening index with increased SSC	Romero-Trigueros et al. (2017)
Mandarins	Regulated deficit irrigation maintained fruit quality with enhanced soluble solids and juice proline contents, hardiness, and thicker peel with reduced chilling injury incidence	Conesa et al. (2014a, b)
Nectarine	Mild water stress potentially reduced fruit size and yield while improved overall quality	Lopez et al. (2016); Falagán et al. (2015)
Pear	Deficit irrigation improved fruit composition related to firmness; soluble solids and acidity increased at harvest irrespective of change in fruit maturity. Also reduced weight loss during storage	Lopez et al. (2011)
Plum	Improved yield in plants treated with regulated deficit irrigation (20–60%)	Samperio et al. (2015)
Pomegranate	Increased bioactive compounds, without affecting size and marketable yield with improved quality and health-promoting attributes of fruits	Galindo et al. (2017); Peña-Estévez et al. (2016)
Sugar apple	Increased antioxidants, ascorbic acid, and sugar contents	Kowitcharoen et al. (2018)
Tomato	Bioactive compounds significantly influenced by regulated deficit irrigation, while changes in antioxidants were cultivar-dependent	Bogale et al. (2016)

(Falagán et al. 2015). DI before fruit growth increases proline content, total soluble solids, and total acidity with reduced maturity index of "Fortune" mandarins during shelf and cold storage (Table 4.1). Moreover, the same treatment also resulted in reduced commercial losses and thicker skin owing to reduced chilling injury (Conesa et al. 2014a, b). Sustained deficit irrigation (SDI) at 30% showed higher firmness, peel redness, soluble solids, ascorbic acid, protocatechuic acid, and phloretin as well as phenolics of pomegranate throughout the postharvest life (Pena et al. 2013). Water stress during the late ripening stage produced early harvest and improved quality of pomegranate (Galindo et al. 2017). SDI at 78% less ET_O increased health-related compounds, sensory attributes, and physicochemical quality of pomegranate arils during postharvest shelf life (Peña-Estévez et al. 2016). Application of SDI and RDI improved harvest quality and biochemical attribute composition and postharvest performance of pomegranates (Laribi et al. 2013).

Partial root zone drying irrigation and RDI improved yield, antioxidants, bioactive compounds, and lycopene in tomato fruit (Bogale et al. 2016). Drought stress during preharvest stage led to improved sugar accumulation and antioxidant activity of sugar apple at harvest as well as during postharvest storage. Similarly, drought treatment showed higher ethylene production, respiration rate, and concentration of abscisic acid in sugar apple (Kowitcharoen et al. 2018). DI in combination with thinning resulted in early harvest, better biochemical composition, reduced weight loss, and better marketability after cold storage of pear fruits (Lopez et al. 2011).

4.4 Postharvest Climatic Factors Affecting Quality of Edible Plant's Products

Besides preharvest climatic factors, postharvest climate-related conditions also significantly influence quality of edible products. The use of various climatic-related factors such as ultraviolet radiations, carbon dioxide, and ozone has been found effective in managing overall quality of various produce under simulated conditions.

4.4.1 Ultraviolet Radiations

Ultraviolet (UV) radiations have been increased due to ozone (O_3) layer depletion under the present climate change scenario (Bais et al. 2015). UV radiation leads to numerous harmful effects on the crop plants. At the same time, UV irradiation treatment of harvested products has been found effective in extending storage/shelf life and maintaining quality of various fresh edible plant products under simulated conditions (La Cava and Sgroppo 2015; Manzocco et al. 2016; Lu et al. 2018; Aiamla-or et al. 2019). It has been reported that low-dose cyclic UV-C application retained quality and suppressed browning of calyx in strawberry fruit (Araque et al. 2018). UV-C irradiation and blue light treatment showed better surface color and higher level of different health-related antioxidant compounds (Avila-Sosa et al. 2017). Postharvest treatment of UV-C led to extended shelf life and improved micro- and macronutrients in amaranth and African nightshade (Gogo et al. 2017). Combined treatment with pulsed light and UV-C led to better color and higher lycopene, soluble solids, and phenolics in tomato (Table 4.2) (Pataro et al. 2015). Postharvest UV-C application enhanced flavonoids and phenolic acids due to upregulation of phenylpropanoid pathway-related genes in tomato (Liu et al. 2018). In the same way, combined application of ultrasonic and UV-C treatments substantially enhanced different bioactive compounds of tomato during storage (Esua et al. 2019). UV-C treatment also preserved higher phytonutrients and delayed color changes in persimmon and cucumber fruits (Imaizumi et al. 2018). The combination of preharvest spray of $CaCl_2$ and postharvest treatment with UV-B maintained

Table 4.2 Effect of ultraviolet (UV) radiations on postharvest quality of edible plant products

Commodity	Inferences	References
Amaranth	UV-C reduced weight loss, while lignin and cellulose/hemicellulose contents increased	Gogo et al. (2017)
African nightshade	UV-C reduced weight loss, whereas lignin and cellulose/hemicellulose contents increased	Gogo et al. (2017)
Broccoli	UV-B irradiation maintained the quality of broccoli florets and delayed reduction of hue angle value as well as chlorophyll content and also enhanced glucosinolates	Aiamla-or et al. (2019); Lu et al. (2018)
Cucumber	UV-C increased brightness and maintained quality	Imaizumi et al. (2018)
Garlic	UV-C reduced microbial count and maintained antioxidant activity and exhibited higher flavonoids and quercetin	Park and Kim (2015)
Grapefruit	UV-C resulted in vitamin C and antioxidant activity reduction and improved storage life by minimizing microbial growth	La Cava and Sgroppo (2015)
Hawthorn	Lower doses of UV-C with blue light induced increased bioactive compounds including total flavonoids, phenolics, ascorbic acid contents, and antioxidant activity	Avila-Sosa et al. (2017)
Lilly bulb	UV-C inhibited microbial growth and browning index and increased total phenolic contents, antioxidants, and PAL activity in minimally processed lily bulbs during storage	Huang et al. (2017)
Lotus root	Maintained quality of fresh lotus and exhibited low browning degree, PPO, and POD activities; however, soluble solid contents and hardness were not affected by UV-C application	Wang et al. (2019)
Mangosteen	UV-C have fungicidal potential and reduced fruit rot incidence, induced POD and PAL activities, and delayed weight loss, respiration rate, and color development of peel	Sripong et al. (2019)
Oyster mushroom	UV-C resulted in lower soluble solid contents, protein, and ion leakage and showed higher CAT and PAL enzyme activities	Wang et al. (2017)
Pineapple	Enhanced storage life by minimizing microbial growth and increased availability at consumer end	Manzocco et al. (2016)
Satsuma mandarin	Flavonoids and total phenolic contents increased due to exposure of UV-C irradiations in processed fruits	Shen et al. (2013)
Strawberry	UV-C reduced fruit softening and pectin solubilization, improved firmness, and decreased PG and PME activities	Araque et al. (2019)
Table grapes	UV-B and UV-C maintained total phenolics and antioxidant potential	Sheng et al. (2018)
Tomato	UV-C irradiation enhanced individual phenolic and flavonoid contents (caffeic acid, p-coumaric acid, trans-ferulic acid, chlorogenic acid, gallic acid, protocatechuic acid, rutin, and quercetin) during storage in the dark conditions	Liu et al. (2018)
Tomatoes	UV-C treatment increased bioactive compounds and antioxidant activities	Esua et al. (2019)

quality and preserved higher glucosinolate concentration in microgreens of broccoli during storage (Lu et al. 2018). Treatment of broccoli florets with UV-B radiation resulted in reduced degradation of chlorophyll concentration due to suppression of chlorophyll-degrading genes such as *BoNYC1* and *BoSGR* (Table 4.2) (Aiamla-or et al. 2019). UV-C-treated juice of grapefruit had less yeasts and molds and aerobic bacteria along with higher concentration of bioactive compounds and related quality attributes during refrigerated storage (La Cava and Sgroppo 2015). Similarly, UV-C application resulted in better surface color, inhibited microbial growth, and retained freshness of treated lotus root slices (Wang et al. 2019) and fresh-cut (Manzocco et al. 2016) and whole pineapple fruits (Sari et al. 2016). The surface color was better due to inhibition of browning because degradation of color occurs due to higher activities of some pro-oxidant enzymes (Ali et al. 2016a, b, 2018). Postharvest application of UV-B and UV-C preserved biochemical quality to some extent, whereas phenolic compounds significantly increased in UV-C-treated grapes during storage (Table 4.2). Similarly, expression of flavonoid, phenylpropanoid, and stilbenoid pathway-related genes was also higher in UV-C treatment, than UV-B or control (Sheng et al. 2018). Repeated low-dose UV-C treatment suppressed softening and cell wall disassembly along with lower pectin solubilization of strawberry fruit (Araque et al. 2019). Postharvest UV-C radiation treatment maintained surface color and suppressed browning in oyster (Wang et al. 2017) and button (Lei et al. 2018) mushrooms. Application of UV-C had no negative impact on biochemical quality, and it enhanced flavonoids and phenolics of Satsuma mandarins during storage (Shen et al. 2013). It has also been observed that combined treatment of UV-C radiation and O_3 efficiently maintained quality by preserving higher antioxidant capacity and phenolic contents along with higher antioxidant enzymes activities of rocket (*Eruca sativa*) leaves (Gutiérrez et al. 2018). UV-C radiation was also found effective in inhibiting fruit rot of harvested mangosteen (Table 4.2). Application of UV-C treatment inhibited rotting of *Lasiodiplodia theobromae*-inoculated fruits due to induction of higher activities of POD, PAL, CHT, and 1, 3-glucanase enzymes (Sripong et al. 2019). Similarly, UV-C irradiation reduced microbial population and preserved bioactive compounds of peeled garlic cloves (Park and Kim 2015). Likewise, UV-C application suppressed activities of PPO, PAL, and POD that in turn inhibited browning and enhanced total soluble sugars and starch content in minimally processed lily bulbs (Huang et al. 2017).

4.4.2 Ozone

Ozone (O_3) is a gas with antioxidant potential (Karaca 2010). Its concentration has been declining in the stratosphere leading to various detrimental effects on the crop plants. Besides its role as a barrier to different harmful radiations, its role has also been reported in managing various quality-related attributes of different edible plant products. The treatment of low bush blueberries with O_3 and chlorine lowered microbial load (molds, yeast, and mesophilic bacteria) and thus conserved quality

(Crowe et al. 2012). Treatment with O_3 led to higher firmness, lower disease incidence, and suppressed ethylene production in bell peppers, zucchini, and cucumbers (Table 4.3). Moreover, it also maintained higher biochemical quality and sugar contents (Glowacz et al. 2015; Glowacz and Rees 2016). Application of O_3 delayed the changes in antioxidant enzyme activity reduction and conserved bioactive compounds in pepper fruits (Sachadyn-Król et al. 2016). Postharvest treatment of different citrus varieties with O_3 showed lower color changes, oleocellosis incidence, weight loss, and higher biochemical characteristics along with suppressed in vivo and in vitro growth of various fungal pathogens of citrus (García-Martín et al. 2018). Treatment with O_3 reduced firmness and weight losses along with maintained surface color and soluble solids in carrots (Souza et al. 2018). In another study, O_3 application was effective in reducing microbial load and weight loss and preserved color due to higher retention of anthocyanins in black mulberry fruit (Tabakoglu and Karaca 2018). It has been observed that O_3 treatment is also suitable in extending minimally processed edible produce such as rocket leaves (Table 4.3). Combined treatment of O_3 and UV radiation efficiently maintained quality by preserving higher antioxidant capacity and phenolic metabolism along with higher antioxidant enzyme activities (Gutiérrez et al. 2018). Ozonation and drying were effective in reducing fungal pathogens in seeds of naturally contaminated wheat (Granella et al. 2018). Application of O_3 also has appropriate potential of preserving grain product quality (Table 4.3). The quality of wheat, rice, and maize products (cake, noodle, and bread) can effectively be preserved with O_3 treatments. It also has the ability to enhance grain product functionalities along with ensuring food safety (Zhu 2018). Although higher O_3 level is a type of environmental pollution and it has a certain level of toxicity, at the same time its use is suitable in preserving quality and reducing microbial population such as disease-causing pathogens and mycotoxin accumulation that could be a step toward food safety (Table 4.3). However, at the same time, increasing O_3 pollution under climate change scenario can drastically reduce the yield of crops because its effects generally depend on its concentration, water status, temperature, crop type, and cultivars (Schauberger et al. 2019).

4.4.3 Carbon Dioxide

With the advent of climate change, the concentration of carbon dioxide (CO_2) has significantly increased in the world. The elevated levels of CO_2 in combination with other abiotic stresses negatively impact different crop plants (Kumar et al. 2019; Lamichaney et al. 2019). The elevated CO_2 may either have positive effects on crops under simulated conditions. The increased level of climatic CO_2 reduces grain quality during storage. It has also been noted that elevated temperature in combination with climate change induced increased CO_2 and lowered total protein concentration and different micronutrients in the grains during postharvest storage (Chakraborty and Newton 2011). Elevated atmospheric CO_2 and heat stress also negatively affected grain quality in wheat (Nuttall et al. 2017).

Table 4.3 Effect of elevated CO_2 and ozone on postharvest quality of edible plant products

Chemical	Commodity	Inferences	References
CO_2	Button mushroom	Browning index reduced with maintained flavor and enhanced antioxidant enzymes activities under elevated CO_2 conditions	Lin et al. (2017)
	Oyster mushroom	Higher CO_2 (30%) increased shelf life with enhanced antioxidant enzymes activities with better sensory quality	Li et al. (2013); Zhang et al. (2015)
	Persimmon	Soluble tannin contents reduced in CO_2-treated fruits and postharvest storage life was enhanced with increased antioxidant enzymes activities	Min et al. (2018)
	Strawberry	Storage life of fresh fruits prolonged for 12 days. It also delayed loss of chlorophyll and anthocyanin contents	Li et al. (2018); Li et al. (2019); Shin et al. (2008)
Ozone	Bell pepper	Glucose, fructose, and total phenolic contents increased in bell pepper exposed to lower ozone application, while weight loss was reduced with maintained texture in cucumber and zucchini during storage	Glowacz et al. (2015)
	Blueberries	Microbial log count such as mesophilic bacteria, yeast, and mold was reduced in ozone-treated fruits	Crowe et al. (2012)
	Carrot	Ozone treatment (in aqueous form) increased soluble solid content and shelf life	Souza et al. (2018)
	Chili peppers	Reduced disease incidence, weight loss, and maintained fruit firmness which ultimately extended its storage life	Glowacz and Rees (2016)
	Citrus	Continuous or intermittent treatment decreased decay and disease incidence and also delayed the color loss	García-Martín et al. (2018)
	Cucumber	Glucose, fructose, and total phenolic contents increased in bell pepper exposed to lower ozone application, while weight loss was reduced with maintained texture in cucumber and zucchini during storage	Glowacz et al. (2015)
	Hot pepper	Flavonoid contents (quercetin 3-*O*-rhamnoside and quercetin 3-*O*-rhamnoside-7-*O*-glucoside) increased in exposed pericarp of fruits	Sachadyn-Król et al. (2016)
	Mulberry	Reduced microbial count especially *Enterobacteriaceae* and weight loss	Tabakoglu and Karaca (2018)
	Rocket	Extended shelf life of minimally processed rocket and acted as a sanitizing agent against microbial growth but did not trigger its bioactive compounds	Gutiérrez et al. (2018)
	Wheat	Reduced filamentous fungi and inhibited mycotoxins in wheat kernel	Granella et al. (2018); Zhu (2018)
	Zucchini	Glucose, fructose, and total phenolic contents increased in bell pepper exposed to lower ozone application, while weight loss was reduced with maintained texture in cucumber and zucchini during storage	Glowacz et al. (2015)

It has also been reported in various studies that simulated increased or pure CO_2 treatments showed positive effects on the postharvest quality of various edible produce during storage (Table 4.3). High CO_2 treatment showed higher sensory quality, lower lipid peroxidation, and oxidative damage along with higher activities of CCO, CAT, POD, and SOD enzymes that ultimately conserved color and quality of *Pleurotus eryngii* mushroom during postharvest storage (Li et al. 2013). In the same way, application of 30% CO_2 maintained visual color and prolonged *P. eryngii* shelf life (Zhang et al. 2015). Combined application of 1-MCP and 90% CO_2 concentration delayed browning, decreased soluble tannins, suppressed ethylene production, and conserved higher activities of different antioxidant enzymes with prolonged storage life of persimmon (Min et al. 2018). Besides increased CO_2 concentration in store houses, its higher concentration has also been used in modified air packaging to maintain quality of packaged produce. The higher in-package CO_2 concentration conserved postharvest quality and flavor, reduced browning and oxidative stress, and increased antioxidant enzyme activities in button mushrooms (*Agaricus bisporus*) leading to its extended storage potential (Lin et al. 2017). Red color is an important visual quality indicator in fruits (Shah et al. 2017; Ali et al. 2018). The elevated level of CO_2 has been found effective in suppressing loss of red color during postharvest in strawberry (Table 4.3). Higher concentration (20%) of CO_2 resulted in conserved firmness, color, flavonoids, phenolics, antioxidant activities, and antiproliferative potential of strawberry fruit (Shin et al. 2008). It was noted that 20% elevated CO_2 concentration led to higher energy charge (ADP, ATP, and AMP) and mediated γ-aminobutyric acid shunt pathway due to higher activities of energy metabolism-related enzymes eventually leading to prolonged storage life of strawberry (Li et al. 2018). Exogenous treatment with 20% CO_2 delayed chlorophyll degradation due to suppression of chlorophyllase enzyme (Table 4.3). In addition, the development of red color was delayed due to downregulation of *FaPAO*, *FaRCCR*, and *FaChl b reductase* expression with extended storage life of strawberry (Li et al. 2019).

4.5 Climate Change and Food Safety

Food safety of edible plant products is very important with respect to consumer or end user. Increased contamination of various food-borne pathogens will eventually lead to certain serious ailments in the consumers if not handled appropriately. Different factors influence the concentration of pathogens during preharvest and postharvest stages. Among different pathogens mycotoxins are most detrimental and critical; those need to be addressed efficiently in order to reduce their concentration in the edible plant products during postharvest storage.

4.5.1 Effect of Climate Change on Aflatoxins

Different changes in climate have direct or indirect impact on contamination of various edible products (Medina et al. 2017). Climate change significantly influences the concentration of different mycotoxins in edible plant products (Magan et al. 2011). Prolonged water stress and elevated temperature lead to higher fungal infections in stressed maize plants. *Fumonisins* and *Fusarium verticillioides* contamination led to substantial increase in load of *Aspergillus flavus* and aflatoxin levels in grains of maize at harvest and during storage (Giorni et al. 2007). The concentration of deoxynivalenol was found to be correlated with the eoccurrence of *Fusarium graminearum* in maize. Due to prolonged drought conditions, *Aspergillus flavus* incidence also increased under dry environment that eventually increased the concentration of aflatoxins (Sanchis and Magan 2004). The incidence of *F. verticillioides* and *A. flavus* during growth period increased under longer dry periods that ultimately resulted in higher sterigmatocystin and aflatoxins in maize grains (Giorni et al. 2007). Extended periods of drought led to pod cracking in peanuts during production stage that eventually resulted in higher *A. flavus* and aflatoxins concentration. In the same way, lack of rain and irrigation water during fruit developmental stages and subsequent maturation period resulted in splitting of hulls in pistachio. The heavy rains in the later stages negatively affected quality and promoted buildup of mycotoxins during its postharvest stages (Cotty and Jaime-Garcia 2007). The contamination of aflatoxin B1 has been increasing in maize grown in Europe due to climate change (Battilani et al. 2016). Climate-based changes in temperature (high) and water (drought) also had a significant impact on ochratoxin A in fresh grapes (Chiotta et al. 2014; Gil-Serna et al. 2014). It has been explained on the basis of climatic modeling that increased temperature would substantially reduce the mycotoxin production and growth of *Alternaria* as higher temperature results in minimal production and growth in tomato (Fels-Klerx et al. 2016).

Stored foods with high water contents especially fruits and vegetables are generally considered alive as these actively respire during postharvest stage (Ali et al. 2019). Poor storage management during postharvest may lead to substantial loss of dry matter and mycotoxin accumulation (Magan et al. 2011). So, the potential effects of the climate change should be carefully considered to prevent accumulation of toxic compounds. Under elevated humidity and temperature, increased mycotoxigenic mold infestation may occur during storage (Magan et al. 2011). Mycotoxin levels have been found to increase under current climatic changes in various edible products (Moretti et al. 2019). Increase in CO_2, drought stress, and global temperature during preharvest stage significantly increased *A. flavus* and AFB_1 production in stored maize grains (Medina et al. 2014, 2015). Increased temperature during production also significantly increased mycotoxins such as ochratoxin A contamination in grapes-based products during postharvest storage and consumption among the consumers (Paterson et al. 2018).

4.5.2 Effect of Climate Change on Insect Pest Infestations

It has been reported that extended droughts and increased temperature are predicted to have significant influence on population dynamics, geographical distribution, and status of insect pests of various stored products (Roy et al. 2009). Moreover, hot climate is expected to enhance mobility, overwintering, and increased diversity with enhanced infestation of insect pests on different stored products eventually leading to increased postharvest losses of grains in the world (DeLucia et al. 2012; Moses et al. 2015). Present models of the climatic predictions show that diseases and pests are traveling at the rate of 3–5 km year^{-1} toward the poles (Medina et al. 2015). Furthermore, increased temperature has direct association with the metabolic activities such as physiological, biochemical, reproductive, and behavioral responses that will subsequently increase infestation level and postharvest losses of grains (Thomas and Blanford 2003). Climate changes in subtropical and tropical regions may lead to increased invasion and migration of pests and change in host plant and insect interactions with decreased efficiency of protection-related strategies (Sharma 2010). This will eventually cause increased postharvest losses in the stored grain (Sharma 2010). Postharvest losses of grains and cereals are about 40%, and these can feed 20 million people (Suleiman et al. 2013). The major causes of the said losses are insect pest and diseases (especially molds) during production and postharvest stages (Suleiman et al. 2013). Due to increased climate changes, higher insect pest infestations are projected in the forthcoming years, and the cost of managing the postharvest losses of grains and related products will also increase subsequently leading to food insecurity in the world (Stathers et al. 2013). In the same way, climate changes will lead to prolong drought and heat stress with increased outbreak of diseases and insect pests eventually leading to increased cost of supply chain with escalated losses during transportation, postharvest storage, and subsequent distribution of the products (De-Pinto et al. 2012). Stored insects pests and temperature are two major affecting biotic and abiotic factors in the deterioration of stored grains (Moses et al. 2015). Temperature also affects various physicochemical damages of grains and growth of insect pests (Astuti et al. 2013). Several studies described that there was a positive association between insect pest outbreak in the stored grains and increased climatic temperature (Qiu 2014; Moses et al. 2015). In general, grains are stored to ensure their continuous supply during the whole year. Any preharvest infestation of insect pests and disease will lead to increased contamination and losses of grains during postharvest. The level of insect pest and disease infestation directly depends on the climatic temperature (Mannaa and Kim 2017).

4.6 Climate Change Effect on Cold Chain of Edible Produce

Cold chain is very important to ensure continuous and safe supply of edible produce with conserved quality. The lack of cold chain may lead to detrimental effects on the quality. At the same time, it has been reported that some seasonal changes associated with climate change impact food poisoning (James and James 2010). Hot summer months may lead to increased probability of food poisoning. So, it is expected that global warming-induced increased global temperature will bring higher food poisoning chances (Schmidhuber and Tubiello 2007; James and James 2010). Multiplication of microorganisms in foods is favored by high temperatures. For instance, the growth of salmonellas highly depends upon the temperature as its growth starts at 7 °C and reaches to optimal at about 37 °C (Bentham 2002). In the same way, warmer summer temperature in combination with humid environment can significantly increase microbial survival in the environment subsequently leading to increased chances of food contamination and risk of pathogenic infections (Charron et al. 2005). The climate-induced increased temperature may reduce the efficiency of cold chain-related structures. The temperature in most of the domestic refrigerator systems in the world is 5–6 °C. It has also been reported that many of the refrigerator systems operate at significantly higher temperature range (James et al. 2008). So, temperature ranges need to be reduced to ensure conserved quality and enhanced shelf life (James and James 2010). Keeping food at lower temperature range will lead to increased use of energy leading to increased ambient temperature due to higher energy use.

4.7 Conclusion

Climate change affects production of various plant-based fresh products by changing agroecological environments and influencing growth of crops during preharvest stages. Climate change has also shown a significant impact on preharvest physiology that ultimately affects postharvest quality and storage potential of various edible produce. Climate change-induced alterations in precipitation, temperature, CO_2, solar radiation, O_3, and UV radiations directly influence agricultural crop production during preharvest production stage. It affects growth and population of various insect pests and toxigenic fungi eventually leading to negative effects such as aflatoxins in stored products. Climate change negatively affects stored grain quality by reducing protein concentration and micronutrients along with increased free acid formation and cooking time. However, simulated studies, which have been conducted by using increased concentration of UV radiations, CO_2, temperature, drought, and O_3, have shown improved secondary metabolites and reduced pathogen population in different fruits and vegetables during controlled conditions. So, effects of climate change are different under actual field conditions and controlled environments. Thus further detailed and comprehensive research work is still required to know about the influences of climate change on quality of freshly harvested plant-based edible products.

References

Aiamla-or S, Shigyo M, Yamauchi N (2019) UV-B treatment controls chlorophyll degradation and related gene expression in broccoli (*Brassica oleracea* L. Italica Group) florets during storage. Sci Hortic 243:524–527

Ali Q, Ashraf M, Anwar F (2010) Seed composition and seed oil antioxidant activity of maize under water stress. J Am Oil Chem Soc 87:1179–1187

Ali Q, Ashraf M, Anwar F, Al-Qurainy F (2012) Trehalose-induced changes in seed oil composition and antioxidant potential of maize grown under drought stress. J Am Oil Chem Soc 89:1485–1493

Ali S, Khan AS, Malik AU (2016a) Postharvest L-cysteine application delayed pericarp browning, suppressed lipid peroxidation and maintained antioxidative activities of litchi fruit. Postharvest Biol Technol 121:135–142

Ali S, Khan AS, Malik AU, Shahid M (2016b) Effect of controlled atmosphere storage on pericarp browning, bioactive compounds and antioxidant enzymes of litchi fruits. Food Chem 206:18–29

Ali S, Khan AS, Malik AU, Shaheen T, Shahid M (2018) Pre-storage methionine treatment inhibits postharvest enzymatic browning of cold stored ‘Gola’ litchi fruit. Postharvest Biol Technol 140:100–106

Ali S, Nawaz A, Ejaz S, Haider STA, Alam MW, Javed HU (2019) Effects of hydrogen sulfide on postharvest physiology of fruits and vegetables: an overview. Sci Hortic 243:290–299

Alikhani-Koupaei M, Fatahi R, Zamani Z, Salimi S (2018) Effects of deficit irrigation on some physiological traits, production and fruit quality of ‘Mazafati’ date palm and the fruit wilting and dropping disorder. Agric Water Manag 209:219–227

Araque LCO, Rodoni LM, Darré M, Ortiz CM, Civello PM, Vicente AR (2018) Cyclic low dose UV-C treatments retain strawberry fruit quality more effectively than conventional pre-storage single high fluence applications. LWT 92:304–311

Araque LCO, Ortiz CM, Darré M, Rodoni LM, Civello PM, Vicente AR (2019) Role of UV-C irradiation scheme on cell wall disassembly and surface mechanical properties in strawberry fruit. Postharvest Biol Technol 150:122–128

Astuti LP, Mudjiono G, Rasminah S, Rahardjo BT (2013) Influence of temperature and humidity on the population growth of *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) on Milled Rice. J Entomol 10:86–94

Avila-Sosa R, Avila-Crisostomo E, Reyes-Arcos EA, Cid-Pérez TS, Navarro-Cruz AR, Ochoa-Velasco CE (2017) Effect of blue and UV-C irradiation on antioxidant compounds during storage of Hawthorn (*Crataegus mexicana*). Sci Hortic 217:102–106

Bais AF, McKenzie RL, Bernhard G, Aucamp PJ, Ilyas M, Madronich S, Tourpali K (2015) Ozone depletion and climate change: Impacts on UV radiation. Photochem Photobiol Sci 14(1):19–52

Barnabás B, Jäger K, Fehér A (2008) The effect of drought and heat stress on reproductive processes in cereals. Plant Cell Environ 31(1):11–38

Battilani P, Toscano P, Van der Fels-Klerx HJ, Moretti A, Leggieri MC, Brera C, Robinson T (2016) Aflatoxin B1 contamination in maize in Europe increases due to climate change. Sci Rep 6:24328

Bekhradi F, Luna MC, Delshad M, Jordan MJ, Sotomayor JA, Martínez-Conesa C, Gil MI (2015) Effect of deficit irrigation on the postharvest quality of different genotypes of basil including purple and green Iranian cultivars and a Genovese variety. Postharvest Biol Technol 100:127–135

Bentham G (2002) Food poisoning and climate change. Health effects of climate change in the UK—2001/2002. Department of Health, London, pp 81–84. Section 4.2

Bindi M, Fibbi L, Miglietta F (2001) Free air CO_2 Enrichment (FACE) of grapevine (*Vitis vinifera* L.): II. Growth and quality of grape and wine in response to elevated CO_2 concentrations. Eur J Agron 14:145–155

Bisbis MB, Gruda N, Blanke M (2018) Potential impacts of climate change on vegetable production and product quality—a review. J Clean Prod 170:1602–1620

Blankenship SM (1987) Night-temperature effects on rate of apple fruit maturation and fruit quality. Sci Hortic 33(3–4):205–212

Bogale A, Nagle M, Latif S, Aguila M, Müller J (2016) Regulated deficit irrigation and partial root-zone drying irrigation impact bioactive compounds and antioxidant activity in two select tomato cultivars. Sci Hortic 213:115–124

Chakraborty S, Newton AC (2011) Climate change, plant diseases and food security: an overview. Plant Pathol 60(1):2–14

Charron D, Waltner-Toews D, Maarouf AR (2005) Zoonoses: climate change affects the modes by which diseases are passed from animals to humans. Altern J 31(3):24

Chiotta ML, Sosa DM, Ponsone ML, Chulze SN (2014) Effect of water activity and temperature on growth of Aspergillus carbonarius and Aspergillus tubingensis and their interactions on ochratoxin A production. World Mycotoxin J 8:99e105

Chmielewski F-M, Muller A, Runs EB (2004) Climate changes and trends in phenology of fruit trees and field crops in Germany, 1961-2000. Agric For Meteorol 121(1–2):69–78

Conesa MA, Galmes J, Ochogavía JM, March J, Jaume J, Martorell A, Francis DM, Medrano H, Jocelyne KCR, Cifre J (2014a) The postharvest tomato fruit quality of long shelf-life Mediterranean landraces is substantially influenced by irrigation regimes. Postharvest Biol Technol 93:114–121

Conesa MR, García-Salinas MD, José M, Fernández-Trujillo JP, Domingo R, Pérez-Pastor A (2014b) Effects of deficit irrigation applied during fruit growth period of late mandarin trees on harvest quality, cold storage and subsequent shelf-life. Sci Hortic 165:344–351

Controy JP, Seneweera S, Basrra AS, Rogers G, Nissen-Wooller B (1994) Influence of rising atmospheric CO_2 concentrations and temperature on growth, yield and grain quality of cereal crops. Aust J Plant Physiol 21:741–758

Coombe BG (1987) Influence of temperature on composition and quality of grapes. Acta Hortic 206:23–35

Corollaro ML, Manfrini L, Endrizzi I, Aprea E, Demattè ML, Charles M, Bergamas-chi M, Biasioli F, Zibordi M, Corelli Grappadelli L, Gasperi F (2015) The effect of two orchard light-management practices on the sensory quality of apple: fruit thinning by shading or photo-selective nets. J Hortic Sci Biotechnol 90:99–107

Cotty PJ, Jaime-Garcia R (2007) Influences of the climate on aflatoxin producing fungi and aflatoxin contamination. Int J Food Microbiol 119:109–115

Crowe KM, Bushway A, Davis-Dentici K (2012) Impact of postharvest treatments, chlorine and ozone, coupled with low-temperature frozen storage on the antimicrobial quality of lowbush blueberries (*Vaccinium angustifolium*). LWT-Food Sci Technol 47(1):213–215

DeLucia EH, Nabity PD, Zavala JA, Berenbaum MR (2012) Climate change: resetting plant-insect interactions. Plant Physiol 160(4):1677–1685

De-Pinto A, Demirag U, Haruna A, Koo J, Asamoah M (2012) Climate change, agriculture, and food crop production in Ghana. Ghana strategy support program. Policy Note # 3. International Food Policy Institute

Diamantidis G, Thomai T, Genitsariotis M, Nanos G, Bolla N, Sfakiotakis E (2002) Scald susceptibility and biochemical/physiological changes in respect to low preharvest temperature in ‘Starking Delicious’ apple fruit. Sci Hortic 92:361–366

Dwivedi SL, Nigam SN, Rao RCN, Singh U, Rao KVS (1996) Effect of drought on oil, fatty acids and protein contents of groundnut (*Arachis hypogaea* L.) seeds. Field Crop Res 48:125–133

Eden MA, Hill RA, Beresford R, Stewart A (1996) The influence of inoculum concentration, relative humidity, and temperature on infection of greenhouse tomatoes by *Botrytis cinerea*. Plant Pathol 45:798–806

Esua OJ, Chin NL, Yusof YA, Sukor R (2019) Effects of simultaneous UV-C radiation and ultrasonic energy postharvest treatment on bioactive compounds and antioxidant activity of tomatoes during storage. Food Chem 270:113–122

Falagán N, Artés F, Artés-Hernández F, Gómez PA, Pérez-Pastor A, Aguayo E (2015) Comparative study on postharvest performance of nectarines grown under regulated deficit irrigation. Postharvest Biol Technol 110:24–32

Farneti B, Schouten RE, Qian T, Dieleman JA, Tijskens LMM, Woltering EJ (2013) Greenhouse climate control affects postharvest tomato quality. Postharvest Biol Technol 86:354–361

Fels-Klerx HJ, Liu C, Battilani P (2016) Modelling climate change impacts on mycotoxin contamination. World Mycotoxin J 9:717–726

Ferguson I, Volz R, Woolf A, Cavalieri RP (1999) Pre-harvest factors affecting physiological disorders of fruit. Postharvest Biol Technol 15:255–262

Fujisawa M, Kobayashi K (2010) Apple *(Malus pumila var. domestica)* phenology is advancing due to rising air temperature in northern Japan. Glob Chang Biol 16:2651–2660

Galindo A, Calín-Sánchez Á, Griñán I, Rodríguez P, Cruz ZN, Girón IF, Torrecillas A (2017) Water stress at the end of the pomegranate fruit ripening stage produces earlier harvest and improves fruit quality. Sci Hortic 226:68–74

García-Galiano SG, Gimenez PO, Martínez-Perez JA, Giraldo-Osorio JD (2015) Improving evaluation of climate change impacts on the water cycle by remote sensing ET-retrieval. Remote Sens GIS Hydrol Water Resour 368:239–244

García-Martín JF, Olmo M, García JM (2018) Effect of ozone treatment on postharvest disease and quality of different citrus varieties at laboratory and at industrial facility. Postharvest Biol Technol 137:77–85

Gil-Serna J, Vazquez C, Garcıa Sandino F, Marquez Valle A, Gonzalez-Jaen MT, Patiño B (2014) Evaluation of growth and ochratoxin A production by *Aspergillus steynii* and *Aspergillus westerdijkiae* in green-coffee based medium under different environmental conditions. Food Res Int 61:127–131

Giorni P, Magan N, Pietri A, Bertuzzi T, Battilani P (2007) Studies on Aspergillus Section Flavi isolated in northern Italy from maize. Int J Food Microbiol 113:330–338

Glowacz M, Rees D (2016) Exposure to ozone reduces postharvest quality loss in red and green chilli peppers. Food Chem 210:305–310

Glowacz M, Colgan R, Rees D (2015) Influence of continuous exposure to gaseous ozone on the quality of red bell peppers, cucumbers and zucchini. Postharvest Biol Technol 99:1–8

Gogo EO, Opiyo AM, Hassenberg K, Ulrichs C, Huyskens-Keil S (2017) Postharvest UV-C treatment for extending shelf life and improving nutritional quality of African indigenous leafy vegetables. Postharvest Biol Technol 129:107–117

Grab S, Craparo A (2011) Advance of apple and pear tree full bloom dates in response to climate change in the southwestern Cape, South Africa: 1973–2009. Agric For Meteorol 151:406–413

Granella SJ, Christ D, Werncke I, Bechlin TR, Coelho SRM (2018) Effect of drying and ozonation process on naturally contaminated wheat seeds. J Cereal Sci 80:205–211

Gruda N (2005) Impact of environmental factors on product quality of greenhouse vegetables for fresh consumption. Crit Rev Plant Sci 24(3):227–247

Gutiérrez DR, Chaves AR, Rodríguez SDC (2018) UV-C and ozone treatment influences on the antioxidant capacity and antioxidant system of minimally processed rocket (Eruca sativa Mill.). Postharvest Biol Technol 138:107–113

Hall AJ, McPherson HG, Crawford RA, Seager NG (1996) Using early-season measurements to estimate fruit volume at harvest in kiwifruit. N Z J Crop Hortic Sci 24:379–391

Henson R (2008) The rough guide to climate change, 2nd edn. Penguin Books, London

Högy P, Fangmeier A (2008) Effects of elevated atmospheric CO_2 on grain quality of wheat. J Cereal Sci 48(3):580–591

Högy P, Fangmeier A (2009) Atmospheric CO_2 enrichment affects potatoes: 2 tuber quality traits. Eur J Agron 30:85–94

Huang H, Ge Z, Limwachiranon J, Li L, Li W, Luo Z (2017) UV-C treatment affects browning and starch metabolism of minimally processed lily bulb. Postharvest Biol Technol 128:105–111

Hussein Z, Fawole OA, Opara UL (2018) Preharvest factors influencing bruise damage of fresh fruits—a review. Sci Hortic 229:45–58

Imaizumi T, Yamauchi M, Sekiya M, Shimonishi Y, Tanaka F (2018) Responses of phytonutrients and tissue condition in persimmon and cucumber to postharvest UV-C irradiation. Postharvest Biol Technol 145:33–40

James SJ, James C (2010) The food cold-chain and climate change. Food Res Int 43(7):1944–1956

James SJ, Evans J, James C (2008) A review of the performance of domestic refrigeration. J Food Eng 87:2–10

Jang EH, Lim ST, Kim SS (2009) Effect of storage temperature for paddy on consumer perception of cooked rice. Cereal Chem 86:549–555

Kalnay E, Cai M (2003) Impact of urbanization and land-use change on climate. Nature 423:528–531

Karaca H (2010) Use of ozone in the citrus industry. Ozone Sci Eng 32(2):122–129

Kong M, Lampinen B, Shackel K, Crisosto CH (2013) Fruit skin side cracking and ostiole-end splitting shorten postharvest life in fresh figs (*Ficus carica* L.), but are reduced by deficit irrigation. Postharvest Biol Technol 85:154–161

Kowitcharoen L, Wongs-Aree C, Setha S, Komkhuntod R, Kondo S, Srilaong V (2018) Pre-harvest drought stress treatment improves antioxidant activity and sugar accumulation of sugar apple at harvest and during storage. Agric Nat Resour 52(2):146–154

Kumar A, Nayak AK, Das BS, Panigrahi N, Dasgupta P, Mohanty S, Pathak H (2019) Effects of water deficit stress on agronomic and physiological responses of rice and greenhouse gas emission from rice soil under elevated atmospheric CO_2. Sci Total Environ 650:2032–2050

La Cava EL, Sgroppo SC (2015) Evolution during refrigerated storage of bioactive compounds and quality characteristics of grapefruit [*Citrus paradisi* (Macf.)] juice treated with UV-C light. LWT-Food Sci Technol 63(2):1325–1333

Lamichaney A, Swain DK, Biswal P, Kumar V, Singh NP, Hazra KK (2019) Elevated atmospheric carbon–dioxide affects seed vigour of rice (*Oryza sativa* L.). Environ Exp Bot 157:171–176

Laribi AI, Palou L, Intrigliolo DS, Nortes PA, Rojas-Argudo C, Taberner V, Pérez-Gago MB (2013) Effect of sustained and regulated deficit irrigation on fruit quality of pomegranate cv. ‘Mollar de Elche’ at harvest and during cold storage. Agric Water Manag 125:61–70

Lau OL (1998) Effect of growing season, harvest maturity, waxing, low O_2 and elevated CO_2 on flesh browning disorders in ‘Braeburn’ apples. Postharvest Biol Technol 14:131–141

Lei J, Li B, Zhang N, Yan R, Guan W, Brennan CS, Peng B (2018) Effects of UV-C treatment on browning and the expression of polyphenol oxidase (PPO) genes in different tissues of *Agaricus bisporus* during cold storage. Postharvest Biol Technol 139:99–105

Leonardis A, Fragasso M, Beleggia R, Ficco D, de Vita P, Mastrangelo A (2015) Effects of heat stress on metabolite accumulation and composition, and nutritional properties of durum wheat grain. Int J Mol Sci 16(12):30382–30404

Li P, Zhang X, Hu H, Sun Y, Wang Y, Zhao Y (2013) High carbon dioxide and low oxygen storage effects on reactive oxygen species metabolism in *Pleurotus eryngii*. Postharvest Biol Technol 85:141–146

Li D, Li L, Xiao G, Limwachiranon J, Xu Y, Lu H, Luo Z (2018) Effects of elevated CO_2 on energy metabolism and γ-aminobutyric acid shunt pathway in postharvest strawberry fruit. Food Chem 265:281–289

Li D, Zhang X, Li L, Aghdam MS, Wei X, Liu J, Luo Z (2019) Elevated CO_2 delayed the chlorophyll degradation and anthocyanin accumulation in postharvest strawberry fruit. Food Chem 285:163–170

Lide DR (2009) CRC handbook of chemistry and physics, 90th edn. CRC Press, Boca Raton

Lin Q, Lu Y, Zhang J, Liu W, Guan W, Wang Z (2017) Effects of high CO_2 in-package treatment on flavor, quality and antioxidant activity of button mushroom (*Agaricus bisporus*) during postharvest storage. Postharvest Biol Technol 123:112–118

Liu C, Zheng H, Sheng K, Liu W, Zheng L (2018) Effects of postharvest UV-C irradiation on phenolic acids, flavonoids, and key phenylpropanoid pathway genes in tomato fruit. Sci Hortic 241:107–114

Liu QH, Xiu WU, Chen BC, Jia-Qing MA, Gao J (2014) Effects of low light on agronomic and physiological characteristics of rice including grain yield and quality. Rice Sci 21(5):243–251

Lloyd J, Farquhar GD (2008) Effects of rising temperatures and CO_2 on the physiology of tropical forest trees. Philos Trans R Soc Lond B Biol Sci 363:1811–1817

Lobos TE, Retamales JB, Ortega-Farías S, Hanson EJ, López-Olivari R, Mora ML (2016) Pre-harvest regulated deficit irrigation management effects on post-harvest quality and condition of V. corymbosum fruits cv. Brigitta. Sci Hortic 207:152–159

Lopez G, Echeverria G, Bellvert J, Mata M, Behboudian MH, Girona J, Marsal J (2016) Water stress for a short period before harvest in nectarine: Yield, fruit composition, sensory quality, and consumer acceptance of fruit. Sci Hortic 211:1–7

Lopez G, Larrigaudière C, Girona J, Behboudian MH, Marsal J (2011) Fruit thinning in 'Conference' pear grown under deficit irrigation: implications for fruit quality at harvest and after cold storage. Sci Hortic 129(1):64–70

Lu Y, Dong W, Alcazar J, Yang T, Luo Y, Wang Q, Chen P (2018) Effect of preharvest CaCl2 spray and postharvest UV-B radiation on storage quality of broccoli microgreens, a richer source of glucosinolates. J Food Compos Anal 67:55–62

Magan N, Medina A, Aldred D (2011) Possible climate-change effects on mycotoxin contamination of food crops pre-and postharvest. Plant Pathol 60(1):150–163

Malik AU, Singh Z (2006) Improved fruit retention, yield and fruit quality in mango with exogenous application of polyamines. Sci Hortic 110:167–174

Mannaa M, Kim KD (2017) Influence of temperature and water activity on deleterious fungi and mycotoxin production during grain storage. Mycobiology 45(4):240–254

Manzocco L, Plazzotta S, Maifreni M, Calligaris S, Anese M, Nicoli MC (2016) Impact of UV-C light on storage quality of fresh-cut pineapple in two different packages. LWT-Food Sci Technol 65:1138–1143

McGarry A (1993) Mechanical properties of carrots. Postharvest biology and handling of fruit, vegetables and flowers. Meeting of the Association of Applied Biologists, London

Medina AA, Rodriguez N, Magan P (2014) Effect of climate change on *Aspergillus flavus* and aflatoxins. Front Microbiol 5:348. https://doi.org/10.3389/fmicb.2014.00348

Medina A, Rodriguez A, Magan N (2015) Climate change and mycotoxigenic fungi: impacts on mycotoxin production. Curr Opin Food Sci 5:99–104

Medina Á, González-Jartín JM, Sainz MJ (2017) Impact of global warming on mycotoxins. Curr Opin Food Sci 18:76–81

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kübler K, Bissolli P, Braslavská OG, Briede A, Chmielewski FM (2006) European phenological response to climate change matches the warming pattern. Glob Chang Biol 12:1969–1976

Min D, Dong L, Shu P, Cui X, Zhang X, Li F (2018) The application of carbon dioxide and 1-methylcyclopropene to maintain fruit quality of 'Niuxin' persimmon during storage. Sci Hortic 229:201–206

Moretti CL, Mattos LM, Calbo AG, Sargent SA (2010) Climate changes and potential impacts on postharvest quality of fruit and vegetable crops: a review. Food Res Int 43(7):1824–1832

Moretti A, Pascale M, Logrieco AF (2019) Mycotoxin risks under a climate change scenario in Europe. Trends Food Sci Technol 84:38–40

Moses JA, Jayas DS, Alagusundaram K (2015) Climate change and its implications on stored food grains. Agric Res 4(1):21–30

Mowatt CM (1997) Factors influencing the susceptibility of apples to bruising. Unpublished PhD Thesis, Massey University, Palmerston North

Ndindeng SA, Mapiemfu DL, Fantong W, Nchinda VP, Ambang Z, Manful JT (2014) Postharvest adaptation strategies to the effects of temperature variations and farmer-miller practices on the physical quality of rice in Cameroon. Am J Clim Chang 3:178–192

Nuttall JG, O'Leary GJ, Panozzo JF, Walker CK, Barlow KM, Fitzgerald GJ (2017) Models of grain quality in wheat—a review. Field Crop Res 202:136–145

Oosthuyse SA (1998) Effect of environmental conditions at harvest on the incidence of lenticel damage in mango. SA Mango Growers' Assoc Yearbook 18:15–17

Park MH, Kim JG (2015) Low-dose UV-C irradiation reduces the microbial population and preserves antioxidant levels in peeled garlic (*Allium sativum* L.) during storage. Postharvest Biol Technol 100:109–112

Pataro G, Sinik M, Capitoli MM, Donsì G, Ferrari G (2015) The influence of post-harvest UV-C and pulsed light treatments on quality and antioxidant properties of tomato fruits during storage. Innovative Food Sci Emerg Technol 30:103–111

Paterson RRM, Venâncio A, Lima N, Guilloux-Bénatier M, Rousseaux S (2018) Predominant mycotoxins, mycotoxigenic fungi and climate change related to wine. Food Res Int 103:478–491

Pena ME, Artés-Hernández F, Aguayo E, Martínez-Hernández GB, Galindo A, Artés F, Gómez PA (2013) Effect of sustained deficit irrigation on physicochemical properties, bioactive compounds and postharvest life of pomegranate fruit (cv. 'Mollar de Elche'). Postharvest Biol Technol 86:171–180

Peña ME, Artés-Hernández F, Aguayo E, Martínez-Hernández GB, Galindo A, Artés F, Gómez PA (2013) Effect of sustained deficit irrigation on physicochemical properties, bioactive compounds and postharvest life of pomegranate fruit (cv. 'Mollar de Elche'). Postharvest Biol Technol 86:171–180

Peña-Estévez ME, Gómez PA, Artés F, Aguayo E, Martínez-Hernández GB, Otón M, Galindo A, Artés-Hernández F (2015) Quality changes of fresh-cut pomegranate arils during shelf life as affected by deficit irrigation and postharvest vapour treatments. J Sci Food Agric 95:2325–2336

Peña-Estévez ME, Artés-Hernández F, Artés F, Aguayo E, Martínez-Hernández GB, Galindo A, Gómez PA (2016) Quality changes of pomegranate arils throughout shelf life affected by deficit irrigation and pre-processing storage. Food Chem 209:302–311

Qiu J (2014) Global warming may worse locust swarms. http://www.nature.com/news/2009/091007/full/news.2009.978.html. Accessed 24 Aug 2017

Rehman ZUR, Shah WH (1999) Biochemical changes in wheat during storage at three temperatures. Plant Food Hum Nutr 54:109–117

Romero-Trigueros C, Parra M, Bayona JM, Nortes PA, Alarcón JJ, Nicolás E (2017) Effect of deficit irrigation and reclaimed water on yield and quality of grapefruits at harvest and postharvest. LWT-Food Sci Technol 85:405–411

Rosales MA, Ríos JJ, Castellano R, López-Carrión AI, Romero L, Ruiz JM (2007) Proline metabolism in cherry tomato exocarp in relation to temperature and solar radiation. J Hortic Sci Biotechnol 82(5):739–744

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL, Estrella N, Seguin B, Tryjanowski P (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453:353–357

Roy HE, Beckmann BC, Comont RF, Hails RS, Harrington R, Medlock J, Purse B, Shortall CR (2009) Nuisance insects and climate change. Department Environ, Food Rural Affairs, London. Available online: Nora.nerc.ac.uk./8332. Accessed 30 Jan 2020

Sachadyn-Król M, Materska M, Chilczuk B, Karaś M, Jakubczyk A, Perucka I, Jackowska I (2016) Ozone-induced changes in the content of bioactive compounds and enzyme activity during storage of pepper fruits. Food Chem 211:59–67

Samperio A, Moñino MJ, Vivas A, Blanco-Cipollone F, Martín AG, Prieto MH (2015) Effect of deficit irrigation during stage II and post-harvest on tree water status, vegetative growth, yield and economic assessment in 'Angeleno' Japanese plum. Agric Water Manag 158:69–81

Sanchis V, Magan N (2004) Environmental profiles for growth and mycotoxin production. In: Magan N, Olsen M (eds) Mycotoxins in food: detection and control. Woodhead Publishing Ltd, Cambridge, pp 174–189

Sari LK, Setha S, Naradisorn M (2016) Effect of UV-C irradiation on postharvest quality of 'Phulae' pineapple. Sci Hortic 213:314–320

Schauberger B, Rolinski S, Schaphoff S, Müller C (2019) Global historical soybean and wheat yield loss estimates from ozone pollution considering water and temperature as modifying effects. Agric For Meteorol 265:1–15

Schmidhuber J, Tubiello FN (2007) Global food security under climate change. Proc Natl Acad Sci U S A 104(50):19703–19708

Sehgal A, Sita K, Siddique KH, Kumar R, Bhogireddy S, Varshney RK, Nayyar H (2018) Drought or/and heat-stress effects on seed filling in food crops: impacts on functional biochemistry, seed yields, and nutritional quality. Front Plant Sci 9:1705. https://doi.org/10.3389/fpls.2018.01705

Selahle KM, Sivakumar D, Jifon J, Soundy P (2015) Postharvest responses of red and yellow sweet peppers grown under photo-selective nets. Food Chem 173:951–956

Shah HMS, Khan AS, Ali S (2017) Pre-storage kojic acid application delays pericarp browning and maintains antioxidant activities of litchi fruit. Postharvest Biol Technol 132:154–161

Sharma HC (2010) Global warming and climate change: impact on arthropod biodiversity, pest management, and food security. In: Thakur R, Gupta PR, Verma AK (eds) Souvenir of the national symposium on perspectives and challenges of integrated pest management for sustainable agriculture, Nauni, Solan, Himachal Pradesh, pp 1–14

Shen Y, Sun Y, Qiao L, Chen J, Liu D, Ye X (2013) Effect of UV-C treatments on phenolic compounds and antioxidant capacity of minimally processed Satsuma mandarin during refrigerated storage. Postharvest Biol Technol 76:50–57

Sheng K, Zheng H, Shui S, Yan L, Liu C, Zheng L (2018) Comparison of postharvest UV-B and UV-C treatments on table grape: changes in phenolic compounds and their transcription of biosynthetic genes during storage. Postharvest Biol Technol 138:74–81

Shibairo SI, Upadhyaya MK, Toivonen PMA (1998) Influence of preharvest water stress on postharvest moisture loss of carrots (*Daucus carota* L.). J Hortic Sci Biotechnol 73:347–352

Shin Y, Ryu JA, Liu RH, Nock JF, Polar-Cabrera K, Watkins CB (2008) Fruit quality, antioxidant contents and activity, and antiproliferative activity of strawberry fruit stored in elevated CO_2 atmospheres. J Food Sci 73(6):S339–S344

Sites JW, Reitz HJ (1949) The variation of individual 'Valencia' oranges from different locations on the tree as a guide to sampling methods and spot picking for quality. 1. Soluble solids in the juice. Proc Am Soc Hortic Sci 54:1

Sites JW, Reitz HJ (1950a) The variation of individual 'Valencia' oranges from different locations on the tree as a guide to sampling methods and spot picking for quality. II. Titratable acidity and the soluble solids titratable acidity ration of the juice. Proc Ser Soc Hortic Sci 55:73

Sites JW, Reitz HJ (1950b) The variation of individual 'Valencia' oranges from different locations on the tree as a guide to sampling methods and spot picking for quality. III. Vitamin C and juice content of the fruit. Proc Ser Soc Hortic Sci 56:103

Smith G, Glennie JD (1987) Blackheart development in growing pineapples. Trop Agric 64:7–11

Souza LPD, Faroni LRDA, Heleno FF, Cecon PR, Gonçalves TD, da Silva GJ, Prates LHF (2018) Effects of ozone treatment on postharvest carrot quality. LWT 90:53–60

Spayd SE, Tarara JM, Mee DL, Ferguson JC (2002) Separation of sunlight and temperature effects on the composition of *Vitis vinifera* cv. Merlot berries. Am J Enol Vitic 53:171–182

Sripong K, Jitareerat P, Uthairatanakij A (2019) UV irradiation induces resistance against fruit rot disease and improves the quality of harvested mangosteen. Postharvest Biol Technol 149:187–194

Stathers T, Lamboll R, Mvumi MB (2013) Post-harvest agriculture in a changing climate. Rural Focus 21 47(4):12–14

Sugiura T, Ogawa H, Fukuda N, Moriguchi T (2013) Changes in the taste and textural attributes of apples in response to climate change. Sci Rep 3:2418

Suleiman R, Rosentrater K, Bern CJ (2013) Effects of deterioration parameters on storage of maize: a review. J Nat Sci Res 3:147–165

Tabakoglu N, Karaca H (2018) Effects of ozone-enriched storage atmosphere on postharvest quality of black mulberry fruits (*Morus nigra* L.). LWT-Food Sci Technol 92:276–281

Tahir II, Johansson E, Olsson ME (2009) Improvement of apple quality and storability by a combination of heat treatment and controlled atmosphere storage. Hortic Sci 44:1648–1654

Thomas MB, Blanford S (2003) Thermal biology in insect-parasite interactions. Trends Ecol Evol 18:344–350

Thomas JMG, Boote KJ, Allen LH, Gallo-Meagher M, Davis JM (2003) Elevated temperature and carbon dioxide effects on soybean seed composition and transcript abundance. Crop Sci 43(4):1548–1557

Thomas JMG, Prasad PVV, Boote KJ, Allen LH Jr (2009) Seed composition, seedling emergence and early seedling vigour of red kidney bean seed produced at elevated temperature and carbon dioxide. J Agron Crop Sci 195(2):148–156

Thompson AK (2003) Fruits and vegetables harvesting, handling and storage, 2nd edn. Blackwell Publishing, Oxford, pp 1–8

Thompson AK, Burden OJ (1995) Harvesting and fruit care. In: Gowen S (ed) Bananas and plantains. Chapman and Hall, London, pp 403–433

Toivonen PM, Hodges DM (2011) Abiotic stress in harvested fruits and vegetables. In: Abiotic stress in plants-mechanisms and adaptations. InTech, China, pp 39–58

Vega Pina A, Nieto Angel D, Mena Nevarez G (2000) Effect of water stress and chemical spray treatments on postharvest quality in mango fruits cv. Haden, in Michoacan, Mexico. Acta Hortic 509:617–630

Wang Q, Chu L, Kou L (2017) UV-C Treatment maintains quality and delays senescence of oyster mushroom (*Pleurotus ostreatus*). Sci Hortic 225:380–385

Wang D, Chen L, Ma Y, Zhang M, Zhao Y, Zhao X (2019) Effect of UV-C treatment on the quality of fresh-cut lotus (*Nelumbo nucifera* Gaertn.) root. Food Chem 278:659–664

Webb LB, Whetton PH, Barlow EWR (2011) Observed trends in wine grape maturity in Australia. Glob Chang Biol 17:2707–2719

Woolf AB, Ferguson IB (2000) Postharvest responses to high fruit temperatures in the field. Postharvest Biol Technol 21:7–20

Woolf AB, Wexler A, Prusky D, Kobiler E, Lurie S (2000) Direct sunlight influences postharvest temperature responses and ripening of five avocado cultivars. J Am Soc Hortic Sci 125:370–376

Wurr DCE, Fellows JR, Phelps K (1996) Investigating trends in vegetable crop response to increasing temperature associated with climate change. Sci Hortic 662:55–263

Yamada H, Kobayashi S (1999) Relationship between watercore and maturity or sorbitol in apples affected by preharvest fruit temperature. Sci Hortic 80(3–4):189–202

Zhang L, Gao J, Hu H, Li P (2015) The activity and molecular characterization of a serine proteinase in *Pleurotus eryngii* during high carbon dioxide and low oxygen storage. Postharvest Biol Technol 105:1–7

Zhu F (2018) Effect of ozone treatment on the quality of grain products. Food Chem 264:358–366

Chapter 5
Plant Adaptation and Tolerance to Environmental Stresses: Mechanisms and Perspectives

Ali Raza, Farwa Ashraf, Xiling Zou, Xuekun Zhang, and Hassan Tosif

Contents

Abstract Environmental stresses such as waterlogging, drought, salinity, high and low temperature, and elevated CO_2 levels affect plant development and pose an increasing warning to sustainable agriculture. Environmental stresses have become a matter of contention due to concerns about the outcomes of climate change on plant resources, genetic diversity, and world food safety. Plant responses to these

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stress factors are highly intricate and include modifications at the cellular, molecular, and genetic levels. Now, it has been scientifically proven that plant responds differently to multiple stresses as compared to individual stresses. As the changing climate will expose the plants to interactive effects simultaneously, therefore there is a dire need for further research in plant developmental responses to these stress factors; otherwise, this will have a negative effect on sustainable agriculture. Therefore, in this chapter, recent advancement in mechanisms and perspectives of plant adaptation and tolerance to several environmental stresses have been discussed.

Keywords Bioinformatics · Climate change · Environmental stresses · Plant physiology · Phytohormones · Stress tolerance · Transcription factors

5.1 Plant Responses to Environmental Stress Factors: An Overview

Plant responses to various environmental stresses are extremely variable and highly complicated, which may include changes at the physiological, cellular, and transcriptional level. Recent studies indicate that plant responds differently to multiple stresses as they respond to individual stress, by the activation of specific gene expressions, which are needed in particular environmental stress. Plants have developed to grow in their environment where plants are frequently subjected to various environmental conditions, as they are sessile and have well-emerged mechanisms that allowed them to recognize minute environmental changes to avoid damage and to conserve energy for growth and development. Plants can activate specific responses to confer stress, so it became difficult to study multiple responses at a time by available techniques. This phenomenon is quite accurate for both biotic and abiotic stresses. There is a dire need for vast research in plant studies in order to evaluate the multiple stresses and how plants can tolerate these stresses (Atkinson and Urwin 2012; Zhu 2016). In this regard, conventional and modern breeding platforms can help us to select plants for the improvement of dsirable traits; such as 1) development of environmental stress resistance plants, 2) to increase sustainable yield production, and 3) to enhance the content of micronutrients to develop nutritious crops.

5.1.1 Multiple Environmental Stresses: A Challenge in Agriculture

Essentially, plants require water, carbon, and vital mineral nutrients for growth and normal development (Cramer et al. 2011). Most of the time, plants do not grow in standard conditions, which limit their genetic potential to achieve maximum height and reproductive stage (Bray et al. 2000). This fact is observed by comparing the maximum crop yield and the average crop yield. This difference in yield is due to suboptimal environmental conditions, which induce damaging the physiological changes which occur within the plants, called stresses (Simontacchi et al. 2015; Shao et al. 2008; Zhu 2016).

Abiotic stresses such as cold, high temperature, drought, salinity, and nutrient imbalance are those environmental stresses which limit the plant growth and production below the threshold level. In addition to this, plants must have to defend themselves against various pathogens and pests, which may include fungi, bacteria, nematodes, and herbivore pests. Each plant activates a specific response mechanism to a particular stress to avoid damage (Hammond-Kosack 2000). Plant responses can be elastic (reversible) and plastic (irreversible). The duration of stress can also vary which directly affects the plant response. The plant reaction toward stress factors depends on the specific tissue or organ, which is affected by the corresponding stress factor. For instance, the transcriptional responses are different and depend on stress, which is either tissue- or cell-specific in roots. Water stress, for example, affects the plant cell wall enzymatically and nonenzymatically which may inhibit plant growth (Cramer et al. 2011). Under field conditions, drought and temperature are the major principal stresses and have a remarkable effect on different crops (Raza et al. 2019a).

5.2 How Can Climate Change Affect Plant Developmental Responses?

Climate change is one of the main reasons which widely affects plant growth and reproduction. This changing climatic conditions and increasing population led to the demand of stress-tolerant plant species to meet the environmental conditions and energy demand (Takeda and Matsuoka 2008; Raza et al. 2019a; Newton et al. 2011).

As plants are sessile, they have to tolerate fluctuating environmental conditions in order to survive. The climatic catastrophe, which may be in the form of drought, salinity, elevated temperature, and elevated CO_2, represents a concerned issue toward the sustainable development of agriculture. Naturally, plants are blessed with the ability to sense climate change and adapt accordingly. With changing the environment, plants evolved and have developed precise molecular and cellular mechanisms that enable them to survive in harsh conditions. However, unfortunately, there is not enough research on how plants evolved currently at present, and this knowledge gap should be minimized to develop the plant species, which can tolerate not only individual stresses but also multiple stresses (Ahuja et al. 2010). Recent researches in “omics” approach led to better understanding of transcriptome, proteome, and metabolomics of plants by linking with stress perceptions and responses. These approaches are also studied in other crop and woody plant species besides a model plant *Arabidopsis* (Coolen et al. 2016; Varoquaux et al. 2019; Razzaq et al. 2019; Zhang et al. 2019; You et al. 2019).

5.2.1 Elevated CO_2 Levels Affect Plant Development and Morphology

The CO_2 levels in the atmosphere have elevated to 440 ppm from 280 ppm due to increased industrial activity (Meehl et al. 2007). Increased levels of CO_2 directly affect plant developmental processes and photosynthetic exchange of gas. Plants are also affected indirectly by CO_2 as it is the cause of the greenhouse effect that causes global warming and other drastic changes in climate. Studies in C3 plants have found that the elevation in CO_2 level contributes to increased aboveground biomass. In grassland species, the aboveground biomass has been found to increase by 33%, but it also depends on nutrient and water availability in soil. In dry and hot areas, there is low aboveground biomass due to low water and nitrogen availability (Reich et al. 2014). Studies also indicated that root biomass also increased due to increased CO_2 levels (Madhu and Hatfield 2013). The increased production of shoot biomass led to an increase in seed yield, as is observed in most plant species such as soybean, peanut, wheat, bean, and rice (Hatfield et al. 2011). Soybean, the model plant, has shown increased leaf length and the number of leaf nodes, increased seed yield and pod number, and elongated root (Bishop et al. 2015; Gray et al. 2016).

5.2.2 Effects of Elevated Temperature

The global average temperature has been increased to 0.85 from 1880 to 2012, due to increasing concentrations of CO_2 and other greenhouse gases (Hartmann et al. 2013). By the end of the century, there is a prediction of increasing global mean temperature from 1.0 to 3.7 °C. This increasing temperature makes the plants undergo heat stress due to changing frequency, intensity, and duration of heat waves. The effects of elevation in CO_2 are quite consistent across many plant species, while the elevation in temperature causes the plants to behave differently in different regions across the globe. In the Arctic, for instance, the surface temperature increases much faster as compared to other regions (Gray et al. 2016). The elevation in temperature affects plant development based on their growing regions. The yield of some plants increased, while the yield of the same plants decreased when grown in different regions. For example, soybean had a maximum yield in the Midwestern USA as compared to low yield in the Southern USA (Hatfield et al. 2011). The plant physiology and development are also affected by temperature, which in turn affects the yield of the plant. This reduction in plant yield is also due to decreasing the activity of carbon assimilation enzyme *Rubisco* either by a reduction in activity of *Rubisco* actives or by reduction in the generation of ribulose-1,5 biphosphate (RuBP). The C3 and C4 plants have different photosynthetic functions and behave accordingly in their optimal range of temperatures (Sage et al. 2008). This mechanism is quite clear that plant development depends on species-specific temperature optimum.

5.2.3 *Effects of Drought Stress on Plant Physiology*

Climate change is one of the major reasons for water stress. This increasing water stress is affecting plant growth in different regions of the world. It is predicted that the drought will increase in those areas which are already under water stress. Drought can cause damaging hydrologic imbalances due to prolonged dry weather affecting plant development and morphology (Gray et al. 2016). Drought stress can be observed in different plant organs and tissues. This stress often leads to elongation of root and reduction in shoot growth. This means that root elongates at the expense of shoot. For instance, the two grass species (*H. lanatus* and *A. pratensis*) showed increased nutrient and metabolite content in roots as compared to shoots (Gargallo-Garriga et al. 2014). This property proves the functional equilibrium theory in which plants will try to optimize the limiting resource by shifting allocation among tissues. This adaptive behavior will help the plants grow in water-deficit areas by the reduction in transpiration rates as plants invest more in roots than in shoots.

5.2.4 *Multiple Environmental Stress Effects on Plant Development*

There is limited research on how plants behave when a number of stresses are inflicted upon them at a time. Researchers have studied each stress independently but still challenging to comprehend multiple stresses. Climate change is one of the main reasons for the increasing number of stresses, and thus plants have to behave accordingly. In soybean, for instance, seed yield is increased by the elevation of CO_2 which diminishes due to drought stress (Ruiz-Vera et al. 2018; Gray et al. 2016). In maize, high CO_2 and elevated temperature do not contribute to an increase in seed yield (Ruiz-Vera et al. 2015, 2018). These effects demonstrated that the influence of one climate change factor is affected by the presence of another climate change factor on plant development and physiology. In order to comprehend the interactive effects of changing climate, there is a need to study how plants reacted to climate change at the molecular and cellular level.

5.3 How Transgenic Plants Respond to Different Environmental Stresses?

The transgenic approach has helped us to understand the ways of stress tolerance. Transgenic plants have developed to study the abiotic stress factors in greenhouses, growth rooms, and under a controlled environment. These studies have helped to understand the behavior of the number of transgenic plants in stress conditions like drought, salinity, and low and high temperature (Ashraf and Foolad 2007; Wang et al. 2016a; Gilliham et al. 2017). Some examples of transgenic plants showing resistance to different environmental stresses are described in Table 5.1.

There is a comparable difference which exists between conventional and transgenic approaches to tolerate water stress. The genes of significant metabolic and defensive pathways can be engineered through transgenic approaches such as osmoprotectant producing pathways and antioxidant defense approaches (Singh et al. 2015; Wang et al. 2016a). Microarray techniques are proving helpful in several stress-inducible genes, but their function at the molecular level is still unknown. Recently, the study was carried out to enhance the photosynthetic properties of different C3 crops either by the introgression of C4 genes or by the overexpression of C3 genes (Ashraf and Harris 2013).

Among other abiotic stresses, high salinity is exceptionally damaging for plants. In transgenic plants, compartmentation and diversion of harmful ions such as Na^+ and Cl^- from delicate areas of plants like mesophyll to apoplast or vacuole took place to avoid the deleterious effects of high salinity (Sperling et al. 2014). Transgenic plants, mostly halophytes, have increased salinity tolerance due to overexpression of the ion transporter gene (Flowers and Colmer 2008). The physiological and molecular responses are determinant of plant survival under low temperatures (John et al. 2016; Sergeant et al. 2014). Transgenic plants at transcriptional as well as translational levels show cold tolerance mechanisms. Biotechnological and molecular approaches are used to alter gene expression in such a way that it increases the concentration of several metabolites to avoid cold stress (John et al. 2016). The expression of altered genes, which have been evaluated most recently, is said to be controlled by core binding factor (CBF) or dehydration responsive element binding (DREB) binding factors (Agarwal et al. 2017).

High temperature, another abiotic factor, has to be tolerated by plants in this fluctuating environmental temperature (Mittler et al. 2012). High temperature directly affects the proteome, transcriptome, metabolome, and liposome which makes it challenging for the plants to survive. Molecular chaperones such as heat shock protein (HSP) are highly valuable in avoiding the harmful effect of high temperature (Xu et al. 2013). Five major HSPs play a central role in avoiding stress. These HSPs may also combine with other co-chaperones to repair damaged proteins by refolding, thereby protecting plant cellular functions. Any reduction in the HSPs is responsible for the abnormal development of plants (Kotak et al. 2007).

Pest-resistant crops are highly useful in limiting the biotic stress caused by pests and fungi. The development of these bio-friendly plants helps to improve plant tolerance to a certain fungicide or a pesticide (Mahmood et al. 2014). In the literature, it is well reported that resistance to pests can be brought about by enhancing the complex multigene enzymes activities such as glutathione-*S*-transferase, esterases, and cytochrome P450s (Bass and Field 2011).

Another factor, nutrient use efficiency (NUE), becomes reduced due to leaching, surface runoff, volatilization, or microbial consumption. Efficient means are required to maximize the nutrient use efficiency to diminish mineral losses (Salim and Raza 2020; Baligar and Fageria 2015). There are not enough molecular approaches used to date to improve the NUE of plants. However, despite the limiting

Table 5.1 Transgenic plants indicating tolerance to different environmental stresses via gene expression

TFs type/ subfamily	Gene	Donor plant	Accepter plant	Stress type tolerance	References
MYB	*OsMYB3R-2*	*Oryza sativa*	*Arabidopsis thaliana*	Freezing, drought, and salinity	Dai et al. (2007)
	TaMYB56-B	*Triticum aestivum*	*Arabidopsis thaliana*	Freezing and salinity	Zhang et al. (2012)
	AtMYB44	*Arabidopsis thaliana*	*Glycine max*	Drought and salinity	Seo et al. (2012)
	MdSIMYB1	*Malus domestica*	*Nicotiana tabacum*	Drought, salinity, and cold	Wang et al. (2014b)
	FtMYB9	*Fagopyrum tataricum*	*Arabidopsis thaliana*	Drought and salinity	Gao et al. (2017)
	GaMYB85	*Gossypium raimondii*	*Arabidopsis thaliana*	Drought	Butt et al. (2017)
	TaODORANT1	*Triticum aestivum*	*Nicotiana tabacum*	Drought and salinity	Wei et al. (2017)
	GhMYB73	*Gossypium hirsutum*	*Arabidopsis thaliana*	Salinity	Zhao et al. (2019)
	ZmMYB3R	*Zea mays*	*Arabidopsis thaliana*	Drought and salinity	Wu et al. (2019)
DREB/CBF/AP2/ ERF	*AhERF019*	*Arachis hypogaea*	*Arabidopsis thaliana*	Drought, salinity, and heat	Wan et al. (2014)
	SsDREB	*Suaeda salsa*	*Nicotiana tabacum*	Salinity	Zhang et al. (2015b)
	DaCBF7	*Deschampsia antarctica*	*Oryza sativa*	Cold	Byun et al. (2015)
	GhCBF3	*Gossypium hirsutum*	*Arabidopsis thaliana*	Drought and salinity	Ma et al. (2016)
	ERF76	*Populus*	*Nicotiana tabacum*	Salinity	Yao et al. (2016)
	NnDREB1	*Nelumbo nucifera*	*Arabidopsis thaliana*	Drought	Cheng et al. (2017)
	ThDREB	*Tamarix hispida*	*Nicotiana tabacum* and *Tamarix hispida*	Drought and salinity	Yang et al. (2017)
	CcHRD	*Christolea crassifolia*	*Solanum lycopersicum*	Drought	Guo et al. (2017b)
	JcDREB2	*Jatropha curcas*	*Oryza sativa*	Salinity	Tang et al. (2017)
	LbDREB	*Limonium bicolor*	*Populus ussuriensis*	Salinity	Zhao et al. (2018)
	MhSHN1	*Malus hupehensis*	*Nicotiana tabacum*	Salinity and osmotic stresses	Zhang et al. (2018)
	CmERF053	*Chrysanthemum morifolium*	*Arabidopsis thaliana*	Drought	Nie et al. (2018)
	IbRAP2-12	*Ipomoea batatas*	*Arabidopsis thaliana*	Drought and salinity	Li et al. (2019)

(continued)

Table 5.1 (continued)

TFs type/ subfamily	Gene	Donor plant	Accepter plant	Stress type tolerance	References
NAC	*EcNAC1*	*Eleusine coracana*	*Nicotiana tabacum*	Salinity and osmotic	Ramegowda et al. (2012)
	TaNAC67	*Triticum aestivum*	*Arabidopsis thaliana*	Drought, salinity, and freezing	Mao et al. (2014)
	MlNAC9	*Miscanthus lutarioriparius*	*Arabidopsis thaliana*	Drought, salinity, and cold	Zhao et al. (2016b)
	TaNAC47	*Triticum aestivum*	*Arabidopsis thaliana*	Drought, salinity, and freezing	Zhang et al. (2016)
	ZmNAC55	*Zea mays*	*Arabidopsis thaliana*	Drought	Mao et al. (2016)
	GhNAC2	*Gossypium herbaceum*	*Arabidopsis thaliana*	Drought and salinity	Gunapati et al. (2016)
	ShNAC1	*Solanum habrochaites*	*Solanum lycopersicum*	Drought, salinity, and cold	Liu et al. (2018)
	GmNAC109	*Glycine max*	*Arabidopsis thaliana*	Drought and salinity	Yang et al. (2019b)
	SlNAC2	*Solanum lycopersicum*	*Arabidopsis thaliana*	Drought and salinity	Borgohain et al. (2019)
	AtJUB1	*Arabidopsis thaliana*	*Solanum lycopersicum*	Drought and salinity	Alshareef et al. (2019)
WRKY	*TaWRKY44*	*Triticum aestivum*	*Nicotiana tabacum*	Drought, salinity, and osmotic	Wang et al. (2015)
	GhWRKY41	*Gossypium herbaceum*	*Nicotiana benthamiana*	Drought and salinity	Chu et al. (2015)
	TaWRKY93	*Triticum aestivum*	*Arabidopsis thaliana*	Drought, salinity, and low temperature	Qin et al. (2015)
	GhWRKY25	*Gossypium herbaceum*	*Nicotiana benthamiana*	Drought and salinity	Liu et al. (2016)
	PeWRKY83	*Phyllostachys edulis*	*Arabidopsis thaliana*	Salinity	Wu et al. (2017)
	GhWRKY6-like	*Gossypium herbaceum*	*Arabidopsis thaliana*	Salinity	Ullah et al. (2018)
	VvWRKY2	*Vitis vinifera*	*Nicotiana tabacum*	Salinity and osmotic	Mzid et al. (2018)
	MuWRKY3	*Macrotyloma uniflorum*	*Arachis hypogaea*	Drought	Kiranmai et al. (2018)
	GhWRKY91	*Gossypium hirsutum*	*Arabidopsis thaliana*	Drought	Gu et al. (2019)

bZIP	*GmbZIP132*	*Glycine max*	*Arabidopsis thaliana*	Salinity	Liao et al. (2008)
	ZmbZIP72	*Zea mays*	*Arabidopsis thaliana*	Drought and salinity	Ying et al. (2012)
	MsZIP	*Medicago sativa*	*Nicotiana tabacum*	Drought and salinity	Li et al. (2013)
	TabZIP60	*Triticum aestivum*	*Arabidopsis thaliana*	Drought, salinity, and freezing	Zhang et al. (2015a)
	BnaABF2	*Brassica napus*	*Arabidopsis thaliana*	Drought and salinity	Zhao et al. (2016a)
	VqbZIP39	*Vitis quinquangularis*	*Arabidopsis thaliana*	Drought, salinity, and oxidative	Tu et al. (2016)
	TabZIP14-B	*Triticum aestivum*	*Arabidopsis thaliana*	Salinity and freezing	Zhang et al. (2017)
	OsbZIP16	*Oryza sativa*	*Arabidopsis thaliana*	Drought	Pandey et al. (2018)
	VvABF2	*Vitis vinifera*	*Arabidopsis thaliana*	Osmotic	Liu et al. (2019)
	IbbZIP1	*Ipomoea batatas*	*Arabidopsis thaliana*	Drought and salinity	Kang et al. (2019)
LEA	*PMA80 and PMA1959*	*Triticum aestivum*	*Oryza sativa*	Dehydration	Cheng et al. (2002)
	CaLEA6	*Capsicum annuum*	*Nicotiana tabacum*	Drought and high salinity	Kim et al. (2005)
	BnaLEA	*Brassica napus*	*Brassica campestris*	Drought and salinity	Park et al. (2005)
	LEA (DQ663481)	*Tamarix androssowii*	*Nicotiana tabacum*	Drought	Wang et al. (2006)
	TaLEA3	*Triticum aestivum*	*Leymus chinensis*	Drought	Wang et al. (2009)
	IbLEA14	*Ipomoea batatas*	*Calli*	Salinity and osmotic	Park et al. (2011b)
	OsLEA3-2	*Oryza sativa*	*Arabidopsis thaliana*	Drought and salinity	Duan and Cai (2012)
	SiLEA14	*Setaria italica*	*Arabidopsis thaliana*	Salinity and osmotic	Wang et al. (2014a)

knowledge, it has been acknowledged that transcription factors and associated kinases are improving the NUE of plants (Salim and Raza 2020; Canales et al. 2014).

Heavy metal toxicity leads to necrosis and stunted growth of plants, and it is one of the major determinants to assess agricultural productivity (Liu et al. 2014b). It not only affects the plant at the cellular level but also at the molecular level by impairing transcription and replication mechanisms (User 2013). Phytoremediation is a highly useful technique in eliminating environmental contaminants (Glick 2003). Moreover, rhizoremediation, including plants and also their rhizospheric microbes which naturally either exist or are introduced in plants, can help to eliminate or reduce contamination levels and encourage normal plant development (Rainbird et al. 2018).

5.4 Role of Transcription Factors (TFs) in Stress Management

Plants have developed a number of defense processes to tolerate abiotic stresses. It is becoming essential to assess these mechanisms to produce new varieties of genetically stress-tolerant plants. Due to the progress in novel genetic fields such as genomics, transcriptomics, and proteomics, now it is not only easy to dissect the whole defense mechanism but also have the ability to enhance the resistance in plants (Liu et al. 2014a). Molecular markers contribute to the utilization of candidate genes in the genetic engineering of crops (Raza et al. 2019b). As it becomes easy to study the stress signaling pathway, therefore, the generic signaling pathway consists of key steps such as signal perception, signal transduction, stress-responsive gene expression, concerning physiological processes, and metabolic reactions (Zhu 2016; Pérez-Clemente et al. 2013). Firstly, plants via sensors/receptors present in the cell wall or membrane receive the extracellular stimuli. The second messenger, which includes inositol phosphate, sugar, reactive oxygen species (ROS), calcium ions (Ca^{2+}), cyclic nucleotides (cAMP and cGMP), and nitric oxide (NO), converts the extracellular signals into intracellular signals. Thereupon, these secondary messengers activate the required signaling pathway to transduce the signal (Newton et al. 2016; Bhargava and Sawant 2013). The phosphorylation and dephosphorylation of proteins are carried out with the help of protein kinase and phosphatases, respectively, in most of the signaling pathways and quite effective in signal relay mechanism (Jaiwal and Singh 2003). For example, in plant abiotic stress, the mitogen-activated protein kinases (MAPKs) pathways and calcium-dependent protein kinases (CDPKs) pathways are known to play an important role (Simeunovic et al. 2016; Huang et al. 2012; Rayapuram et al. 2018). The protein kinases or phosphatases activate transcription factors at the end of phosphorylation chain and further bind TFs precisely to *cis*-elements in the promoter region of stress-related genes and modulate their transcription process (Simeunovic et al. 2016). At the same time, further upstream components regulate TFs to their transcript level and undergo a number of alterations at the posttranscriptional level, like ubiquitination and simulation. After posttranscriptional modification, it forms a multiplex regulatory network to inflect the response of stress-related genes that regulate physiological activities and metabolic reactions (Simeunovic et al. 2016; Zhu 2016; Mizoi et al. 2013). A model for plant abiotic stress responses is described in Fig. 5.1.

All these steps contribute to form a genetic pathway for abiotic stress-related signal transduction in plants. Various TFs have been identified and characterized through a considerable research, which are elaborated in abiotic stress responses in plants either in ABA-dependent pathways or in ABA-independent pathways (Simeunovic et al. 2016; Umezawa et al. 2006; Zhu 2016; Golldack et al. 2011). Several studies were carried out to engineer these TFs to overcome plant stress tolerance, and some worth noting results have been reported (Table 5.2).

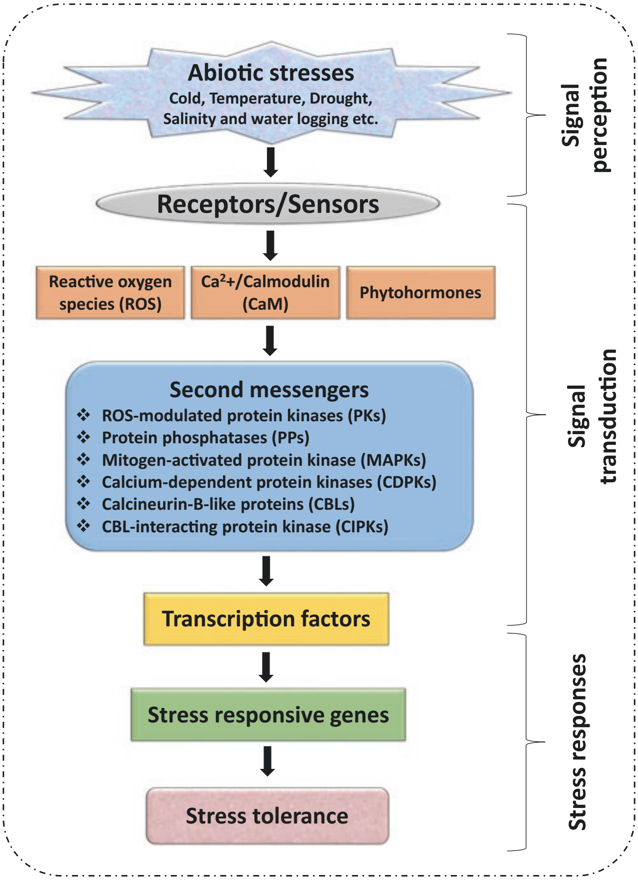

Fig. 5.1 Signaling pathways of plant abiotic stresses. Some key factors plays a vital role in signaling pathways such as perception of stress, transcriptional regulation, expression of stress-responsive genes, and physiological responses for the development of abiotic stress tolerance plants

Table 5.2 The potential role of transcription factors (TFs) in relation to different abiotic stresses

TFs type/ subfamily	Plant name	Gene name	Effect on plant growth	References
MYB	*Arabidopsis thaliana*	*AtMYBL*	Candidate gene for salt stress tolerance and increased leaf senescence	Zhang et al. (2010)
	Oryza sativa	*OsMYB2*	Positive regulator of salinity, cold, and dehydration stress	Yang et al. (2012)
	Malus domestica	*MdoMYB121*	A candidate gene for drought, salinity, and cold stress tolerance	Cao et al. (2013)
	Oryza sativa	*OsMYB91*	Salinity stress tolerance and coordinate plant growth	Zhu et al. (2015)
	Betula platyphylla	*BplMYB46*	Increased salinity and osmotic stress tolerance and involved in secondary wall biosynthesis	Guo et al. (2017a)
	Oryza sativa	*OsMYB6*	Positive regulator to salinity and drought tolerance	Tang et al. (2019)
DREB/ CBF/AP2/ ERF	*Oryza sativa*	*OsDREB1F*	Increased drought, salinity, and low-temperature tolerance via ABA-dependent pathway	Wang et al. (2008)
	Caragana korshinskii	*CkDREB*	Increased salinity and osmotic stress tolerance	Wang et al. (2011)
	Arabidopsis thaliana	*AtERF71/ HRE2*	Positive regulator of osmotic stress tolerance and hypoxia as well	Park et al. (2011a)
	Lepidium latifolium	*LlaDREB1b*	A candidate gene for cold, drought, and salinity stress tolerance	Gupta et al. (2013)
	Populus hopeiensis	*PhCBF4a and PhCBF4b*	Positive regulator of dehydration, salinity, and cold stress tolerance	Wang et al. (2014c)
	Oryza sativa	*OsEREBP1*	Drought and submergence stress tolerance	Jisha et al. (2015)
	Hemarthria compressa	*HcDREB2*	Drought, salinity, and cold stress tolerance and an ABA-independent gene	Chen et al. (2016)
	Musa Acuminata	*MaERF10*	Cold tolerance MeJA-induced gene	Qi et al. (2016)
	Brassica oleracea var. italica	*BoERF1*	Positive regulator to salinity tolerance	Jiang et al. (2019)

(continued)

Table 5.2 (continued)

TFs type/ subfamily	Plant name	Gene name	Effect on plant growth	References
NAC	*Gossypium hirsutum*	*GhNAC1–GhNAC6*	Associated with drought, salinity, and cold stress and tolerance via ABA-mediated pathway	Meng et al. (2009)
	Oryza sativa	*OsNAC5*	Induced by and increased resistance to drought, salinity, and cold stress via ABA and JA pathways	Takasaki et al. (2010)
	Brassica napus	*BnNAC485*	Enhance resistance to various abiotic stresses via the ABA-mediated pathway	Ying et al. (2014)
	Gossypium herbaceum	*GhNAC2*	Enhance resistance to drought and salinity through the activation of ABA and JA pathways and the suppression of the ethylene pathway	Gunapati et al. (2016)
	Oryza sativa	*OsNAC2*	ABA-dependent gene increased salinity and drought stress tolerance	Shen et al. (2017)
	Solanum lycopersicum	*SlNAC35*	Enhanced chilling tolerance via the regulation of CBF-COR pathways	Wang et al. (2018)
WRKY	*Hordeum vulgare*	*HvWRKY38*	A positive regulator in cold and drought stress tolerance	Mare et al. (2004)
	Oryza sativa	*OsWRKY11*	Increased heat and drought stress tolerance	Wu et al. (2009)
	Arabidopsis thaliana	*AtWRKY28*	Salinity tolerance via the upregulation of many downregulated genes	Babitha et al. (2013)
	Camellia sinensis	*CsWRKY2*	Increased cold and drought stress tolerance through the ABA pathway	Wang et al. (2016a, b)
	Chrysanthemum	*DgWRKY5*	Positive regulator of salinity tolerance	Liang et al. (2017)
	Triticum aestivum	*TaWRKY2*	Enhanced drought stress tolerance and promotes grain yield	Gao et al. (2018)

(continued)

Table 5.2 (continued)

TFs type/ subfamily	Plant name	Gene name	Effect on plant growth	References
bZIP	*Oryza sativa*	*OsABF2*	Positive regulator of salinity, drought, and oxidative stress tolerance through the ABA-dependent pathway	Hossain et al. (2010)
	Oryza sativa	*OsbZIP52/ RISBZ5*	A negative regulator in cold and drought stress responses	Liu et al. (2012)
	Vitis vinifera	*VvbZIP23*	Enhanced drought, salinity, and cold stress tolerance	Tak and Mhatre (2013)
	Oryza sativa	*OsbZIP71*	Enhanced drought and salinity stress tolerance through ABA-mediated pathway	Liu et al. (2014a)
	Solanum lycopersicum	*SlbZIP1*	Drought and salt stress tolerance based on the ABA-mediated pathway	Zhu et al. (2018)
	Oryza sativa	*OsbZIP62*	Positive regulator of drought stress tolerance based on ABA signaling pathway	Yang et al. (2019a)
LEA	*Oryza sativa*	*OsLEA3-1*	Increased drought stress tolerance	Xiao et al. (2007)
	Oryza sativa	*OsLEA3-2*	Positive regulator of different abiotic stresses mainly drought and salinity	Duan and Cai (2012)
	Zea mays	*Rab28*	Positive regulator of drought stress tolerance	Amara et al. (2013)

5.5 Regulation of Environmental Responses in Plants by Oxidative Stress

The growth of plants depends on the exposing environment. Due to the continuous fluctuating environment, these plants are open to a number of stress factors and other extreme meteorological conditions such as drought and floods, heat and frost waves, and others, which are mainly encouraged by climate change (Raza et al. 2019a; Walter et al. 2013). The dose-response connection is a property of the stress factor. These stress factors inflict the stress on plants from a specific intensity level of stress; according to classical stress theory, low doses of stress does not cause much damage to plants, but instead, they can stimulate metabolism and growth—a phenomenon called eustress (Poschenrieder et al. 2013).

Oxidative stress, which is mainly a disproportion between oxidizing (ROS) and reducing (antioxidants) factors, is a common property of all environmental stresses (Potters et al. 2010). ROS are produced by aerobic plant metabolism as a by-product. These ROS are either excited or reduced forms of oxygen. Various forms of ROS, for example, superoxide ($O^{\cdot -}_2$), hydrogen peroxide (H_2O_2), and hydroxyl radical

($HO^{\cdot}$), are obtained when atmospheric oxygen undergoes univalent reduction (Sgherri et al. 2018; Gill and Tuteja 2010).

Almost all environmental stresses are responsible for enhancing the rate of ROS. The most common processes observed are disruption of photosynthesis and reduction in stomatal conductance results in the making of ROS. Increase in photorespiration is due to the reduction in stomatal conductance which causes increases in 70% of H_2O_2. During a water shortage, excessive photorespiration causes stomata to close to reduce transpiration results in CO_2 deficiency which leads to limited photosynthesis (Sgherri et al. 2018; Dat et al. 2000; Noctor et al. 2002; Nayyar and Gupta 2006).

Oxidative stress can be induced by some stress factors directly, such as transition metals, e.g., iron and copper, that activate the Haber–Weiss pathway and elevate the production of $HO^{\cdot}$ (Bhattacharjee 2019; Ravet and Pilon 2013). In addition to metals, ozone can also induce ROS production directly which results in apoplast breakdown and formation of H_2O_2 and $HO^{\cdot}$. Further, metabolic changes cause a secondary oxidative burst, which further increases the synthesis of ROS (Fiscus et al. 2005). In addition, these metabolic abnormalities induce oxidative stress indirectly mainly by UV-B radiation (Hideg et al. 2013). Nevertheless, many researchers believe that UV-B has the ability to convert H_2O_2 to $HO^{\cdot}$, which directly leads to the damage of oxidative tissues (Czégény et al. 2014). Plants to avoid oxidative stress have evolved many approaches. Both enzymatic and non-enzymatic antioxidants are helpful to control ROS concentration, of which the two most important are superoxide dismutase (SOD) which catalyzes the production of H_2O_2 and catalase (CAT) which eliminates H_2O_2 in peroxisomes. The vital non-enzymatic antioxidants are tocopherols, ascorbate, glutathione (GSH), carotenoids, and flavonoids which have a significant part in ROS elimination and in repairing cell damage (Kacienė et al. 2015).

5.6 Phytohormones: Role in Plant Responses to Environmental Stresses

As it is evident, Ca^{2+}- and ROS-mediated plant responses to environmental stresses do not contribute much as the stress response mechanism is highly complex. Phytohormones have the ability to mitigate stress response because of the highly intricate link among plant hormones and their capability to regulate physiological functions (Verma et al. 2016). A group of nine different plant hormones mediates the production of highly efficient response, and their signaling pathways are interconnected to help in the plant's defense mechanism. The major phytohormones are auxins, gibberellin (GA), cytokinin (CK), abscisic acid (ABA), ethylene (ET) , salicylic acid (SA), jasmonate (JA), brassinosteroid (BRs), and strigolactones (STs) . For abiotic stresses and pathogens, ABA, SA, JA, and ethylene are recognized to have a significant role (Raza et al. 2019c; Nakashima and Yamaguchi-Shinozaki 2013). The levels of ABA are increased in abiotic stresses like salinity, drought, and low and high temperature (Raza et al. 2019c; Lata and Prasad 2011). Comparatively,

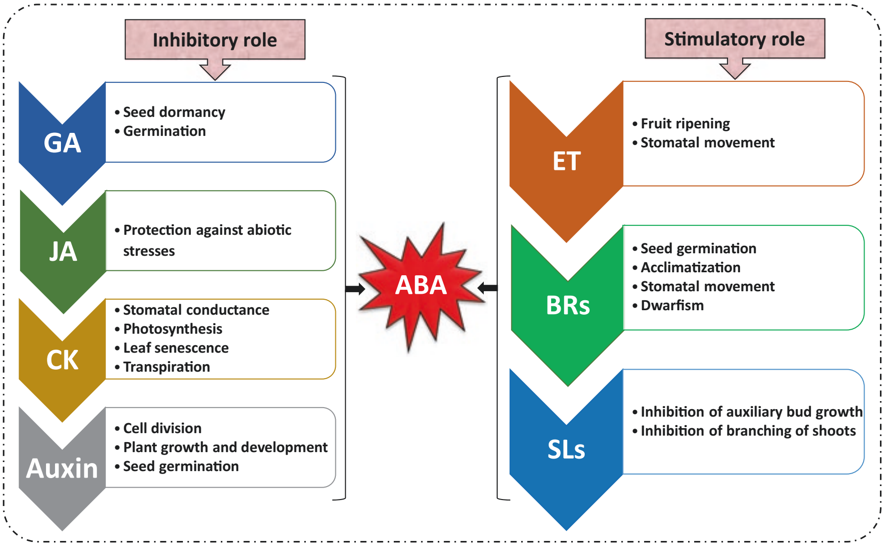

Fig. 5.2 Hormonal cross-talk related to different environmental stresses in the plant with a relation to ABA. Abbreviations are explained in the text. Modified from Raza et al. (2019a)

other hormones such as SA, JA, and ethylene have a key role in biotic stresses as well, and their levels increase with the pathogen infection (Bari and Jones 2009). The possible role of hormones related to different stresses in plants is described in Fig. 5.2. However, the stress response process is not only limited to these hormones. Recent research in plant hormones has provided considerable evidence for the cross talk of ABA, SA, JA, and ET with auxins, GA, and CK in regulating plant defense responses (Bari and Jones 2009; Raza et al. 2019c; Nishiyama et al. 2013).

5.7 Interaction of Plants with Other Organisms and Viruses in Stress Management

Microbes or microbial community plays a vital role to mitigate environmental constraints. The soil contains a pool of microbial population that comprises of bacteria, fungi, actinomycetes, protozoa, and algae. The maximum number of bacteria is found around the area of plant roots commonly called the rhizosphere, as compared to bulk soil. Bacteria can infect plants in three ways. Firstly, the bacteria may be harmful, beneficial, or neutral to plants. Secondly, plant growth-promoting bacteria (PGPB) includes both free-living and those that form symbiotic relationships with plants. Lastly, bacterial endophytes that colonize in plants interior and cyanobacteria make symbiotic relationship with fungi. The symbiotic relationship of PGPB with plants helps them to avoid environmental stresses and protects plants from dying. Over the past decade, bacteria belonging to the diverse genera have been stated to bestow host plants under

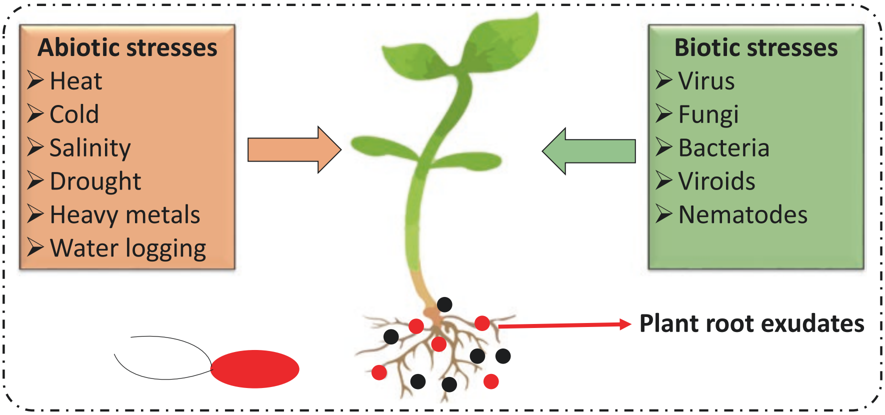

Fig. 5.3 Environmental stresses affecting plant–microbe interaction

different abiotic stress environments (Ho et al. 2017). Figure 5.3 shows the factors that affect the plant–microbe interaction during both abiotic and biotic stresses.

PGPB also help plants to combat biotic stresses in two different ways: directly by phytohormone production or by assisting the uptake of certain nutrients that promote plant growth or indirectly when PGPB minimizes or eliminates the harmful effects of pathogens. For example, the growth of phytopathogenic fungi is inhabited by 2,4-diacetyl phloroglucinol (DAPG) produced by *P. Fluorescens* (Voisard et al. 1994). The new approach to developing entomopathogenic bacteria has been in use to handle resistant pests. Several species are used as biological control of pests includes *Aschersonia*, *Agerata*, *Verticillium*, *Sphaerostilbe*, *Podonectria*, *Myriangium*, *Hirsutella*, *Metarhizium*, and *Bacillus thuringiensis*. *Brevibacillus laterosporus* is considered to be productive against insects like Coleoptera, Lepidoptera, nematodes, and phytopathogenic fungi (Boets et al. 2004; Saikia et al. 2011).

5.8 Usage of Bioinformatics Tools for Expression Analysis of Plant Transcriptome

Bioinformatics has been incorporated in different subjects of sciences, including plant breeding (Barh et al. 2013). Table 5.3 shows a list of bioinformatics tools for gene expression analysis based on statistical data analysis in plant breeding programs. The consistency and predictability of plant breeding programs, reduction in time, and the cost of stress-tolerant varieties are now possible with the help of OMICs tools (Van Emon 2015). These tools can enhance the nutritional content of food crops and maximize the agricultural production for food, feed, and energy (Davies 2010; Van Emon 2015). Transcriptomics, a subcategory of OMICs, appeals several scientists especially in plant breeding subjects (Shariatipour and Heidari 2017). It allows us to classify genes differentially present in diverse cell populations or in reaction to altered treatments. Microarray, a high-throughput technique, has

Table 5.3 A lists of bioinformatics tools for gene expression analysis

Tools	Link URL	References
MAExplorer	http://maexplorer.sourceforge.net/index.html	Lemkin et al. (1999)
GeneXPress	http://genexpress.stanford.edu/	Segal et al. (2004)
Onto-Tools	http://vortex.cs.wayne.edu/Projects.html	Khatri et al. (2004)
GenePattern	http://software.broadinstitute.org/cancer/software/genepattern/	Reich et al. (2006)
Partek Genomics Suite	https://www.partek.com/applications/	Downey (2006)
GEPAS	http://www.gepas.org	Tárraga et al. (2008)
RSEQtools	http://archive.gersteinlab.org/proj/rnaseq/rseqtools/	Habegger et al. (2010)
AltAnalyze	http://www.altanalyze.org/	Emig et al. (2010)
geWorkbench	http://wiki.c2b2.columbia.edu/workbench/index.php/Home	Floratos et al. (2010)
JMP Genomics	https://www.jmp.com/en_us/software/genomics-data-analysis-software.html	Segall et al. (2010)
IGV	http://software.broadinstitute.org/software/igv/	Robinson et al. (2011)
Chipster	https://chipster.csc.fi/index.shtml	Kallio et al. (2011)
S-Mart	https://urgi.versailles.inra.fr/Tools/S-Mart	Zytnicki and Quesneville (2011)
GeneProf	https://bio.tools/geneprof	Halbritter et al. (2012)
ArrayExpress	https://www.ebi.ac.uk/arrayexpress/	Kolesnikov et al. (2014)
GenoExp	https://bioinformaticshome.com/tools/descriptions/GenoExp.html	Manor and Segal (2015)
NetworkAnalyst	https://www.networkanalyst.ca/	Xia et al. (2015)
ExAtlas	https://lgsun.grc.nia.nih.gov/exatlas/	Sharov et al. (2015)
MSigDB	http://software.broadinstitute.org/gsea/msigdb	Liberzon et al. (2015)
TRUFA	https://trufa.ifca.es/web/	Kornobis et al. (2015)
TRAPLINE	https://usegalaxy.org/u/mwolfien/p/trapline%2D%2D-manual	Wolfien et al. (2016)
Expression Atlas	https://www.ebi.ac.uk/gxa/home	Papatheodorou et al. (2017)

the ability to measure gene expression and thereby produce functional data for numerous genes at once (Schulze and Downward 2001; Oktem et al. 2008). However, to overcome environmental distress and to improve plant varieties, it is crucial to investigate the role of bioinformatics.

5.9 Plant Evolution-Adaptive and Neutral Processes

The K-Pg dividing line is commonly linked with its related extinction events, which comprise the last five important mass extinction events in the Phanerozoic Eon (Rohde and Muller 2005). Several environmental issues, such as the rise in volcanism and global warming, were responsible for this mass extinction which leads to unfavorable conditions for the existence of the number of living organisms (Robertson et al. 2013).

In order to study the present-day challenges, the production of polyploids is being observed, which are often exposed to changing and unstable environment. In the Arctic, for example, there is an excess of latterly establishing polyploids. The adaptive and neutral processes have the ability to describe these phenomena and the consequences thereof for plant evolution. Both these processes help in the enhancement of polyploidy establishment under changing environment and distress conditions. An unreduced gamete formation might be increased by the adaptive processes in addition to other processes such as hybridization and extinction of the background diploid population. This is likely to lead to other polyploids being established even in the unavailability of any active adaptive benefit. On the other hand, transgressive segregation and genomic vulnerability of polyploids may lead toward the heterotic phenotypes, enhanced phenotypic irregularity, and plasticity. If it is considered useful, then it might be quickly selected under the changing environmental conditions, which is likely to lead to more polyploids being established even in the lake of enhanced polyploid formation (Vanneste et al. 2014). It is imperative that the environment plays a crucial role in polyploid formation regardless of which process contributes more as described in Fig. 5.4.

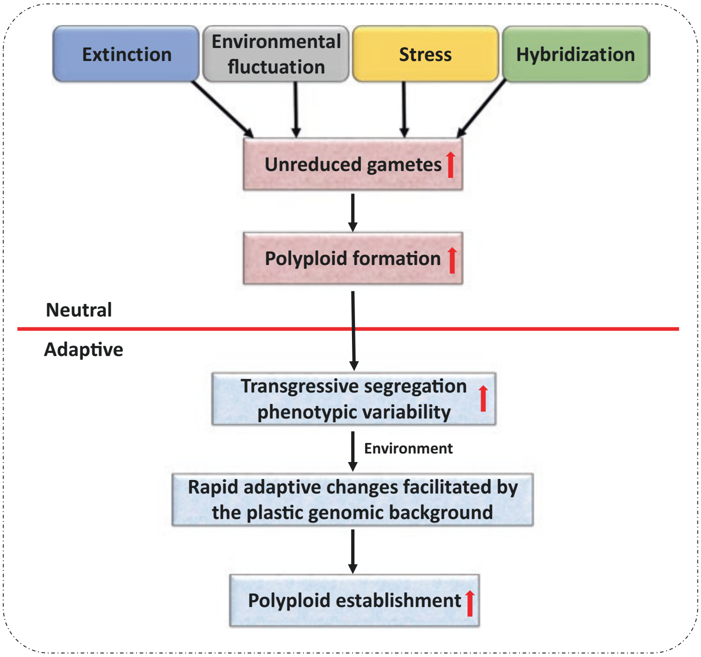

Fig. 5.4 Systematic diagram of neutral and adaptive action likely involved in the enhancement of polyploid formation under different environmental stresses and/or fluctuations

5.10 Conclusion and Future Perspectives

Environmental stresses are responsible for reversible and irreversible changes in the plants. These changes can be biochemical, physiological, and genomic types, including at transcriptional and posttranscriptional levels. Climate change is the major reason for the environmental distress and is responsible for increasing drought and salinity and low and high temperature. These changes minimize the plant plasticity for development and agricultural productivity. However, it has been reported that the world population projected to reach 9.8 billion in 2050, and 11.2 billion in 2100 (United Nation 2017). To overcome the food demands in coming years, it is very important to generate climate-resiliet plants. Plant biotechnology played a vital role in the establishment of stress-resistant plant varieties. However, care should be taken in creating transgenic varieties to introduce genes that have the ability to tolerate interactive stress factors, precisely at the entire plant level. Currently, there is less understanding of plant responses to harsh climate conditions in several experiments related to molecular changes. A more holistic approach is needed which requires data from several biological kinds of research to study individual and multiple stress conditions. Nevertheless, the integration of OMICS approaches could help us to identify stress related genes and regulators, which ultimately leads towards the manipulation of candidate genes for the development of climate-resilient plants. Additionally, a powerful genome editing tool such as CRISPR/Cas system together with conventional and modern breeding technologies should be utilize to cope with environmental stresses and to secure the world food security for sustainable agriculture.

References

Agarwal PK, Gupta K, Lopato S, Agarwal P (2017) Dehydration responsive element binding transcription factors and their applications for the engineering of stress tolerance. J Exp Bot 68:2135–2148

Ahuja I, de Vos RC, Bones AM, Hall RD (2010) Plant molecular stress responses face climate change. Trends Plant Sci 15:664–674

Alshareef NO, Wang JY, Ali S, Al-Babili S, Tester M, Schmöckel SM (2019) Overexpression of the NAC transcription factor JUNGBRUNNEN1 (JUB1) increases salinity tolerance in tomato. Plant Physiol Biochem 140:113–121

Amara I, Capellades M, Ludevid MD, Pagès M, Goday A (2013) Enhanced water stress tolerance of transgenic maize plants over-expressing LEA Rab28 gene. J Plant Physiol 170:864–873

Ashraf M, Foolad M (2007) Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environ Exp Bot 59:206–216

Ashraf M, Harris P (2013) Photosynthesis under stressful environments: an overview. Photosynthetica 51:163–190

Atkinson NJ, Urwin PE (2012) The interaction of plant biotic and abiotic stresses: from genes to the field. J Exp Bot 63:3523–3543

Babitha K, Ramu S, Pruthvi V, Mahesh P, Nataraja KN, Udayakumar M (2013) Co-expression of *AtbHLH17* and *AtWRKY28* confers resistance to abiotic stress in *Arabidopsis*. Transgenic Res 22:327–341

Baligar VC, Fageria NK (2015) Nutrient use efficiency in plants: an overview. In: Nutrient use efficiency: from basics to advances. Springer, New Delhi, pp 1–14

Barh D, Zambare V, Azevedo V (2013) Omics: applications in biomedical, agricultural, and environmental sciences. CRC Press, Boca Raton. https://doi.org/10.1201/b14289

Bari R, Jones JD (2009) Role of plant hormones in plant defence responses. Plant Mol Biol 69:473–488

Bass C, Field LM (2011) Gene amplification and insecticide resistance. Pest Manag Sci 67:886–890

Bhargava S, Sawant K (2013) Drought stress adaptation: metabolic adjustment and regulation of gene expression. Plant Breed 132:21–32

Bhattacharjee S (2019) ROS and oxidative stress: origin and implication. In: Reactive oxygen species in plant biology. Springer, New Delhi, pp 1–31

Bishop KA, Betzelberger AM, Long SP, Ainsworth EA (2015) Is there potential to adapt soybean (Glycine max M err.) to future [CO_2]? An analysis of the yield response of 18 genotypes in free-air CO_2 enrichment. Plant Cell Environ 38:1765–1774

Boets A, Arnaut G, Van Rie J, Damme N (2004) Toxins. U.S. Patent No. 6,706,860, U.S. Patent and Trademark Office, Washington, DC

Borgohain P, Saha B, Agrahari R, Chowardhara B, Sahoo S, van der Vyver C, Panda SK (2019) *SlNAC2* overexpression in *Arabidopsis* results in enhanced abiotic stress tolerance with alteration in glutathione metabolism. Protoplasma 256:1065–1077

Bray E, Bailey-Serres J, Weretilnyk E (2000) Biochemistry and molecular biology of plants. Am Soc Plant Physiol, Rockville, pp 1158–1203

Butt HI et al (2017) *GaMYB85*, an R2R3 MYB gene, in transgenic Arabidopsis plays an important role in drought tolerance. BMC Plant Biol 17:142

Byun MY et al (2015) Constitutive expression of *DaCBF7*, an Antarctic vascular plant Deschampsia antarctica CBF homolog, resulted in improved cold tolerance in transgenic rice plants. Plant Sci 236:61–74

Canales J, Moyano TC, Villarroel E, Gutiérrez RA (2014) Systems analysis of transcriptome data provides new hypotheses about *Arabidopsis* root response to nitrate treatments. Front Plant Sci 5:22

Cao Z-H, Zhang S-Z, Wang R-K, Zhang R-F, Hao Y-J (2013) Genome wide analysis of the apple MYB transcription factor family allows the identification of *MdoMYB121* gene confering abiotic stress tolerance in plants. PLoS One 8:e69955

Chen Y, Huang L, Yan H, Zhang X, Xu B, Ma X (2016) Cloning and characterization of an ABA-independent DREB transcription factor gene, *HcDREB2*, in Hemarthria compressa. Hereditas 153:3

Cheng Z, Targolli J, Huang X, Wu R (2002) Wheat LEA genes, PMA80 and PMA1959, enhance dehydration tolerance of transgenic rice (*Oryza sativa* L.). Mol Breed 10:71–82

Cheng L, Yang J, Yin L, Hui L, Qian H, Li S-Y, Li L-J (2017) Transcription factor *NnDREB1* from lotus improved drought tolerance in transgenic *Arabidopsis thaliana*. Biol Plant 61:651–658

Chu X et al (2015) The cotton WRKY gene *GhWRKY41* positively regulates salt and drought stress tolerance in transgenic *Nicotiana benthamiana*. PLoS One 10:e0143022

Coolen S, Proietti S, Hickman R, Davila Olivas NH, Huang PP, Van Verk MC, Van Pelt JA, Wittenberg AH, De Vos M, Prins M, Van Loon JJ (2016) Transcriptome dynamics of Arabidopsis during sequential biotic and abiotic stresses. Plant J 86:249–267

Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K (2011) Effects of abiotic stress on plants: a systems biology perspective. BMC Plant Biol 11:163. https://doi.org/10.1186/1471-2229-11-163

Czégény G, Wu M, Dér A, Eriksson LA, Strid Å, Hideg É (2014) Hydrogen peroxide contributes to the ultraviolet-B (280–315 nm) induced oxidative stress of plant leaves through multiple pathways. FEBS Lett 588:2255–2261

Dai X, Xu Y, Ma Q, Xu W, Wang T, Xue Y, Chong K (2007) Overexpression of an R1R2R3 MYB gene, *OsMYB3R-2*, increases tolerance to freezing, drought, and salt stress in transgenic Arabidopsis. Plant Physiol 143:1739–1751

Dat J, Vandenabeele S, Vranová E, Van Montagu M, Inzé D, Van Breusegem F (2000) Dual action of the active oxygen species during plant stress responses. Cell Mol Life Sci 57:779–795

Davies H (2010) A role for "omics" technologies in food safety assessment. Food Control 21:1601–1610

Downey T (2006) Analysis of a multifactor microarray study using Partek genomics solution. Methods Enzymol 411:256–270

Duan J, Cai W (2012) *OsLEA3-2*, an abiotic stress induced gene of rice plays a key role in salt and drought tolerance. PLoS One 7:e45117

Emig D, Salomonis N, Baumbach J, Lengauer T, Conklin BR, Albrecht M (2010) AltAnalyze and DomainGraph: analyzing and visualizing exon expression data. Nucleic Acids Res 38:W755–W762

Fiscus EL, Booker FL, Burkey KO (2005) Crop responses to ozone: uptake, modes of action, carbon assimilation and partitioning. Plant Cell Environ 28:997–1011

Floratos A, Smith K, Ji Z, Watkinson J, Califano A (2010) geWorkbench: an open source platform for integrative genomics. Bioinformatics 26:1779–1780

Flowers TJ, Colmer TD (2008) Salinity tolerance in halophytes. New Phytol 179:945–963

Gao F et al (2017) Overexpression of a tartary buckwheat R2R3-MYB transcription factor gene, *FtMYB9*, enhances tolerance to drought and salt stresses in transgenic Arabidopsis. J Plant Physiol 214:81–90

Gao H, Wang Y, Xu P, Zhang Z (2018) Overexpression of a WRKY transcription factor *TaWRKY2* enhances drought stress tolerance in transgenic wheat. Front Plant Sci 9:997

Gargallo-Garriga A et al (2014) Opposite metabolic responses of shoots and roots to drought. Sci Rep 4:6829

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 48:909–930

Gilliham M, Able JA, Roy SJ (2017) Translating knowledge about abiotic stress tolerance to breeding programmes. Plant J 90:898–917

Glick BR (2003) Phytoremediation: synergistic use of plants and bacteria to clean up the environment. Biotechnol Adv 21:383–393

Golldack D, Lüking I, Yang O (2011) Plant tolerance to drought and salinity: stress regulating transcription factors and their functional significance in the cellular transcriptional network. Plant Cell Rep 30:1383–1391

Gray SB et al (2016) Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean. Nat Plants 2:16132

Gu L, Ma Q, Zhang C, Wang C, Wei H, Wang H, Yu S (2019) The cotton *GhWRKY91* transcription factor mediates leaf senescence and responses to drought stress in transgenic *Arabidopsis thaliana*. Front Plant Sci 10:1352

Gunapati S et al (2016) Expression of *GhNAC2* from *G. herbaceum*, improves root growth and imparts tolerance to drought in transgenic cotton and Arabidopsis. Sci Rep 6:24978

Guo H et al (2017a) Expression of the MYB transcription factor gene *BplMYB46* affects abiotic stress tolerance and secondary cell wall deposition in *Betula platyphylla*. Plant Biotechnol J 15:107–121

Guo X, Zhang L, Zhu J, Wang A, Liu H (2017b) Christolea crassifolia HARDY gene enhances drought stress tolerance in transgenic tomato plants. Plant Cell Tissue Org Cult 129:469–481

Gupta SM, Pandey P, Negi P, Pande V, Grover A, Patade VY, Ahmed Z (2013) DRE-binding transcription factor gene (LlaDREB1b) is regulated by various abiotic stresses in *Lepidium latifolium* L. Mol Biol Rep 40:2573–2580

Habegger L, Sboner A, Gianoulis TA, Rozowsky J, Agarwal A, Snyder M, Gerstein M (2010) RSEQtools: a modular framework to analyze RNA-Seq data using compact, anonymized data summaries. Bioinformatics 27:281–283

Halbritter F, Vaidya HJ, Tomlinson SR (2012) GeneProf: analysis of high-throughput sequencing experiments. Nat Methods 9:7

Hammond-Kosack K (2000) Responses to plant pathogens. In: Biochemistry and molecular biology of plants. American Society of Plant Physiologists, Rockville, MD, pp 1102–1109

Hartmann DL, Klein Tank AMG, Rusticucci M, Alexander L, Brönnimann S, Charabi Y, Dentener F, Dlugokencky E, Easterling D, Kaplan A, Soden B, Thorne P, Wild M, Zhai PM (2013) Observations: atmosphere and surface supplementary material. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. www.climatechange2013.org; www.ipcc.ch

Hatfield JL, Boote KJ, Kimball BA, Ziska LH, Izaurralde RC, Ort D, Thomson AM, Wolfe D (2011) Climate impacts on agriculture: implications for crop production. Agron J 103:351–370

Hideg É, Jansen MA, Strid Å (2013) UV-B exposure, ROS, and stress: inseparable companions or loosely linked associates? Trends Plant Sci 18:107–115

Ho Y-N, Mathew DC, Huang C-C (2017) Plant-microbe ecology: interactions of plants and symbiotic microbial communities. In: Plant ecology-traditional approaches to recent trends. InTech, Rijeka, pp 93–119

Hossain MA, Cho J-I, Han M, Ahn C-H, Jeon J-S, An G, Park PB (2010) The ABRE-binding bZIP transcription factor *OsABF2* is a positive regulator of abiotic stress and ABA signaling in rice. J Plant Physiol 167:1512–1520

Huang G-T et al (2012) Signal transduction during cold, salt, and drought stresses in plants. Mol Biol Rep 39:969–987

Jaiwal PK, Singh RP (2003) Improvement strategies of leguminosae biotechnology. Springer Science & Business Media

Jiang M, Ye Z-H, Zhang H-J, Miao L-X (2019) Broccoli plants over-expressing an ERF transcription factor gene *BoERF1* facilitates both salt stress and sclerotinia stem rot resistance. J Plant Growth Regul 38:1–13

Jisha V, Dampanaboina L, Vadassery J, Mithöfer A, Kappara S, Ramanan R (2015) Overexpression of an AP2/ERF type transcription factor *OsEREBP1* confers biotic and abiotic stress tolerance in rice. PLoS One 10:e0127831

John R, Anjum N, Sopory S, Akram N, Ashraf M (2016) Some key physiological and molecular processes of cold acclimation. Biol Plant 60:603–618

Kacienė G, Žaltauskaitė J, Milčė E, Juknys R (2015) Role of oxidative stress on growth responses of spring barley exposed to different environmental stressors. J Plant Ecol 8:605–616

Kallio MA et al (2011) Chipster: user-friendly analysis software for microarray and other high-throughput data. BMC Genomics 12:507

Kang C, Zhai H, He S, Zhao N, Liu Q (2019) A novel sweetpotato bZIP transcription factor gene, *IbbZIP1*, is involved in salt and drought tolerance in transgenic Arabidopsis. Plant Cell Rep 38:1373–1382. https://doi.org/10.1007/s00299-019-02441-x

Khatri P, Bhavsar P, Bawa G, Draghici S (2004) Onto-Tools: an ensemble of web-accessible, ontology-based tools for the functional design and interpretation of high-throughput gene expression experiments. Nucleic Acids Res 32:W449–W456

Kim H-S, Lee JH, Kim JJ, Kim C-H, Jun S-S, Hong Y-N (2005) Molecular and functional characterization of CaLEA6, the gene for a hydrophobic LEA protein from *Capsicum annuum*. Gene 344:115–123

Kiranmai K et al (2018) A novel WRKY transcription factor, *MuWRKY3* (Macrotyloma uniflorum lam. Verdc.) enhances drought stress tolerance in transgenic groundnut (*Arachis hypogaea* L.) plants. Front Plant Sci 9:346

Kolesnikov N et al (2014) ArrayExpress update—simplifying data submissions. Nucleic Acids Res 43:D1113–D1116

Kornobis E, Cabellos L, Aguilar F, Frías-López C, Rozas J, Marco J, Zardoya R (2015) TRUFA: a user-friendly web server for de novo RNA-seq analysis using cluster computing. Evol Bioinform Online 11:97–104. https://doi.org/10.4137/EBO.S23873

Kotak S, Larkindale J, Lee U, von Koskull-Döring P, Vierling E, Scharf K-D (2007) Complexity of the heat stress response in plants. Curr Opin Plant Biol 10:310–316

Lata C, Prasad M (2011) Role of DREBs in regulation of abiotic stress responses in plants. J Exp Bot 62:4731–4748

Lemkin P, Thornwall G, Wagner U, Henninghausen L (1999) MAExplorer–microarray exploratory data analysis. Nat Genet 23:57–57

Li Y, Sun Y, Yang Q, Fang F, Kang J, Zhang T (2013) Isolation and characterization of a gene from *Medicago sativa* L., encoding a bZIP transcription factor. Mol Biol Rep 40:1227–1239

Li Y, Zhang H, Zhang Q, Liu Q, Zhai H, Zhao N, He S (2019) An AP2/ERF gene, *IbRAP2-12*, from sweetpotato is involved in salt and drought tolerance in transgenic Arabidopsis. Plant Sci 281:19–30

Liang Q-Y et al (2017) Chrysanthemum WRKY gene *DgWRKY5* enhances tolerance to salt stress in transgenic chrysanthemum. Sci Rep 7:4799

Liao Y, Zhang JS, Chen SY, Zhang WK (2008) Role of soybean *GmbZIP132* under abscisic acid and salt stresses. J Integr Plant Biol 50:221–230

Liberzon A, Birger C, Thorvaldsdóttir H, Ghandi M, Mesirov JP, Tamayo P (2015) The molecular signatures database hallmark gene set collection. Cell Syst 1:417–425

Liu C, Wu Y, Wang X (2012) bZIP transcription factor *OsbZIP52/RISBZ5*: a potential negative regulator of cold and drought stress response in rice. Planta 235:1157–1169

Liu C et al (2014a) *OsbZIP71*, a bZIP transcription factor, confers salinity and drought tolerance in rice. Plant Mol Biol 84:19–36

Liu J-G, Qu P, Zhang W, Dong Y, Li L, Wang M-X (2014b) Variations among rice cultivars in subcellular distribution of Cd: the relationship between translocation and grain accumulation. Environ Exp Bot 107:25–31

Liu X, Song Y, Xing F, Wang N, Wen F, Zhu C (2016) *GhWRKY25*, a group I WRKY gene from cotton, confers differential tolerance to abiotic and biotic stresses in transgenic *Nicotiana benthamiana*. Protoplasma 253:1265–1281

Liu H, Zhou Y, Li H, Wang T, Zhang J, Ouyang B, Ye Z (2018) Molecular and functional characterization of *ShNAC1*, an NAC transcription factor from *Solanum habrochaites*. Plant Sci 271:9–19

Liu J, Chu J, Ma C, Jiang Y, Ma Y, Xiong J, Cheng Z-M (2019) Overexpression of an ABA-dependent grapevine bZIP transcription factor, *VvABF2*, enhances osmotic stress in Arabidopsis. Plant Cell Rep 38:587–596

Ma L-F, Li Y, Chen Y, Li X-B (2016) Improved drought and salt tolerance of *Arabidopsis thaliana* by ectopic expression of a cotton (*Gossypium hirsutum*) CBF gene. Plant Cell Tissue Org Cult 124:583–598

Madhu M, Hatfield J (2013) Dynamics of plant root growth under increased atmospheric carbon dioxide. Agron J 105:657–669

Mahmood Q, Bilal M, Jan S (2014) Herbicides, pesticides, and plant tolerance: an overview. In: Emerging technologies and management of crop stress tolerance, vol 1. Elsevier, pp 423–448

Manor O, Segal E (2015) GenoExp: a web tool for predicting gene expression levels from single nucleotide polymorphisms. Bioinformatics 31:1848–1850

Mao X, Chen S, Li A, Zhai C, Jing R (2014) Novel NAC transcription factor *TaNAC67* confers enhanced multi-abiotic stress tolerances in Arabidopsis. PLoS One 9:e84359

Mao H, Yu L, Han R, Li Z, Liu H (2016) *ZmNAC55*, a maize stress-responsive NAC transcription factor, confers drought resistance in transgenic Arabidopsis. Plant Physiol Biochem 105:55–66

Mare C, Mazzucotelli E, Crosatti C, Francia E, Cattivelli L (2004) *Hv-WRKY38*: a new transcription factor involved in cold-and drought-response in barley. Plant Mol Biol 55:399–416

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao Z-C (2007) Global climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 747–845

Meng C, Cai C, Zhang T, Guo W (2009) Characterization of six novel NAC genes and their responses to abiotic stresses in *Gossypium hirsutum* L. Plant Sci 176:352–359

Mittler R, Finka A, Goloubinoff P (2012) How do plants feel the heat? Trends Biochem Sci 37:118–125

Mizoi J, Ohori T, Moriwaki T, Kidokoro S, Todaka D, Maruyama K, Kusakabe K, Osakabe Y, Shinozaki K, Yamaguchi-Shinozaki K (2013) GmDREB2A; 2, a canonical DEHYDRATION-RESPONSIVE ELEMENT-BINDING PROTEIN2-type transcription factor in soybean, is posttranslationally regulated and mediates dehydration-responsive element-dependent gene expression. Plant Physiol 161:346–361

Mzid R et al (2018) The grapevine *VvWRKY2* gene enhances salt and osmotic stress tolerance in transgenic *Nicotiana tabacum*. 3 Biotech 8:277

Nakashima K, Yamaguchi-Shinozaki K (2013) ABA signaling in stress-response and seed development. Plant Cell Rep 32:959–970

Nayyar H, Gupta D (2006) Differential sensitivity of C3 and C4 plants to water deficit stress: association with oxidative stress and antioxidants. Environ Exp Bot 58:106–113

Newton AC, Johnson SN, Gregory PJ (2011) Implications of climate change for diseases, crop yields and food security. Euphytica 179:3–18

Newton AC, Bootman MD, Scott JD (2016) Second messengers. CSH Perspect Biol 8:a005926

Nie J et al (2018) The AP2/ERF transcription factor *CmERF053* of chrysanthemum positively regulates shoot branching, lateral root, and drought tolerance. Plant Cell Rep 37:1049–1060

Nishiyama R et al (2013) Arabidopsis AHP2, AHP3, and AHP5 histidine phosphotransfer proteins function as redundant negative regulators of drought stress response. Proc Natl Acad Sci U S A 110:4840–4845

Noctor G, Veljovic-Jovanovic S, Driscoll S, Novitskaya L, Foyer CH (2002) Drought and oxidative load in the leaves of C3 plants: a predominant role for photorespiration? Ann Bot 89:841–850

Oktem HA, Eyidogan F, Selçuk F, Oz MT, Teixeira da Silva JA, Yucel M (2008) Revealing response of plants to biotic and abiotic stresses with microarray technology. Genes Genomes Genomics 2:14–48

Pandey AS, Sharma E, Jain N, Singh B, Burman N, Khurana JP (2018) A rice bZIP transcription factor, *OsbZIP16*, regulates abiotic stress tolerance when over-expressed in Arabidopsis. J Plant Biochem Biotechnol 27:393–400

Papatheodorou I et al (2017) Expression Atlas: gene and protein expression across multiple studies and organisms. Nucleic Acids Res 46:D246–D251

Park B-J, Liu Z, Kanno A, Kameya T (2005) Genetic improvement of Chinese cabbage for salt and drought tolerance by constitutive expression of a *B. napus* LEA gene. Plant Sci 169:553–558

Park H-Y et al (2011a) *AtERF71/HRE2* transcription factor mediates osmotic stress response as well as hypoxia response in Arabidopsis. Biochem Biophys Res Commun 414:135–141

Park S-C, Kim Y-H, Jeong JC, Kim CY, Lee H-S, Bang J-W, Kwak S-S (2011b) Sweetpotato late embryogenesis abundant 14 (IbLEA14) gene influences lignification and increases osmotic- and salt stress-tolerance of transgenic calli. Planta 233:621–634

Pérez-Clemente RM, Vives V, Zandalinas SI, López-Climent MF, Muñoz V, Gómez-Cadenas A (2013) Biotechnological approaches to study plant responses to stress. BioMed Res Int 2013:654120

Poschenrieder C, Cabot C, Martos S, Gallego B, Barceló J (2013) Do toxic ions induce hormesis in plants? Plant Sci 212:15–25

Potters G, Horemans N, Jansen MA (2010) The cellular redox state in plant stress biology—a charging concept. Plant Physiol Biochem 48:292–300

Qi X-N, Xiao Y-Y, Fan Z-Q, Chen J-Y, Lu W-J, Kuang J-F (2016) A banana fruit transcriptional repressor *MaERF10* interacts with MaJAZ3 to strengthen the repression of JA biosynthetic genes involved in MeJA-mediated cold tolerance. Postharvest Biol Technol 120:222–231

Qin Y, Tian Y, Liu X (2015) A wheat salinity-induced WRKY transcription factor *TaWRKY93* confers multiple abiotic stress tolerance in *Arabidopsis thaliana*. Biochem Biophys Res Commun 464:428–433

Rainbird B, Bentham RH, Soole KL (2018) Rhizoremediation of residual sulfonylurea herbicides in agricultural soils using Lens culinaris and a commercial supplement. Int J Phytoremediation 20:104–113

Ramegowda V, Senthil-Kumar M, Nataraja KN, Reddy MK, Mysore KS, Udayakumar M (2012) Expression of a finger millet transcription factor, *EcNAC1*, in tobacco confers abiotic stress-tolerance. PLoS One 7:e40397

Ravet K, Pilon M (2013) Copper and iron homeostasis in plants: the challenges of oxidative stress. Antioxid Redox Signal 19:919–932

Rayapuram N, Bigeard J, Alhoraibi H, Bonhomme L, Hesse AM, Vinh J, Hirt H, Pflieger D (2018) Quantitative phosphoproteomic analysis reveals shared and specific targets of Arabidopsis mitogen-activated protein kinases (MAPKs) MPK3, MPK4, and MPK6. Mol Cell Proteomics 17:61–80

Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, Xu J (2019a) Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. Plants 8:34

Raza A, Mehmood SS, Shah T, Zou X, Yan L, Zhang X, Khan RS (2019b) Applications of molecular markers to develop resistance against abiotic stresses in wheat. In: Wheat production in changing environments. Springer, Singapore, pp 393–420

Raza A, Mehmood SS, Tabassum J, Batool R (2019c) Targeting plant hormones to develop abiotic stress resistance in wheat. In: Wheat production in changing environments. Springer, Singapore, pp 557–577

Razzaq A, Sadia B, Raza A, Khalid Hameed M, Saleem F (2019) Metabolomics: a way forward for crop improvement. Meta 9:303

Reich PB, Hobbie SE, Lee TD (2014) Plant growth enhancement by elevated CO_2 eliminated by joint water and nitrogen limitation. Nat Geosci 7:920

Reich M, Liefeld T, Gould J, Lerner J, Tamayo P, Mesirov JP (2006) Gene pattern 2.0. Nat Genet 38:500–501

Robertson DS, Lewis WM, Sheehan PM, Toon OB (2013) K-Pg extinction: reevaluation of the heat-fire hypothesis. J Geophys Res Biogeosci 118:329–336

Robinson JT, Thorvaldsdóttir H, Winckler W, Guttman M, Lander ES, Getz G, Mesirov JP (2011) Integrative genomics viewer. Nat Biotechnol 29:24–26

Rohde RA, Muller RA (2005) Cycles in fossil diversity. Nature 434:208–210

Ruiz-Vera UM, Siebers MH, Drag DW, Ort DR, Bernacchi CJ (2015) Canopy warming caused photosynthetic acclimation and reduced seed yield in maize grown at ambient and elevated [CO_2]. Glob Chang Biol 21:4237–4249

Ruiz-Vera UM, Siebers MH, Jaiswal D, Ort DR, Bernacchi CJ (2018) Canopy warming accelerates development in soybean and maize, offsetting the delay in soybean reproductive development by elevated CO_2 concentrations. Plant Cell Environ 41:2806–2820

Sage RF, Way DA, Kubien DS (2008) Rubisco, Rubisco activase, and global climate change. J Exp Bot 59:1581–1595

Saikia R, Gogoi D, Mazumder S, Yadav A, Sarma R, Bora T, Gogoi B (2011) Brevibacillus laterosporus strain BPM3, a potential biocontrol agent isolated from a natural hot water spring of Assam, India. Microbiol Res 166:216–225

Salim N, Raza A (2020) Nutrient use efficiency (NUE) for sustainable wheat production: a review. J Plant Nutr 43:297–315

Schulze A, Downward J (2001) Navigating gene expression using microarrays—a technology review. Nat Cell Biol 3:E190

Segal E, Yelensky R, Kaushal A, Pham T, Regev A, Koller D, Friedman N (2004) GeneXPress: a visualization and statistical analysis tool for gene expression and sequence data. In: Proceedings of the 11th international conference on intelligent systems for molecular biology (ISMB)

Segall RS, Zhang Q, Pierce R (2010) Data mining supercomputing with SAS JMP® genomics. In: Proceedings of 14th world multi-conference on systemics, cybernetics and informatics: WMSCI

Seo JS et al (2012) Expression of the Arabidopsis *AtMYB44* gene confers drought/salt-stress tolerance in transgenic soybean. Mol Breed 29:601–608

Sergeant K, Kieffer P, Dommes J, Hausman J-F, Renaut J (2014) Proteomic changes in leaves of poplar exposed to both cadmium and low-temperature. Environ Exp Bot 106:112–123

Sgherri C, Pinzino C, Quartacci MF (2018) Reactive oxygen species and photosynthetic functioning: past and present. In: Reactive oxygen species in plants: boon or bane—revisiting the role of ROS. Wiley, Chichester, pp 137–155

Shao H-B, Chu L-Y, Jaleel CA, Zhao C-X (2008) Water-deficit stress-induced anatomical changes in higher plants. C R Biol 331:215–225

Shariatipour N, Heidari B (2017) Application of bioinformatics in plant breeding programmes. BAOJ Bioinform 1:1–10

Sharov AA, Schlessinger D, Ko MS (2015) ExAtlas: an interactive online tool for meta-analysis of gene expression data. J Bioinform Comput Biol 13:1550019

Shen J, Lv B, Luo L, He J, Mao C, Xi D, Ming F (2017) The NAC-type transcription factor *OsNAC2* regulates ABA-dependent genes and abiotic stress tolerance in rice. Sci Rep 7:40641

Simeunovic A, Mair A, Wurzinger B, Teige M (2016) Know where your clients are: subcellular localization and targets of calcium-dependent protein kinases. J Exp Bot 67:3855–3872

Simontacchi M, Galatro A, Ramos-Artuso F, Santa-María GE (2015) Plant survival in a changing environment: the role of nitric oxide in plant responses to abiotic stress. Front Plant Sci 6:977

Singh M, Kumar J, Singh S, Singh VP, Prasad SM (2015) Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. Rev Environ Sci Biotechnol 14:407–426

Sperling O, Lazarovitch N, Schwartz A, Shapira O (2014) Effects of high salinity irrigation on growth, gas-exchange, and photoprotection in date palms (*Phoenix dactylifera* L., cv. Medjool). Environ Exp Bot 99:100–109

Tak H, Mhatre M (2013) Cloning and molecular characterization of a putative bZIP transcription factor *VvbZIP23* from Vitis vinifera. Protoplasma 250:333–345

Takasaki H et al (2010) The abiotic stress-responsive NAC-type transcription factor *OsNAC5* regulates stress-inducible genes and stress tolerance in rice. Mol Gen Genomics 284:173–183

Takeda S, Matsuoka M (2008) Genetic approaches to crop improvement: responding to environmental and population changes. Nat Rev Genet 9:444–457

Tang Y et al (2017) *JcDREB2*, a physic nut AP2/ERF gene, alters plant growth and salinity stress responses in transgenic rice. Front Plant Sci 8:306

Tang Y et al (2019) Overexpression of a MYB family gene, *OsMYB6*, increases drought and salinity stress tolerance in transgenic rice. Front Plant Sci 10:168

Tárraga J et al (2008) GEPAS, a web-based tool for microarray data analysis and interpretation. Nucleic Acids Res 36:W308–W314

Tu M, Wang X, Huang L, Guo R, Zhang H, Cai J, Wang X (2016) Expression of a grape bZIP transcription factor, *VqbZIP39*, in transgenic Arabidopsis thaliana confers tolerance of multiple abiotic stresses. Plant Cell Tissue Org Cult 125:537–551

Ullah A, Sun H, Yang X, Zhang X (2018) A novel cotton WRKY gene, *GhWRKY6-like*, improves salt tolerance by activating the ABA signaling pathway and scavenging of reactive oxygen species. Physiol Plant 162:439–454

Umezawa T, Fujita M, Fujita Y, Yamaguchi-Shinozaki K, Shinozaki K (2006) Engineering drought tolerance in plants: discovering and tailoring genes to unlock the future. Curr Opin Biotechnol 17:113–122

United Nation (2017) World population projected to reach 9.8 billion in 2050 and 11.2 billion in 2100. 01, 2017, [online] Available https://www.un.org/development/desa/en/news/population/world-population-prospects-2017.html

User I (2013) Biochemical studies on the effects of zinc and lead on oxidative stress, antioxidant enzymes and lipid peroxidation in okra (*Hibiscus esculentus* cv. Hassawi). Sci Int 1:29–38

Van Emon JM (2015) The omics revolution in agricultural research. J Agric Food Chem 64:36–44

Vanneste K, Maere S, Van de Peer Y (2014) Tangled up in two: a burst of genome duplications at the end of the Cretaceous and the consequences for plant evolution. Philos Trans R Soc Lond B Biol Sci 369:20130353

Varoquaux N, Cole B, Gao C, Pierroz G, Baker CR, Patel D, Madera M, Jeffers T, Hollingsworth J, Sievert J, Yoshinaga Y (2019) Transcriptomic analysis of field-droughted sorghum from seedling to maturity reveals biotic and metabolic responses. Proc Natl Acad Sci 116:27124–27132

Verma V, Ravindran P, Kumar PP (2016) Plant hormone-mediated regulation of stress responses. BMC Plant Biol 16:86

Voisard C et al (1994) Biocontrol of root diseases by Pseudomonas fluorescens CHA0: current concepts and experimental approaches. In: Molecular ecology of rhizosphere microorganisms: biotechnology and the release of GMOs. Wiley, pp 67–89

Walter J, Jentsch A, Beierkuhnlein C, Kreyling J (2013) Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. Environ Exp Bot 94:3–8

Wan L et al (2014) Identification of ERF genes in peanuts and functional analysis of *AhERF008* and *AhERF019* in abiotic stress response. Funct Integr Genomics 14:467–477

Wang Y, Jiang J, Zhao X, Liu G, Yang C, Zhan L (2006) A novel LEA gene from *Tamarix androssowii* confers drought tolerance in transgenic tobacco. Plant Sci 171:655–662

Wang Q, Guan Y, Wu Y, Chen H, Chen F, Chu C (2008) Overexpression of a rice *OsDREB1F* gene increases salt, drought, and low temperature tolerance in both Arabidopsis and rice. Plant Mol Biol 67:589–602

Wang L, Li X, Chen S, Liu G (2009) Enhanced drought tolerance in transgenic Leymus chinensis plants with constitutively expressed wheat TaLEA 3. Biotechnol Lett 31:313–319

Wang X, Chen X, Liu Y, Gao H, Wang Z, Sun G (2011) *CkDREB* gene in Caragana korshinskii is involved in the regulation of stress response to multiple abiotic stresses as an AP2/EREBP transcription factor. Mol Biol Rep 38:2801–2811

Wang M et al (2014a) SiLEA14, a novel atypical LEA protein, confers abiotic stress resistance in foxtail millet. BMC Plant Biol 14:290

Wang RK, Cao ZH, Hao YJ (2014b) Overexpression of a R2R3 MYB gene *MdSIMYB1* increases tolerance to multiple stresses in transgenic tobacco and apples. Physiol Plant 150:76–87

Wang Z et al (2014c) Characterization of two highly similar CBF/DREB1-like genes, *PhCBF4a* and *PhCBF4b*, in *Populus hopeiensis*. Plant Physiol Biochem 83:107–116

Wang X et al (2015) Expression of *TaWRKY44*, a wheat WRKY gene, in transgenic tobacco confers multiple abiotic stress tolerances. Front Plant Sci 6:615

Wang H, Wang H, Shao H, Tang X (2016a) Recent advances in utilizing transcription factors to improve plant abiotic stress tolerance by transgenic technology. Front Plant Sci 7:67

Wang Y, Shu Z, Wang W, Jiang X, Li D, Pan J, Li X (2016b) *CsWRKY2*, a novel WRKY gene from *Camellia sinensis*, is involved in cold and drought stress responses. Biol Plant 60:443–451

Wang G-D, Liu Q, Shang X-T, Chen C, Xu N, Guan J, Meng Q-W (2018) Overexpression of transcription factor *SlNAC35* enhances the chilling tolerance of transgenic tomato. Biol Plant 62:479–488

Wei Q et al (2017) A wheat R2R3-type MYB transcription factor *TaODORANT1* positively regulates drought and salt stress responses in transgenic tobacco plants. Front Plant Sci 8:1374

Wolfien M et al (2016) TRAPLINE: a standardized and automated pipeline for RNA sequencing data analysis, evaluation and annotation. BMC Bioinform 17:21

Wu X, Shiroto Y, Kishitani S, Ito Y, Toriyama K (2009) Enhanced heat and drought tolerance in transgenic rice seedlings overexpressing *OsWRKY11* under the control of HSP101 promoter. Plant Cell Rep 28:21–30

Wu M, Liu H, Han G, Cai R, Pan F, Xiang Y (2017) A moso bamboo WRKY gene *PeWRKY83* confers salinity tolerance in transgenic Arabidopsis plants. Sci Rep 7:11721

Wu J, Jiang Y, Liang Y, Chen L, Chen W, Cheng B (2019) Expression of the maize MYB transcription factor *ZmMYB3R* enhances drought and salt stress tolerance in transgenic plants. Plant Physiol Biochem 137:179–188

Xia J, Gill EE, Hancock RE (2015) NetworkAnalyst for statistical, visual and network-based meta-analysis of gene expression data. Nat Protoc 10:823–844

Xiao B, Huang Y, Tang N, Xiong L (2007) Over-expression of a LEA gene in rice improves drought resistance under the field conditions. Theor Appl Genet 115:35–46

Xu J, Xue C, Xue D, Zhao J, Gai J, Guo N, Xing H (2013) Overexpression of GmHsp90s, a heat shock protein 90 (Hsp90) gene family cloning from soybean, decrease damage of abiotic stresses in *Arabidopsis thaliana*. PLoS One 8:e69810

Yang A, Dai X, Zhang W-H (2012) A R2R3-type MYB gene, *OsMYB2*, is involved in salt, cold, and dehydration tolerance in rice. J Exp Bot 63:2541–2556

Yang G, Yu L, Zhang K, Zhao Y, Guo Y, Gao C (2017) A *ThDREB* gene from *Tamarix hispida* improved the salt and drought tolerance of transgenic tobacco and T. hispida. Plant Physiol Biochem 113:187–197

Yang S et al (2019a) A stress-responsive bZIP transcription factor *OsbZIP62* improves drought and oxidative tolerance in rice. BMC Plant Biol 19:260

Yang X, Kim MY, Ha J, Lee S-H (2019b) Overexpression of the soybean NAC gene *GmNAC109* increases lateral root formation and abiotic stress tolerance in transgenic Arabidopsis plants. Front Plant Sci 10:1036

Yao W, Wang L, Zhou B, Wang S, Li R, Jiang T (2016) Over-expression of poplar transcription factor ERF76 gene confers salt tolerance in transgenic tobacco. J Plant Physiol 198:23–31

Ying S, Zhang D-F, Fu J, Shi Y-S, Song Y-C, Wang T-Y, Li Y (2012) Cloning and characterization of a maize bZIP transcription factor, *ZmbZIP72*, confers drought and salt tolerance in transgenic Arabidopsis. Planta 235:253–266

Ying L, Chen H, Cai W (2014) *BnNAC485* is involved in abiotic stress responses and flowering time in *Brassica napus*. Plant Physiol Biochem 79:77–87

You J, Zhang Y, Liu A, Li D, Wang X, Dossa K, Zhou R, Yu J, Zhang Y, Wang L, Zhang X (2019) Transcriptomic and metabolomic profiling of drought-tolerant and susceptible sesame genotypes in response to drought stress. BMC Plant Biol 19:267

Zhang X, Ju H-W, Chung M-S, Huang P, Ahn S-J, Kim CS (2010) The RR-type MYB-like transcription factor, *AtMYBL*, is involved in promoting leaf senescence and modulates an abiotic stress response in Arabidopsis. Plant Cell Physiol 52:138–148

Zhang L, Zhao G, Xia C, Jia J, Liu X, Kong X (2012) Overexpression of a wheat MYB transcription factor gene, *TaMYB56-B*, enhances tolerances to freezing and salt stresses in transgenic Arabidopsis. Gene 505:100–107

Zhang L, Zhang L, Xia C, Zhao G, Liu J, Jia J, Kong X (2015a) A novel wheat bZIP transcription factor, *TabZIP60*, confers multiple abiotic stress tolerances in transgenic Arabidopsis. Physiol Plant 153:538–554

Zhang X, Liu X, Wu L, Yu G, Wang X, Ma H (2015b) The *SsDREB* transcription factor from the succulent halophyte *Suaeda salsa* enhances abiotic stress tolerance in transgenic tobacco. Int J Genomics 2015:875497

Zhang L, Zhang L, Xia C, Zhao G, Jia J, Kong X (2016) The novel wheat transcription factor *TaNAC47* enhances multiple abiotic stress tolerances in transgenic plants. Front Plant Sci 6:1174

Zhang L et al (2017) A novel wheat C-bZIP gene, *TabZIP14-B*, participates in salt and freezing tolerance in transgenic plants. Front Plant Sci 8:710

Zhang J, Luo H, Guo Z (2018) Overexpression of *Malus hupehensis MhSHN1* gene enhances salt and osmotic stress tolerance in transgenic tobacco plants. Russ J Plant Physiol 65:857–864

Zhang Y, Li D, Zhou R, Wang X, Dossa K, Wang L, Zhang Y, Yu J, Gong H, Zhang X, You J (2019) Transcriptome and metabolome analyses of two contrasting sesame genotypes reveal the crucial biological pathways involved in rapid adaptive response to salt stress. BMC Plant Biol 19:66

Zhao B-Y, Hu Y-F, Li J-j, Yao X (2016a) *BnaABF2*, a bZIP transcription factor from rapeseed (*Brassica napus* L.), enhances drought and salt tolerance in transgenic Arabidopsis. Bot Stud 57:12

Zhao X et al (2016b) The Miscanthus NAC transcription factor *MlNAC9* enhances abiotic stress tolerance in transgenic Arabidopsis. Gene 586:158–169

Zhao H, Zhao X, Li M, Jiang Y, Xu J, Jin J, Li K (2018) Ectopic expression of *Limonium bicolor* (Bag.) Kuntze DREB (LbDREB) results in enhanced salt stress tolerance of transgenic *Populus ussuriensis* Kom. Plant Cell Tissue Org Cult 132:123–136

Zhao Y et al (2019) Over-expression of an R2R3 MYB Gene, *GhMYB73*, increases tolerance to salt stress in transgenic Arabidopsis. Plant Sci 286:28–36

Zhu JK (2016) Abiotic stress signaling and responses in plants. Cell 167:313–324

Zhu N et al (2015) The R2R3-type MYB gene *OsMYB91* has a function in coordinating plant growth and salt stress tolerance in rice. Plant Sci 236:146–156

Zhu M, Meng X, Cai J, Li G, Dong T, Li Z (2018) Basic leucine zipper transcription factor *SlbZIP1* mediates salt and drought stress tolerance in tomato. BMC Plant Biol 18:83

Zytnicki M, Quesneville H (2011) S-MART, a software toolbox to aid RNA-Seq data analysis. PLoS One 6:e25988

Chapter 6
Crop Growth Responses Towards Elevated Atmospheric CO_2

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Contents

Abstract The projected rise in global elevated atmospheric CO_2 level has well-pronounced impact on plant ecophysiology and economic productivity. Elevated atmospheric CO_2 accelerated the leaf-level photosynthesis in C_3 plants, reduced stomatal conductance, and enhanced resource use efficiency. The sensitivity was comparatively less for C_4 and CAM plants. Under sufficient nutrient availability, the net increase in leaf-level assimilation amplified the net grain yield under elevated atmospheric CO_2 exposure. However, the relative response in biomass partitioning pattern often varied among the individual crop species. Thus, the net impact on harvest index (HI) varied from one crop species to another. We also observed that the CO_2

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enrichment facilities have marked influence on the reported magnitude and pattern of crop response towards elevated atmospheric CO_2 environment.

Keywords Elevated CO_2 · Photosynthesis · Leaf area index · Radiation use efficiency · Harvest index

6.1 Introduction

Since early twentieth century, the unprecedented rise in the level of atmospheric greenhouse gases (GHGs) from several nonpoint sources of anthropogenic origin that promptly outpaced the natural course of gradual change in earth's atmospheric GHG composition dynamics. This was hard to ignore that the carbon dioxide accounted for a lion share of ever-increasing atmospheric GHGs levels. The rising atmospheric CO_2 level modified the source-sink dynamics in maintaining net agro-ecosystem productivity, as an indispensable component of global biogeochemical cycles. The anthropogenic CO_2 emission contributed a significant rate of rise (1.585 μmol mol^{-1} $year^{-1}$ over past 5 decades; Fig. 6.1a) in our present atmospheric CO_2 concentration (>400 μmol mol^{-1}; Fig. 6.1b) over the past few decades against the reported level of 280 μmol mol^{-1} atmospheric CO_2 prevailed in the preindustrial revolution era (Dlugokencky et al. 2010). The recently reported rise in atmospheric CO_2 level was the highest in last decade @ 2.29 μmol mol^{-1} $year^{-1}$ between 2010; first time ever recorded in past 26 million years' earth history. Intergovernmental Panel on Climate Change projected the future rise in atmospheric CO_2 level from the combined atmospheric GHGs and aerosol radiative forcing up to 700 ppm by the end of twenty-first century under variable projected emission scenarios (IPCC 2007; Fig. 6.2a, b). Atmospheric CO_2 is the only source of carbon acquisition for plant growth in different agricultural crop species. The nature and magnitude of plant growth response towards the high atmospheric CO_2 concentration often relied on the nature of crop species, status of resource availability and other prevailing microclimate or environmental conditions. Therefore, the projected rise in atmospheric CO_2 exposure will have the variable net exaggerated carbon fertilization impact on its' far-reaching consequences on modelling the plant ecophysiological response, food production and human nutritional security in a future predicted high-CO_2 world (Kimball et al. 2002).

The study of elevated atmospheric CO_2 impact on several crop species is often termed as 'CO_2 fertilization' effect. Extensive research activities studying this CO_2 fertilization impacts on different agricultural crop species was initiated dates back to early 1980s. Since early days, the major challenge was accounted for the measurement of CO_2 flux and ensured uniform exposure of elevated CO_2 to standing agricultural crop species under the more realistic open field condition. With a rapid proliferation of worldwide network on CO_2 fertilization studies in early 1990s, the engineering efforts from our

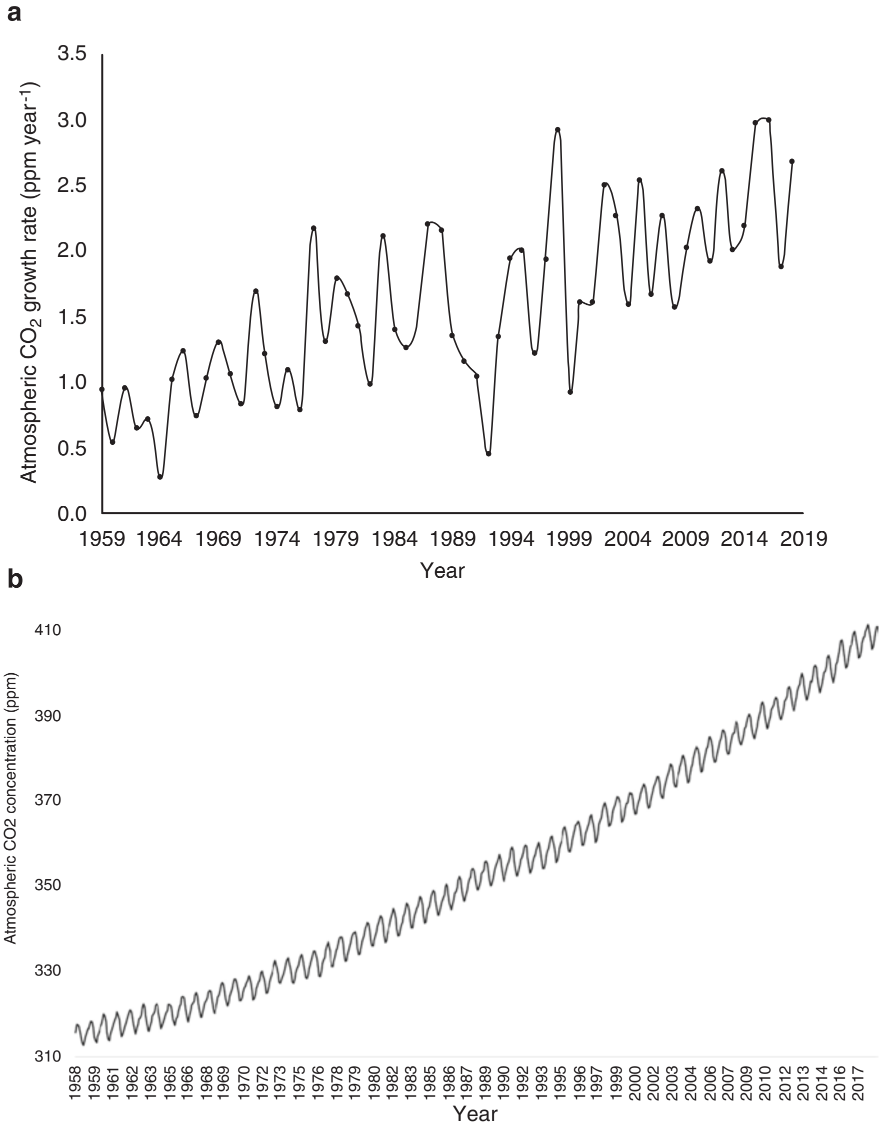

Fig. 6.1 Increasing trend for (**a**) rate of rising (ppm per year), (**b**) quantitative increase of the atmospheric CO$_2$ concentration (ppm) in our globe (Source: https://www.esrl.noaa.gov/gmd/ccgg/trends/data.html)

scientific community were innovated and upgraded the available fabrication of suitable instrumentation/experimental research facilities in this aspect viz. from the century-old closed chamber facilities (plant growth chambers, controlled-environmental chambers, greenhouse, phytotron, etc.) to semiopened open-top chambers (OTCs) and further upgraded to free-air CO$_2$ enrichment (FACE) facilities in the most recent days (Fig. 6.3).

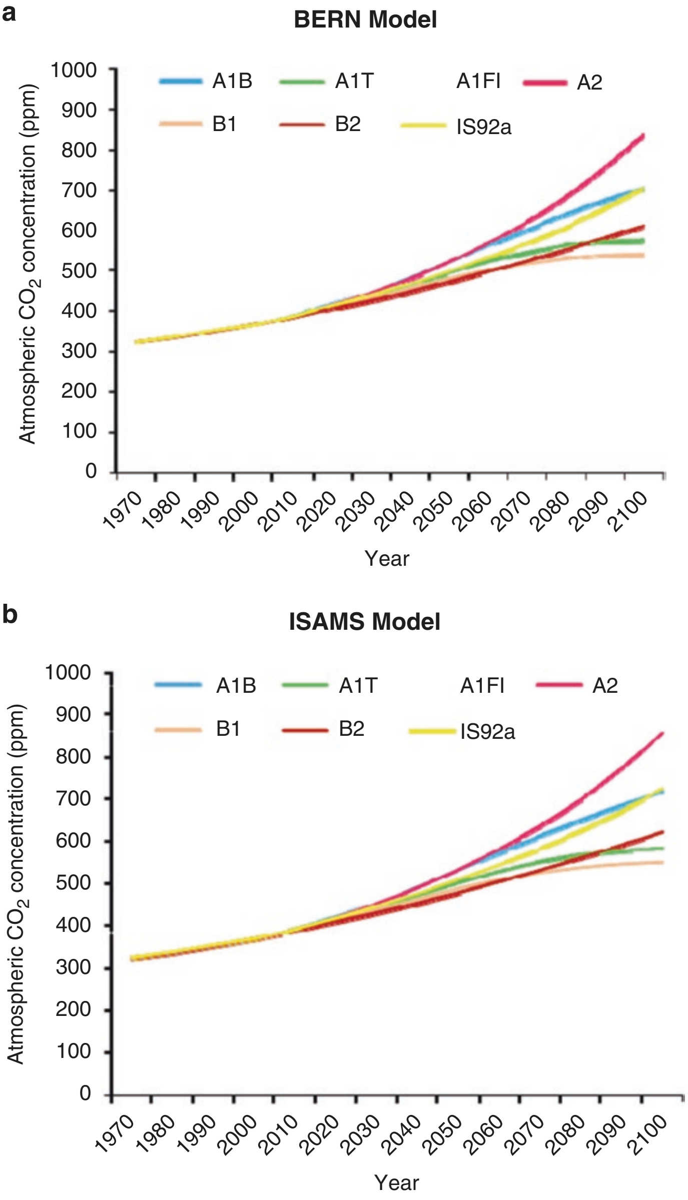

Fig. 6.2 AR4 forcing from the carbon cycle models under different emission scenarios

Fig. 6.3 (**a**) Environmental growth chamber facility at National Phytotron facility ICAR-IARI New Delhi, India; (**b**) open-top chamber facility at ICAR-IARI New Delhi, India; (**c**) Free-air carbon dioxide enrichment facility at ICAR-IARI New Delhi, India

6.2 Crop Growth Response to Elevated CO_2

Plant traits of the agriculturally important crop species are often responsive to changes in local weather variability as well as long-term changes in the prevailing climate condition. The detailed mechanistic study on their response pattern is of our particular interest due to their intrinsic role for sustaining regional food security. The projected rise in elevated atmospheric CO_2 level has the potential to modify the crop ecophysiological processes likewise:

6.2.1 Photosynthesis

During photosynthesis in C_3 plants, the partial pressure difference of CO_2 and O_2 lead to CO_2 diffusion from the outside ambient air into the leaf intercellular spaces through stomata. The diffused CO_2 fractions further move across the cell wall, plasma membrane, cytosol, chloroplast envelope, stroma and reached to final reaction site viz. rubisco to yield two molecules of 3-PGA under the Calvin–Benson–Bassham cycle. Rubisco is specifically evolved under anaerobic environment (Terashima et al. 2011). At lower internal CO_2 concentrations, reduced substrate availability limits the photosynthesis. Any increase CO_2 concentration in plant's surrounding widens the existing diffusion gradient between ambient air and mesophyll cells. The increased diffusive movement of CO_2 from surrounding ambient air to the leaf mesophyll cells finally resulted in higher leaf internal CO_2 concentration at rubisco site with higher CO_2/O_2 ratio that enhanced net CO_2 assimilation rates. Michaelis–Menten constant (Km) signified the higher affinity of rubisco for CO_2 in the carboxylation reaction (8–34 μM) than O_2 in the oxygenation reaction (196–810 μM) at 25 °C (von Caemmerer and Quick 2000). Under ambient environment, photorespiration accounts a significant portion of rubisco activity (25–30% at 25 °C) in C_3 plants, as the present atmospheric O_2 level (~210,000 ppm) is higher than CO_2 (~400 ppm) level. Elevated CO_2 enhanced higher rubisco activation as well as binding of quinine and Mn with photosystem II for enhancement of leaf photosynthetic activity (Long et al. 2004).

Atmospheric CO_2 enrichment in outside environment lead to the higher intercellular CO_2 concentration in chloroplast favoured carboxylation from the increased substrate availability in stroma that activated the reactive sites of rubisco towards enhanced carboxylation and simultaneous inhibition of the photo-respiratory pathways favouring oxygenation of ribulose-1, 5-bisphosphate (RuBP) with the depressed production of 2-phosphoglycolate (Andrews and Lorimer 1987; Pons et al. 2009). Further increase in internal CO_2-substrate availability often restricts the initial amplification of leaf photosynthesis for the limited ability of RuBP regeneration through electron transport cycle. Thus, stimulations in photosynthesis in the post-industrial revolution era were obvious that may gradually saturate at approximately 1000 ppm CO_2 (Poorter and Navas 2003; Körner et al. 2007). Therefore, the future increases in atmospheric CO_2 may have less dramatic impact on plant carbon assimilation so as the crop yield (Long et al. 2004). The increase in the peak photosynthetic rate and light saturation points is obvious under elevated atmospheric CO_2 environment (Meng et al. 2014). Several meta-analytical reviews concluded that elevated CO_2 exposure substantially increased the plant energy conversion efficiency (20%; Slattery et al. 2013), midday photosynthetic rates (70%; Jackson et al. 1994) and light-saturated photosynthetic CO_2 uptake in several C_3 crop species (31%; Ainsworth and Rogers 2007). The amplification was more prominent during vegetative growth stages that gradually reduced with the advancement of reproductive growth stage in rice (Shimono et al. 2009).

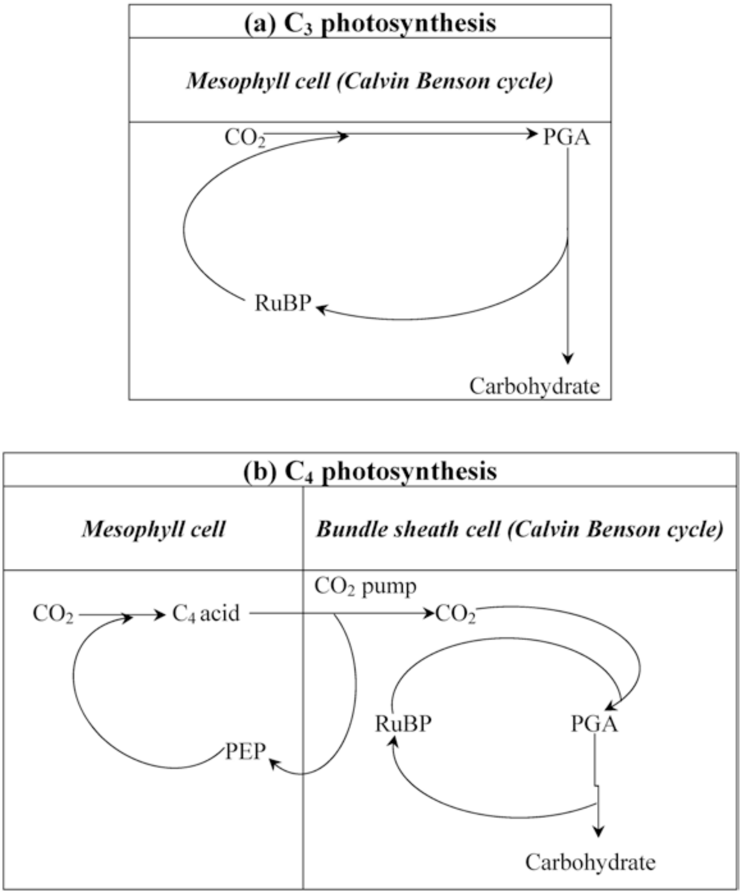

Fig. 6.4 Diagrammatic representation for the basic differences between (**a**) C_3 and (**b**) C_4 photosynthesis

The impact of atmospheric CO_2 elevation on photosynthesis is less obvious in C_4 than C_3 crop species. Available literature review suggested that C_3 crops assimilated ~28% more carbon towards the external elevated atmospheric CO_2 exposure over the C_4 species; preferably due to low CO_2 sensitivity of photosynthetic pigments in C_4 than C_3 species (Ainsworth and Long 2005). The differential compartmentalized carbon assimilation reaction in the active site of rubisco is responsible for the contrasting photosynthetic efficiencies between C_3 and C_4 crop species under elevated CO_2 environment (Fig. 6.4). The typical compartmentalized carboxylation pattern of C_4 photosynthetic pathways explained the root cause of such differential response pattern. The energy-dependent carboxylation in C_4 photosynthetic pathways is much faster than under C_3 pathway. The initial CO_2 capturing by phosphoenol pyruvate (PEP) carboxylase that had a high affinity for the carbon substrate (Bowes 1991), yielded dicarboxylic acids (C_4 acids viz. malic acid in maize) in the mesophyll cells of C_4 plants. Unlike C_3 photosynthesis, the second carboxylation of rubisco takes place in the bundle sheath chloroplasts cells with concentrated CO_2 as delivered from the surrounded mesophyll cells from successive decarboxylation of previously synthesized C_4 acids, after transported by the metabolic pumps. The additional carbon concentrating mechanism in the Hatch–Slack pathway of C_4 photosynthesis is essentially effective to restrict the entry of O_2 at the active site of rubisco and maintain higher CO_2 concentration in the bundle sheath cells in C_4 photosynthetic apparatus (i.e. 3–6 times higher than in the atmosphere; higher CO_2/O_2 ratio than C3 plants). Thus, the high internal CO_2 concentration in bundle sheath cells drastically reduces the net opportunity of oxygenation i.e. photorespiration at whole-leaf level (almost negligible; Crespo et al. 1979) and the net efficiency of photosynthetic quantum yield in C_4 photosynthetic pathway is enhanced (~10 times more than C_3 mesophyll cells) under natural/ambient CO_2 environment (Sage and Coleman 2001). Under sufficient water supply, the increased CO_2 concentration in the bundle sheath chloroplasts may reach up to 10–20 times higher in C_4 species (like maize) than the typical photosynthesizing C_3 plants under ambient atmospheric CO_2 (Furbank et al. 2008). Therefore, maize is appeared to be saturated under the present level of ambient CO_2 (Wand et al. 1999; Kim et al. 2006). However, the elevated CO_2 can alter the photosynthetic rates of the present level of atmospheric CO_2 saturated C_4 species (like maize) towards the amelioration of abiotic stress (water deficit) impact on leaf-level photosynthetic assimilation (Leakey et al. 2004, 2006). The negative consequences of the CO_2 saturation towards the present-day atmospheric CO_2 concentration gave more competitive advantage to the C_4 weeds over cultivated C_3 crop spices that resulted significant reduction in final economic yield in soybean (Ziska 2000) and mung bean (Awasthi et al. 2018). The theoretical assumption about non-sensitivity of C_4 photosynthesis towards the variation in atmospheric CO_2 level was not consistent; because of the variation in CO_2 saturation threshold in C_4 leaves (Ghannoum et al. 2000; Ainsworth and Rogers 2007). The CO_2 saturation level in leaves of C_4 species is the most crucial factor for determining the degree of photosynthetic stimulation under elevated CO_2 environment. The cumulative response varied among the subtypes of C_4 photosynthetic pathways (NADP-ME, NAD-ME, and PCK) or taxonomic lines with different decarboxylation mechanisms (Ghannoum et al. 2002; Muhaidat et al. 2007). Therefore, the aggrandizing response of photosynthesis towards the atmospheric CO_2 enrichment was not identical for all C_4 crop species (Ziska and Bunce 1997). Alike C_3 photosynthesis, the stimulation in leaf photosynthetic rates is obligatory under elevated CO_2 for the rest other C_4 species those remained unsaturated towards the current level of atmospheric CO_2 concentration (Allen et al. 2011). Elevated CO_2 levels exposure intensified CO_2 uptake that often amplified the vegetative growth 44% in C_3 plants, but only 12% for C_4 plants (Poorter and Navas 2003). The magnitude of growth stimulation was comparatively higher at early crop growth stages (Prasad et al. 2009); more prominent in C_4 weed species than C_4 crops grown under elevated CO_2 particularly grown under high irradiance (Ziska and Bunce 1997; Wand et al. 1999) and elevated air temperature regime (Vu et al. 2001; Prasad et al. 2009). Elevated CO_2 exposure accelerated the plants' ability to maintain net photosynthetic rate per unit

N uptake, even under limited N supply (Pal et al. 2005). Recent long-term experimental (20 years) evidences suggested that soil nitrogen supply from net soil N mineralization played the most crucial role in determining such differential response in leaf C assimilation through photosynthetic activity between C_3 and C_4 crop species that may persist up to 3000 ppm atmospheric CO_2 level (Wang et al. 2015; Reich et al. 2018).

The keen impact of high CO_2 environment on the photosynthetic activities in Crassulacean Acid Metabolism (CAM) plants is obvious as it adapts the enzymology of CO_2 fixation in both C_3 and C_4 pathways with a distinct temporal separation (Osmond 2003). The exclusive strategy of CAM photosynthesis engaged rubisco and phosphoenol pyruvate carboxylase (PEPC). Similar to C4 photosynthesis, the nocturnal C acquisition by cytosolic PEPC activity results into malate formation (Phase I) that ends up with dephosphorylation at dawn. The successive initiation of rubisco activity for carbon reduction through Calvin cycle gradually dominates at early morning, as in normal C_3 leaf photosynthesis (Phase II). At midday, malate decarboxylation dominates with increasing rubisco activity for carbohydrate assimilation and the associated increase in partial pressure of intercellular CO_2 favours stomatal closure and suppress transpiration; no exogenous CO_2 is assimilated (Phase III). Thus, complete decarboxylation of malate and the successive utilization of released CO_2 by rubisco in C_3 photosynthesis gradually reduces the intercellular CO_2 concentration that allows stomatal reopening for further nocturnal C acquisition. Simultaneous promotion of C_4 carboxylation by PEP carboxylase gradually dominates in afternoon (phase IV). Such metabolic flexibility often resulted in the inconsistent and contrasting responses of CAM photosynthetic pathways towards elevated atmospheric CO_2 environment.

It was clear that the highest potential stimulation in CAM photosynthesis may occur in phase IV under elevated CO_2 environment. The stomatal reopening at phase IV ensures the higher CO_2 concentration at the active site of dominant primary carboxylase rubisco that is still unsaturated to the present level of ambient atmospheric CO_2. Limited light and stomatal closure from high intercellular CO_2 concentration often limit the net influence of elevated CO_2 on phase II and III of daytime CAM photosynthesis. However, the PEP carboxylase is seemed to be saturated for the present day of atmospheric CO_2 for some CAM species. Elevated CO_2 exposure has no overall impact on the nocturnal CO_2 fixation (phase I) for those particular CAM species but may increase the dark CO_2 fixation for other constitutive CAM species (Ting 1994).

Prevailing air temperature plays the most crucial role in determining the net modified impact of elevated CO_2 exposure on phase I and IV of CAM photosynthesis. Elevated CO_2 accompanied with the increase in air temperature inhibited dark respiration (phase I; Brooks and Farquhar 1985) and photorespiration (phase IV; Drennan and Nobel 2000). Such inhibitory response enhanced the net substrate availability for and dark respiration (phase I) and rubisco activation phase (phase IV), making the net stimulation of CAM photosynthesis under elevated CO_2 more obvious. Moreover, controlled-chamber experimental evidences confirmed the CO_2 saturation of PEP carboxylase at 20 °C night temperature that became CO_2

unsaturated at 25 °C night temperature under present-day ambient CO_2 level (Zhu et al. 1999). Finally, the enhanced response of photosynthetic C assimilation in CAM plants (Phase I and IV) is more obvious under higher air temperature regime.

6.2.1.1 Photosynthetic Acclimation

The initial elevated CO_2 induced stimulation in C_3 leaf-level photosynthesis in the low CO_2 environment is often short-lived and its persistency is still debatable. Many researchers observed the sharp decline in the quantity and activity of photosynthetic enzymes under long-term elevated CO_2 exposure. The phenomenon is popularly known as 'photosynthetic acclimation' or 'downregulation' (Gunderson and Wullschleger 1994; Long et al. 2004; Ainsworth and Rogers 2007; Alonso et al. 2009). The reported decline in leaf photosynthetic activity after moderate to long-term elevated CO_2 exposure was primarily from the source-sink imbalance i.e. bearing the strong negative feedback on photosynthesis either due to source limitation (depletion of intercellular CO_2 as a result of significant increase in mesophyll conductance from partial stomatal closure under elevated CO_2 concentration; (Sanz-Sáez et al. 2010), accumulation of sugars from initial enhancement of leaf-level photosynthesis (Sharma-Natu and Ghildiyal 1994), lowering of soluble protein concentration/rubisco activity (Lawlor and Mitchell 2000), high internal (non-stomatal) resistances (Delucia et al. 1985) or inadequate sink capacity at whole-plant level for effective utilization of photosynthates (Ainsworth et al. 2004; Aranjuelo et al. 2005; Sanz-Sáez et al. 2010). Supercritical level of elevated CO_2 at 3000 and 5000 ppm often emanated photosynthetic downregulation in both C_3 and C_4 species (Wang et al. 2015). Under elevated CO_2 exposure, leaf photosynthetic acclimation was also dependent on vertical profile of leaves within the canopy and the developmental stage (Osborne et al. 1998). Excess C uptake under long-term elevated CO_2 exposure resulted in such downregulation in leaf photosynthetic rates (photosynthetic acclimation) due to nonselective reduction in leaf N concentration and reduced transpiration rate (Kanemoto et al. 2009), thereby the maximum rate of electron transport and rubisco activity (Ellsworth et al. 2004; Aranjuelo et al. 2005) or reallocation of leaf N within different plant organs towards the maximization of nitrogen use efficiency (Nakano et al. 1997) and subsequent dilution of other leaf nutrient elements (Ceulemans and Mousseau 1994). The fact supported the recently observed role of adequate N supply (through external fertilizer application), towards the increase in sink strength as well as subsequent leaf photosynthetic assimilation rates under elevated CO_2 (Ruiz-Vera et al. 2017). Moreover, the relative partitioning pattern of photosynthetic C among different plant storage organs and the extent of leaf-level nutrient dilution (preferably N) varied considerably among the different agricultural crop species (Stitt and Krapp 1999) but the net impact may sustain throughout the life in majority of the agricultural crops (Garcia et al. 1998). The elevated atmospheric CO_2 induced plant growth stimulation overran the increased internal sink capacity of the elevated CO_2 grown plant. This triggers a molecular mechanism for feedback regulation for repression of photosynthetic gene transcription under elevated CO_2 (Van Oosten and Besford 1995). Insufficient sink capacity lead to the reduction in translocation of photosynthetic assimilates from leaf to the respective storage organs from the plant signalling for internal negative feedback from the higher leaf-level starch during the dark period. Under limited N availability, it modified the internal translocation and reduced remobilization pattern of tissue N shoot regrowth (Skinner and Nelson 1994; Kanemoto et al. 2009); thus, finally depressed the initial high atmospheric CO_2 induced stimulation in leaf-level photosynthesis (Griffin and Luo 1999). Finally, the integral impact of the substantial increase in cumulative leaf photosynthetic assimilation over the entire crop growth period (Geiger et al. 1999) and improved energy conversion efficiency under elevated CO_2 environment (Slattery et al. 2013) resulted in higher biomass accumulation at canopy level and economic seed yield for the majority of the C_3 crop species at harvest (Drake et al. 1997; Centritto et al. 2002; Kang et al. 2002; Li et al. 2003).

Unlike C_3 photosynthesis, avoidance of photorespiration under almost CO_2 saturated environment at the active of rubisco in the bundle sheath chloroplast reinforced higher net quantum yield, intrinsic water use efficiency of the daytime C_4 photosynthetic pathways with relatively larger sink capacity of C_4 plants. Therefore, it provides less opportunity for achieving further photosynthetic stimulation and so as its acclimation for the C_4 plants exposed to elevated CO_2 environment. The elevated CO_2 induced enhancement in leaf photosynthesis and successive Rubisco upregulation were most prominent at the early stages of C_4 leaf ontogeny (Prasad et al. 2009). For CAM leaves, nighttime increase in total titratable acidity and malate accumulation via increased PEP carboxylase activity under elevated CO_2 facilitated the downregulation in daytime rubisco activity, upregulation of leaf-level enzyme activities (sucrose–phosphate synthase and sucrose synthase) and increased plant hormones activities (indole-3-acetic acid, gibberellins, isopentenyladenosine, etc.). In absence of any external water deficit stress factors, the daytime activity of PEP carboxylase activity as well as the leaf CO_2 exchange rates remained insensitive to atmospheric CO_2 elevation (Nobel and Israel 1994). However, elevated CO_2 has the potential to increase the leaf-level synthesis of nonstructural carbohydrates in C_4 plants under the water deficit/drought stress with its significant ameliorative impact of on leaf photosynthetic activity (Leakey et al. 2006; Kakani et al. 2011). The degree and extent of such ameliorative impact were independent to the N availability (Markelz et al. 2011). The progressive acclimation in daytime C_3 photosynthesis reduced the resource investment for excess rubisco capacity for CAM plants grown under elevated CO_2 environment. Moreover, the successive slight reduction in daytime phosphoenol pyruvate (PEP) carboxylase activity often had negligible impact over the cumulatively higher dark period PEP carboxylase activity on the net photosynthetic carbon assimilation in some species of CAM plants (Li et al. 2002). Thus, the final increased conversion of stimulated photosynthetic C assimilates into biomass became ~50% in C_3 (Prior et al. 2005), ~35% in CAM (Drennan and Nobel 2000), and ~12% in C_4 (Poorter and Navas 2003) across the respective diverse plant species grown under elevated CO_2 environment.

6.2.2 Stomatal Conductance

Increase in atmospheric CO_2 concentration depressed the long-term developmental responses as the dramatic reduction in stomatal density or stomatal pore size lead to the significant improvement of water use efficiency in several crop species (Woodward and Bazzaz 1988; Lammertsma et al. 2011). An increase in atmospheric CO_2 concentration from 280 ppm in preindustrial era to 340 ppm in late-twentieth century resulted in 67% reduction in stomatal density (Woodward 1987). Similar evidences proved the gene regulated impact on stomatal distribution, development and functioning for differential expression between the ambient and elevated CO_2 grown maize transcripts (Maroco et al. 1999; Kim et al. 2006). Several studies estimated only 5% average decrease (Ainsworth and Rogers 2007) or no significant change (Estiarte et al. 1994; Kumar et al. 2014) in stomatal density under short-term elevated CO_2 exposure. The response may vary from one crop species to other; even among the genotypes of any crop species (Bettarini et al. 1998; Field et al. 2007; Xu et al. 2016). Therefore, the changes in stomatal density of the plant leaves were considered to be the long-term adaptive response towards elevated atmospheric CO_2 concentration (Haworth et al. 2015). The structural plasticity from increased leaf area from short-term exposure, modification in gene expression levels from long-term exposure is the prime reason for changes in stomatal density under elevated CO_2 environment.

Nevertheless, the modification of short-term stomatal behaviour accounted the widespread decrease in leaf-level stomatal conductance in both C_3 and C_4 crops preferably due to the regulation of stomata by guard cells under elevated atmospheric CO_2 environment (Zhu et al. 1998; Bunce 2004). If the leaf diffusive resistances reached the threshold of more than 10–20 s cm^{-1}, elevated atmospheric CO_2 had little impact on regulating plant transpiration over several crop species. Jackson et al. (1994) observed that elevated CO_2 depressed the leaf-level stomatal conductance and reduced transpiration by 50%. However, the actual magnitude of elevated CO_2 induced reduction in transpiration was higher in the C_3 than C_4 crop species (Dugas et al. 1997). Elevated CO_2-induced increase in ABA biosynthesis (Chater et al. 2015) and guard cell hydrogen peroxide and nitric oxide signalling (Shi et al. 2015) modified the channel activity (increased anion channel and decrease in K^+/Ca^{2+}) and organic solute concentration (sucrose and malate) in guard cells. That resulted in the sharp decline turgor pressure and forced the guard cells to shrink followed by closure of stomatal aperture (Fujita et al. 2013; Lawson et al. 2014). The net magnitude of reduction in stomatal conductance also depends on vapour pressure deficit and soil water potential (Wullschleger et al. 2002a). Stomatal conductance and canopy conductance declined with increase in vapour pressure deficit and decline in soil water potential beyond field capacity. With few exceptions, elevated CO_2 studies showed that stomatal conductance was initially reduced in response to elevated CO_2 that was resulting in reduced transpiration as well as the cumulative water consumption at the individual leaf to whole-plant canopy, ecosystem and global scales (Field et al. 1995). For a given leaf-level stomatal opening, C_4 plants have higher carboxylation efficiency as well as increased CO_2 assimilation rate with lower internal resistance than C_3 species. Reduction in leaf-level transpiration rates resulted the increase in daytime leaf temperature by 1 °C (Kim et al. 2006) and also ameliorated the negative impact of moderate drought by conserving soil moisture under maize crop (Leakey et al. 2006). Changes in leaf-level transpiration modified the leaf-level intrinsic water use efficiency under elevated CO_2 exposure. Yoshimoto et al. (2005) observed that elevated CO_2 reduced stomatal conductance and reduced transpiration combined with increased total biomass production and so as the water use efficiency in rice under free-air CO_2 enrichment (FACE) (Medlyn et al. 2001; Ainsworth and Long 2005). The depressive responses were often short-lived in some species (Bunce 1992; Uddling et al. 2010) or absent (Pathare et al. 2017). Under elevated CO_2, stomatal closure is independent apoplastic transfer of 'mesophyll signals' for controlling photosynthetic C assimilation (Fujita et al. 2013). However, the reduction in stomatal conductance in the elevated CO_2-grown gradually nullified the stimulation in rubisco carboxylation rates from the subsequent increase in leaf internal resistance to CO_2 diffusion. Such 'stomatal acclimation' may also occur from the changes in stomatal morphology and CO_2 sensitivity to the guard cells in several C_3/C_4 grassland species (Morison and Gifford 1984; Drake et al. 1997; Maherali et al. 2002). In some tree species (*Larix decidua* Mill. and *Pinus mugo* ssp.), transpiration rates remained unchanged for insensitivity of stomatal aperture dynamics towards elevated CO_2 exposure, but the significant rise in intrinsic water use efficiency became obvious from enhanced photosynthetic assimilation (Streit et al. 2014).

The widely observed reduction of leaf-level transpiration rate often leads to considerable savings in soil moisture utilization for the elevated CO_2 grown plants to preserve soil moisture, improve plant water status and increase carbon gain towards the enhanced plant fitness towards drought environment (Leakey et al. 2009; Hussain et al. 2013). But it did not always translate into an equivalent reduction in soil water uptake (Baker et al. 1996; Wullschleger and Norby 2001; Centritto et al. 2002). Elevated CO_2 often increased leaf area index (LAI) (Ainsworth and Long 2005), which is a primary determinant of both crop productivity and cumulative water use (Wullschleger et al. 2002b). The net reduction in water loss through CO_2-enrichment-induced decrease in leaf-level transpiration was almost cancelled out by the subsequent increase in evapotranspiration from the increased leaf area under adequate N and water supply (Li et al. 2004; Jin et al. 2018). Finally, for a given increased exposure to enriched atmospheric CO_2 concentration had brought a proportional increase in transpiration efficiency or intrinsic water use efficiency at leaf level (either by increasing photosynthetic rate and decreasing in stomatal conductance or both) and further scaling up the impact from leaf to crop canopy level confirmed that the increase in net photosynthetic carbon gain is often not converted into equivalent biomass production. The net impact may also overshadow the CO_2 enrichment induced reduction in transpiration with negligible soil water savings for canopy environment.

6.2.3 Flowering Time/Reproductive Phenology

Flowering determines the potential reproductive success for any plant species, its ability to survive in the natural selection process and adapt environmental change. Under ample supply of sunlight, optimum temperature regime temperature and unlimited nutrient availability, increasing atmospheric CO_2 alters carbon metabolism at cellular level, plant size/vigour and periodic rate of canopy development that has an effective control for determining the time of flowering (Ollerton and Lack 1998). Elevated CO_2 favoured enhanced photosynthetic C assimilation that brought several anatomical and morphological changes; strengthen the sugar signalling of trehalose-6-phosphate (T6P) metabolite for relaying information about tissue carbohydrate availability and controlling gene expression to initiate floral induction phenomenon (Wahl et al. 2013). Several experimental results gave no clear consensus and suggested that in the absence of any biotic or abiotic stress factors with minimal photoperiod sensitivity, the alteration of reproductive phenology/flowering time for different agricultural crops was not consistent under elevated atmospheric CO_2 exposure (Springer and Ward 2007; Craufurd and Wheeler 2009). The response was often cultivar-specific, experimental facility-specific (growth chamber/open-top chamber/free-air CO_2 enrichment and others) and differential responses in elevated CO_2-induced flowering time enabled plant to get complete opportunity for attending optimum growth potential under the modified environmental conditions (Kumar et al. 2014). Depending on species, growing season, varietal specificity and treatment (i.e. type of facility used) with elevated CO_2 exposure, the phonological progress was hastened, delayed, had no effect or had nonlinear effects on the reproductive phenology in different agriculturally important crop species. Accelerated flowering time provides scope for escaping abiotic stress factors from water deficit, heat waves, cold waves, nutrient deficiency, excess light, etc. to ensure maximum resource utilization and explore maximum reproductive potential; while delayed flowering facilitated vegetative growth for more resource acquisition to achieve reproductive success (Roux et al. 2006).

The reproductive traits of wild species were less responsive to elevated CO_2 than the cultivated crop species (Kimball et al. 2002; Jablonski et al. 2002; Ainsworth and Long 2005). Our present discussion will confine for the elevated CO_2 impact on the flowering time of some widely cultivated and agriculturally important crop species only. The brief summary of reported response of reproductive phenology of different agricultural crop species towards elevated atmospheric CO_2 concentration is listed in Table 6.2. Considerable variability in the reported literature suggested that elevated CO_2 impact on the flowering time is highly variable both among and within the species. The persistence of competitive advantage for crop-specific or cumulative coexistence of multiple crop species in natural agro-ecosystem was also uncertain. Therefore, it may be concluded that elevated CO_2 enhanced crop growth and development rates that indirectly influence the flowering time through modification of canopy temperature in the elevated CO_2 grown crop canopy

(Kimball et al. 2002). However, the amplification in growth behaviour could not always be pronounced for creating any consistent impact of elevated atmospheric CO_2 on the reproductive phenology in most of the site-specific suitable cultivated agricultural crop species under any specific localized environment. The elevated CO_2 induced such scattered phenotypic plasticity (i.e. delayed or advanced flowering time) were often short-lived and even disappeared gradually with the generation advancement because it failed to produce any permanent genetic change in the successive generations and also subjected to influence by external biotic and abiotic stress factors in the natural environment (Teng et al. 2009). However, systemic research initiatives on studying the underlying mechanisms and molecular basis of crop species-specific flowering time regulation may unveil the source of observed variability in complex signalling network activation that has the potential to govern flowering time at ecosystem level under elevated CO_2 environment (Kumar et al. 2014; Jagadish et al. 2016). Such research initiatives will enable us for accurate and precise predictions on the probable changes in crop phenology and their impact on terrestrial agro-ecosystem under the projected future elevated CO_2 environmental regimes.

6.2.4 Leaf Area Index

Leaf area index (LAI) is defined as, the total one-sided area of leaf tissue per unit ground surface area. Leaf area index drives both the within- and below-canopy microclimate, determines canopy water interception, radiation extinction, water and carbon gas exchange and therefore be a key component of biogeochemical cycles in ecosystems (Breda 2003). Differences in canopy structure, in terms of the extinction coefficient in the Beer's law and corresponding variation in LAI values for a specific crop species, are the two principal factors for differences in resource use efficiencies from the elevated CO_2 grown crop species to other. Seedlings grown under elevated CO_2 shows dramatic increases in leaf area (Kellomäki and Wang 1997; Tissue et al. 1997). However, the dynamics of pine canopy leaf area production and senescence were unaffected by elevated CO_2, although canopy leaf area senescence for hardwoods was slowed down (McCarthy et al. 2007). In contrast, Norby et al. (2003) found that there was no effect of elevated CO_2 on leaf area index for forest species. Ainsworth and Long (2005) reviewed an average 21% increase in LAI for tree species but no significant change in LAI for herbaceous C_3 grasses. For different agricultural crops (like chickpea), elevated CO_2 exposure increased growth characteristics, viz. shoot length, total number of branches, leaf area per plant, seed yield with significant increase in leaf and shoot dry weight (Pal et al. 2008). In black gram (*Vigna mungo L.*), Vanaja et al. (2007) reported that growth parameters viz. length and weight of root and shoot, root: shoot ratio, leaf area and plant weight significantly increased at 700 ppm CO_2 exposure in the open-top chamber experiment. Weigel and Manderscheid (2012) reported about no statistically significant

CO_2 effect on LAI for barley and wheat but significant reduction for ryegrass. Elevated CO_2 also modified the temporal extent plant LAI response by delaying LAI loss to senescence in soybean (Dermody et al. 2006, 2008) and early attaining of peak LAI in pigeon pea (Saha et al. 2012). In other open-top chamber studies, significant increase in LAI was reported for *Lolium perenne* (Nijs et al. 1989), wheat (Tausz-Posch et al. 2012), sorghum (Ottman et al. 2001), *Cenchrus ciliaris* L. (Bhatt et al. 2007), soybean (Dermody et al. 2008), rice (De Costa et al. 2006; Zeng et al. 2011), pigeon pea (Saha et al. 2012) and chickpea (Saha et al. 2014a, b) for different levels of atmospheric CO_2 enrichment. However, the reducing trend of LAI in atmospheric CO_2 enrichment was evident for maize (Kim et al. 2007), sugarbeet (Erbs et al. 2010) and *Echinochloa crusgalli* L. (Zeng et al. 2011). The short-term exposure of elevated CO_2 increased plant biomass production in rice significantly, without change in LAI (Imai et al. 1985; Anten et al. 2004). This can be further explained by means of a reduced total leaf N in the canopy counterbalancing the increase in LAI for a given leaf N content and arguing the LAI increase under elevated CO_2 can only happen if N uptake from the soil is simultaneously increased (Anten et al. 2004). Thus, lower N availability may be one of the most effective causes for suppressing the amplifying response of LAI towards elevated CO_2 environment (Arnone and Körner 1995; Franklin and Ågren 2002).

The observed response of total canopy leaf area towards atmospheric CO_2 enrichment varied from one crop to another. Sims et al. (1999) also observed no significant difference in total canopy leaf area with elevated CO_2 level of 700 μmol mol^{-1} for sunflower. Meta-analytic studies of the free-air CO_2 enrichment (FACE) claimed for an 11% increase of peak LAI (Kimball et al. 2002), but almost no increase in average LAI of different popular agricultural crop species over the crop period was reviewed (Long et al. 2004). Under N scarce condition, leaf N may be remobilized from older to developing new leaves in elevated CO_2, accelerating senescence of shaded foliage and thus reducing canopy LAI (Hartz-Rubin and DeLucia 2001). Ewert (2004) reviewed the relatively smaller interactions between LAI and elevated CO_2 effects on canopy assimilation. However, the net impact on the LAI dynamics got nullified when 36 mesocosms containing the community of C_3 legume, *Trifolium repens* and a C_4 grass, *Stenotaphrum secundatum* were grown under elevated CO_2 with high P fertilization (Edwards et al. 2005).

6.2.5 Leaf Chlorophyll Content

Chlorophyll is one of the major leaf pigments regulating leaf photosynthesis. Our literature survey gave a brief account of changes in chlorophyll a, b and total chlorophyll content for different agricultural crop species under elevated CO_2 exposure (Table 6.1). Leaf N dynamics have the most crucial role to determine the net response for modified chlorophyll concentration and photosynthetic response for the elevated CO_2 grown crops (Delgado et al. 1994). It is evidently clear that leaf chlorophyll content reduced in majority of crop species under elevated CO_2 exposure except in

Table 6.1 Reported summary of observed response of leaf chlorophyll towards elevated CO_2 environment in different agricultural crops

			Percentage response			
Plant species	Facility used	Level of CO_2 (ambient/elevated)	Chlorophyll a	Chlorophyll b	Total chlorophyll	References
Cotton (*Gossypium hirsutum* L. cv. Stoneville 213)	Growth chamber	350	–	–	−58.1 to −61.4	Delucia et al. (1985)
Water hyacinth (*Eichhorniacrassipes* Mart. Solms)	Growth chamber	330/600	–	–	−26	Spencer and Bowes (1986)
Agave vilmoriniana	Open-top chamber	370/750	−20	−31	−12	Szarek et al. (1987)
Yellow-poplar (*Liriodendron tulipifera* L.)	Open-top chamber	376/(540–676)	0 to −24	−8 to −42		Wullschleger et al. (1992)
White oak (*Quercus alba* L.)	Open-top chamber	376/540–676	−14 to −53	−30 to −73		Wullschleger et al. (1992)
Opuntia ficus-indica (CAM)	Open-top chamber	370/(520–720)	−17 to −61	−24 to −63		Cui et al. (1993)
Maranthes corymbosa	Tents	700	+0.4	−2.1	+2.2	Eamus et al. (1993)
Winter wheat (*Triticum aestivum* cv. MV16)	Open-top chamber	350	–	–	−24.6	Tuba et al. (1994)
Winter wheat (*Triticum aestivum*cv. Coker)	Open-top chamber	350/(525–700)	–	–	−11.6 to −18.6	Sicher and Bunce (1997)
Barley (*Hordeum vulgare* cv. Wyson)	Open-top chamber	350/(525–700)	–	–	−4.8 to −7.1	Sicher and Bunce (1997)
Wheat (*Triticum aestivum*cv Zdar line A)	Growth chamber	350/800	−6.5	−5.7	–	Ulman et al. (2000)
Brassica juncea cv. Bio-183-92	Open-top chamber	350	−32.5	No change	–	Uprety and Mahalaxmi (2000)
Potato (*Solanum tuberosum* L. cv. Bintje)	Open-top chamber	400/720	–	–	−5.9	Katny et al. (2005)
Maize (*Zea mays* L., cv. Pioneer 3733)	Soil–plant–atmosphere research (SPAR) chamber	370	−5.7	−1.9		Kim et al. 2006

(continued)

Table 6.1 (continued)

Plant species	Facility used	Level of CO_2 (ambient/elevated)	Percentage response			References
			Chlorophyll a	Chlorophyll b	Total chlorophyll	
Maize (*Zea mays* L., cv. Pioneer 3733)	Soil–plant–atmosphere research (SPAR) chamber	370/750	–	–	−12.5	Kim et al. (2007)
Soybean (*Glycine max* cv. Clark)	Growth chamber	360/700	–	–	+23.1	Sicher (2010)
Rice (*Oryza sativa* L. cv. Notohikari)	Growth chamber	390/1000	–	–	−14.5	Seneweera et al. (2011)
Tobacco cv. Samsun	Growth chamber	360/700	–	–	−12.5	Sicher (2011)
Chickpea (*Cicer arietinum* L cv. Pusa 1105)	Open-top chamber	400/580	–	–	+25.8	Saha et al. (2013)
Mustard (*Brassica juncea* L.cv. Pusa Bold)	Free-air carbon dioxide enrichment	370/585	–	–	−4.2	Ruhil et al. (2015)
Mung bean (*Vigna radiata* L. cv. Zhonglv 1)	Free-air carbon dioxide enrichment	400/550	+10.9	–	+10.6	Gao et al. (2015)
Mung bean (*Vigna radiata* L. cv Pusa Vishal)	Free-air carbon dioxide enrichment	400/550	+11.6	+ 6.9	+9.9	Dey et al. (2016)
Cowpea (Vigna unguiculata L.cv PusaSukomal)	Free-air carbon dioxide enrichment	400/550	–	–	+27.3	Dey et al. (2017)

legumes. Reduced N availability with enhanced plant growth often resulted in successive leaf N dilution and significant reduction in leaf chlorophyll content in the majority of cereals and other reported crop species (Sicher and Bunce 1997; Uprety and Mahalaxmi 2000; Seneweera et al. 2011). Effective N supplementation from external sources and supportive N management practices have the potential to minimize the depressive impact of elevated CO_2 exposure on tissue N concentration and leaf chlorophyll content to a variable extent (Tausz et al. 2017; Gadpayle et al. 2018). In legumes, the increased nodule's nitrogen fixation capacity might ensure the sufficient N supply to the growing leaves that maintained or even increased leaf chlorophyll content under elevated CO_2 exposure (Al-Rawahy et al. 2013; Saha et al. 2016; Dey et al. 2016). Under elevated CO_2 exposure, modification in leaf chlorophyll content was regulated by the prevailing light environment. High-to-moderate light availability (>500 μmol m^{-2} s^{-1}), depressed leaf chlorophyll content (Wullschleger et al. 1992), but low light (<250 μmol m^{-2} s^{-1}), often promoted the leaf chlorophyll response under elevated CO_2 exposure (Eamus et al. 1993). Increase in leaf chlorophyll content yielded the concomitant rise in PAR harvesting and photon fixation for leaf-level C assimilation with efficient leaf-level resource utilization biochemistry. Any reduction in leaf chlorophyll content depressed the elevated CO_2 induced PS II stimulation under insufficient N availability (Nabity et al. 2012).

6.2.6 Aboveground Biomass Production and Resource Use Efficiencies

The elevated atmospheric CO_2 modified the aboveground biomass accumulation pattern through its deterministic regulation on plants' source-sink balance of several C_3, C_4 and CAM species. However, the net impact of elevated atmospheric CO_2 on modifying canopy photosynthetic capacity and dark respiration process varies across the agricultural crop species; thus, it determines the actual degree of control over source-sink balance. Elevated CO_2 exposure experiments were mostly aimed to determine the effective degree of control and modified resource use pattern of these diverse agricultural crop species. The results of such experimentation became the potential input for formulation of crop simulation models to predict our future agricultural production under modified atmospheric environment in the projected elevated CO_2 world. Ainsworth and Long (2005), reviewed ~31% increase in the light-saturated leaf photosynthetic rate with elevated CO_2 exposure to plant canopy, resulted from 28% increase in the diurnal photosynthetic carbon assimilation. Thus, elevated CO_2 has a consistent fertilization effect on plant aboveground biomass production for both C_3 and C_4 plant species. The major stimulating factor of elevated atmospheric CO_2 on the significant increase in aboveground plant biomass was evident in several agricultural crop species viz. sweet potato (Bhattacharya et al. 1985), berseem (Pal et al. 2004), radish (Usuda 2006), potato tubers (Högy and Fangmeier 2009), wheat (Porteaus et al. 2009; Högy et al. 2010; Lam et al. 2012a; Tausz-Posch et al. 2012), sugarbeet (Manderscheid et al. 2010), barley (Wall et al. 2011), *Brassica* *napus* L. (Franzaring et al. 2008; Frenck et al. 2011), rice (Lieffering et al. 2004; Zeng et al. 2011), pigeon pea (Saha et al. 2011), soybean (Rogers et al. 1986; Lam et al. 2012b), chickpea (Saha et al. 2014a, b), sorghum (Prasad et al. 2009), maize (Meng et al. 2014), etc. The underlying mechanism for such elevated CO_2 fertilization impact may be explained with the increased partitioning of photosynthetically assimilated carbon towards the growing plant organs under variable circumstances and magnitudes. At crop maturity, it often resulted a significant decrease in aboveground stem biomass of C_3 potato with the increasing level of atmospheric CO_2 enrichment (Högy and Fangmeier 2009). Enhanced leaf-level net assimilation rate (NAR) with more tiller numbers or higher LAI often increased the competitive ability of biomass production in C_4 barnyard grass (*Echinochloa crusgalli* L.) over C_3 rice crop grown under elevated atmospheric CO_2 exposure (Zeng et al. 2011). However, increased C_4 plants sink capacity, better water availability and higher nutrient status determined the degree of net plant growth response towards elevated CO_2 exposure (Meng et al. 2014). Accelerated leaf warming from reduced transpiration has the potential to nullify the net impact of elevated CO_2 on aboveground biomass accumulation in C_4 crops (Siebke et al. 2002; Prasad et al. 2006; Kim et al. 2007). C_4 photosynthetic rates often undergo the thermal acclimation within their optimal growth temperature range by adjusting capacity and reallocating N among their photosynthetic components (Dwyer et al. 2007).

6.2.6.1 Tissue Nitrogen Dynamics and N Use Efficiency

Nitrogen availability was identified to be the most important potential limitation factor for determining the plant responsiveness towards the rising atmospheric CO_2 (Leakey et al. 2009). The relative changes in crop response under elevated CO_2 environment were primarily determined by the plant N uptake (Kim et al. 2003; Wang et al. 2013). Under adequate N availability, the most obvious positive impact of elevated atmospheric CO_2 from higher biomass production in C_3 plants were often escorted by the widespread decrease of nitrogen concentration in the vegetative tissues (Cotrufo et al. 1998; Wang et al. 2013; Yang et al. 2006) as well as cereal and legume grains (Taub et al. 2008; Myers et al. 2014; Saha et al. 2015; Chaturvedi et al. 2017a); that was ranging between 6 and 16%. The stimulated crop growth often overshadowed the increased N acquisition under elevated CO_2 environment. Modelling studies predicted elevated CO_2 has the potential to decrease the global mean protein concentration decrease by −9% in 2050 (Asseng et al. 2019). This might have an extensive impact on global nutritional security; thus, became the grave concern for the scientific community. The observed reduction in tissue level N concentration may be explained by the negative allometric relation between tissue N concentration and biomass production (Han et al. 2013; Cai et al. 2016; Tausz et al. 2017). Inhibited the NO_3^- assimilation (Bloom et al. 2012) and/or, photosynthetic downregulation under reduced N availability (Stitt and Krapp 1999) also resulted in the decrease of tissue N concentration and enhanced leaf senescence (Fangmeier et al. 2000). However, elevated CO_2 had negligible impact on the rate of aboveground biomass accumulation per unit rate of increase in plant N and the relative magnitude of N dilution in the crop species with similar canopy volume (Coleman et al. 1993).

Several past studies unveiled the positive impact of elevated CO_2 for increasing leaf-level photosynthetic nitrogen use efficiency i.e. photosynthetic C assimilation per unit of leaf N (Davey et al. 2006; Leakey et al. 2009). Photosynthetic acclimation downregulated plant N uptake that ensured the optimum N distribution within crop canopy towards the maximization of C acquisition under long-term elevated CO_2 exposure (Shimono et al. 2009). That could increase the leaf-level N use efficiency under elevated CO_2 exposure (Drake et al. 1997). But the net response varied greatly with variation in crop growth stages. Meta-analytic review showed that the least impact of the nonspecific leaf N dilution for depressing the net magnitude of accelerated photosynthetic C assimilation under elevated CO_2 (Ainsworth and Long 2005; Ainsworth and Rogers 2007). With sufficient N availability under CO_2 enrichment, the accelerated photosynthetic C assimilation determined the degree of increase in N uptake and regulated internal regulation on plant N distribution, that stimulated root growth for greater N uptake (Yang et al. 2007; Pacholski et al. 2015), enhanced sink strength (Feng et al. 2015) and accelerated leaf senescence (Fangmeier et al. 2000) under elevated CO_2 exposure. That increased the potential for higher net N uptake with successive dilution in foliage (including grain) N under elevated CO_2 exposure (Pritchard et al. 2006; Calfapietra et al. 2007; Leakey et al. 2009; Cai et al. 2016; Walker et al. 2017). Therefore, the efficiency of total N use, N uptake and N utilization at canopy level were higher under sufficient soil moisture availability for the elevated CO_2 grown rice (Yang et al. 2007; Roy et al. 2012), pine and deciduous trees (Peterson et al. 1999), sorghum (Torbert et al. 2004), soybean (Torbert et al. 2004; Lam et al. 2012a; Hao et al. 2016; Li et al. 2017) oilseed rape (Franzaring et al. 2011) and wheat (Xiao et al. 2009; Tausz et al. 2017; Dier et al. 2018).

6.2.6.2 Radiation Use Efficiency

Crop modelling approaches are adapted to periodic variation in the resource utilization pattern for assessing the species-specific constancy of energy conversion by the standing crop canopy and their successive conversion into aboveground dry matter including economic grain yield under non-stressed environmental conditions. One of the simplest approaches is aimed to quantify the source utilization per unit of biomass production. Solar radiation is one of the most important primary natural resource, utilized by any standing crop species. Radiation use efficiency (RUE in g MJ^{-1}) is defined as the ratio of the accumulated aboveground biomass (includes dead-leaf mass) to the cumulated intercepted photosynthetically active radiation (PAR) during the entire/any specific crop growth period without exposure to any biotic/abiotic environmental stress factors. RUE is an integral characteristic of net canopy photosynthesis and plant respiration. RUE accounted leaf-level quantum yield for daily photosynthetic C gain and the successive conversion of photosynthetic C into dry matter at canopy level (Monteith 1981). Crop yield is defined as a function of three regulatory factors viz. (a) cumulative intercepted photosynthetically active radiation (IPAR) over the entire crop growth period, (b) conversion efficiency of IPAR into plant dry matter i.e. radiation use efficiency (RUE) and (c) relative proportion of dry matter partitioning towards economic grain yield over total plant biomass production i.e. harvest index (HI).

$$\mathrm{Y} = \left(\mathrm{IPAR} \times \mathrm{fIPAR}\right) \times \mathrm{RUE} \times \mathrm{HI}$$

Any increase in crop yield under elevated CO_2 exposure relied on the increase in at least one or two components of the abovementioned equation. In this section, we will confine our discussion of all these factors controlling crop yield except harvest index (HI; to be discussed later). Improvement in photosynthetic RUE has the greatest potential to increase crop yield in the projected modified environmental condition in near future. In present atmospheric CO_2 concentration, the potential average crop RUE values were estimated as 4.6% and 6% for the C_3 and C_4 crops (at 30 °C air temperature; Zhang et al. 2008). With the rise in atmospheric CO_2, the relative advantage of C_4 over C_3 plants will disappear in the coming century (Allen et al. 2011). Theoretically, the net increase in crop RUE under elevated CO_2 accounted some potential possibilities likely, (a) significant rise in aboveground biomass production (dry matter or economic grain yield) from enhanced photosynthetic rate in most of the C_3 crop species under sufficient light availability (>1000 μmol m^{-2} s^{-1} PAR flux; Idso et al. 1994) and (b) reduction in cumulative intercepted PAR (IPAR) within the elevated CO_2 crop canopy in absence of any biotic or abiotic environmental stress factors. Moreover, atmospheric CO_2 elevation (~700 μmol mol^{-1}) has the ameliorative impact on leaf-level photosynthetic C assimilation under limited water availability and thus increased 30% peanut RUE (Clifford et al. 2007). However, some crop modelling studies suggested that the primary mechanism of higher biomass accumulation via radiation use efficiency (RUE) was not critical to explain the overall response of crop species towards atmospheric CO_2 enrichment (O'Leary et al. 2015).

The cultivar specificity of RUE was mostly determined by the N uptake ability of the crop that often gradually declines after anthesis. RUE and leaf N concentration was closely related in elevated CO_2 grown rice canopy. Under elevated CO_2, quadratic increase of RUE was evident with increase in specific leaf N weight (Dier et al. 2018). The increase in total nitrogen uptake ensured the dramatic increase in canopy LAI at early crop growth stages that also contributed ~35% increase in rice RUE (Weerakoon et al. 2000). However, the reduction in leaf N concentration at post-heading stage contributed to the sharp decline in crop RUE value under the elevated CO_2 grown rice (De Costa et al. 2006; Shimono et al. 2009). N availability for achieving optimum seasonal light interception is independent to the atmospheric CO_2 level elevation. Therefore, the role of canopy radiation intercepted fraction (% radiation captured by the canopy) is very limited in determining the net crop RUE under elevated CO_2 environment (Weerakoon et al. 2000; Manderscheid et al. 2009). Higher CO_2 assimilation rate under elevated CO_2 exposure with sufficient N availability ensured higher canopy cover and enhanced plant's quantum use efficiency of photosynthesis towards higher biomass production (Manderscheid et al. 1997) i.e. more dry matter accumulation in expense of per unit intercepted canopy radiation fractions as well as the absolute increase in net primary productivity under elevated CO_2 environment (Norby et al. 2003). Elevated CO_2 induced amplification in leaf-level light-saturated photosynthetic rate and higher apparent quantum yield contributed to higher crop RUE under elevated CO_2 exposure (Hui et al. 2001; De Costa et al. 2006). Similar increase in crop RUE was evident over several cultivated crop species under elevated CO_2 environment viz. wheat (Monje and Bugbee 1998; Manderscheid et al. 2003; Mulholland et al. 2007), cotton (Pinter et al. 1996), sunflowers (Hui et al. 2001); soybean (Acock et al. 1985; Dermody et al. 2008), barley (Manderscheid et al. 2009), pigeon pea (Saha et al. 2012), chickpea (Saha et al. 2014a, b), etc. (Table 6.2).

In general, elevated CO_2 induced amplification in leaf-level photosynthesis mostly enhanced aboveground biomass accumulation and so as the crop RUE. However, leaf area index (LAI) and leaf orientation/distribution within the canopy are the two important traits for effective determination of the extent of cumulative radiation interception by the crop canopy. These two traits finally contributed to the accelerated plant growth rate and crop RUE values under elevated CO_2 environment. The limited N availability most probably restricted the amplification of canopy LAI and any detectable changes in cumulative canopy radiation interception in most of the C_3 crop species (Rudorff et al. 1996; DeLucia et al. 2002; Norby et al. 2003). For C_4 corn, the positive impact of elevated CO_2 was absent possibly due to limited sensitivity of leaf photosynthesis towards the present level of ambient atmospheric CO_2 elevation (Kim et al. 2006). Under sufficient N availability, significant increase in LAI resulted in greater leaf expansion rate and more absorption of incident PAR that yielded higher crop RUE value under elevated CO_2 exposure (Pinter et al. 1996; Mulholland et al. 1998; Dermody et al. 2008). There are also some other contrasting possibilities for the reported increase in crop RUE under elevated CO_2 condition.

Elevated CO_2 modified the canopy structure by shifting the distribution of leaf area within the canopy so that more leaf area was concentrated near the top of the canopy, resulted in as much as a 50% reduction in photon flux density in the upper portions of the elevated CO_2 exposed sunflower canopy (Sims et al. 1999). Under elevated CO_2 environment, alike changes in leaf area distribution ensured the proportionate increase in low-intensity leaf-scattered light fraction availability to the older leaves in lower portion canopy (Hui et al. 2001). Enhanced canopy LAI with modified leaf orientation reduced the self-shading and older leaf deaths in the elevated CO_2 grown crop canopy and thereby facilitated the formation of 'closed leaf canopy' structure with more uniform and homogeneous distribution of light (PAR) in any horizontal plane (Charles-Edwards et al. 1986). Such elevated CO_2 induced modification in crop architecture reshaped canopy radiation profile and gradually increased the relative contribution from enhanced leaf photosynthetic C assimilation

Table 6.2 Reported summary of percentage change in crop radiation use efficiency, in relation to magnitude of amplification in leaf area index and canopy radiation capture under elevated CO_2 environment

S. no	Crop species	CO_2 concentration in ppm (ambient/elevated)	Facility used	LAI	Radiation capture (absorbed/intercepted)	Magnitude of RUE amplification under elevated CO_2	References
1.	Soybean (*Glycine max* Merrcv.Forrest)	330/800	Sunlight controlled-environment chamber	+22.80	No change (IPAR)	+40	Acock et al. (1985)
2.	Groundnut (*Arachis hypogaea* L.cv Kadiri-3)	350/700	Controlled-environment glasshouse	+6.70	Increased (IPAR)	+30 to +94	Clifford et al. (2007)
3.	Cotton (*Gossypium hirsutum* L. cv. Deltapine 77)	370/550	Free-air CO_2 enrichment	–	+100 (APAR)	+20 to +23	Pinter et al. (1994)
4.	Cauliflower (*Brassica oleracea* L. botrytis cv Plana F 1)	328/531	Glasshouse experiment	–	No change (IPAR)	+41.5	Wheeler et al. 1995
5.	Winter wheat (*Triticum aestivum* L. cv. Massey and Saluda)	350/500	Open-top chamber	No change	No change (APAR)	+8 to +15	Rudorff et al. (1996)
6.	Maize (*Zea mays* L. cv. Pioneer 3714)	350/500	Open-top chamber	No change	No change (APAR)	No change	Rudorff et al. (1996)
7.	White clover (*Trifolium repens* cv. Karina)	385/(480–660)	Open-top chamber	+40	Increased (IPAR)	+20 to +50	Manderscheid et al. (1997)
8	Spring wheat (*Triticum aestivum* L. cv. Minaret)	350/550–680	Open-top chamber	+ 49	+0.3 to +8 (IPAR)	+3 to+15	Mulholland et al. 1998
9	Wheat (*Triticum aestivum* L. cv. Veery 10)	330/1200	Controlled-environment chamber	Decreased	No change (APAR)	+14	Monje and Bugbee (1998)
10.	Rice (*Oryza sativa* L. cv. IR72)	350/600–700	Open-top chamber	No change	No change (IPAR)	+19 to +31.8	Weerakoon et al. (2000)

11.	Rice (*Oryza sativa* L. cv. BG300)	(363 ± 16)/(567 ± 28)	Open-top chamber	+11.01 to +34.5	No change (IPAR)	+11 to +20	De Costa et al. (2006))
12.	Sunflower (*Helianthus annus* var. mammoth)	399/746	Environmentally controlled plant growth facility	No change	–	+45 to +54	Hui et al. (2001)
13.	Pine (*Pinus taeda* L.)	360/560	Free-air CO_2 enrichment	No change	No effect (APAR)	+27	DeLucia et al. (2002)
14.	Wheat (*Triticum aestivum* L. cv. Minaret)	395/675	Open-top chamber	+35	No effect (APAR)	+27.7 to +37.2	Manderscheid et al. (2003)
15.	Sweetgum (*Liquidambar styraciflua*)	391/542	Free-air CO_2 enrichment	No change	No effect (APAR)	+16.08 to +35.5	Norby et al. (2003)
16.	Soybean (*Glycine max* cv. 93B15, Pioneer Hi-Bred, Johnston, IA, USA)	370/550	Free-air CO_2 enrichment	+9 to +25	+3 (IPAR)	+12	Dermody et al. (2008)
17.	Barley (*Hordeum vulgare* L. cv. Theresa)	375/550	Free-air CO_2 enrichment	No change	+0.5 to +9.3 (APAR)	10–13.5	Manderscheid et al. (2009)
18.	Rice (*Oryza sativa* L. cv. Kirara397, Kakehashi, Akitakomachi, Hitomebore)	365/560	Free-air CO_2 enrichment	–	+0 to +8.8 (IPAR)	10.7–29.2 (at preheading stage)	Shimono et al. (2009)
19.	Pigeon pea (*Cajanus cajan* L. cv. Pusa 992 and PS 2009)	380/550	Open-top chambers	+16.1 to +18	No change (IPAR)	+52.30	Saha et al. (2012)
20.	Maize (*Zea mays* L., cv. ‘Romario’)	378/550	Free-air CO_2 enrichment	No change	No effect (APAR)	No change	Manderscheid et al. (2014)

(continued)

Table 6.2 (continued)

S. no	Crop species	CO_2 concentration in ppm (ambient/ elevated)	Facility used	LAI	Radiation capture (absorbed/ intercepted)	Magnitude of RUE amplification under elevated CO_2	References
21.	Rice (*Oryza sativa* L. cv. Rajshree, Rajendra bhagwati, Swarna sub 1, MTU 7029)	380/480	Open-top chamber	+5.6 to +78.9	+6 to +14 (IPAR)	+8.85 to +14.2	Singh et al. (2013)
22.	Chickpea (*Cicer arietinum* L.cv. Pusa 1105)	(384 ± 13)/ (580 ± 20)	Open-top chamber	+8.2 to +17.3	No change (IPAR)	+24	Saha et al. (2014a, b)
23.	Wheat (*Triticum aestivum* L. cv. Batis)	395/600	Free-air CO_2 enrichment	+4 to +22	+4 to +10	+15 to +22	Dier et al. (2018)

from shaded/ older leaves of lower plant canopy (Idso et al. 1994; Manderscheid et al. 2003). At leaf level, the quantum yield of photosynthesis is higher in shaded leaves (Long and Drake 1991; Osborne et al. 1998). Therefore, elevated CO_2 enabled the developing plant canopy to capture and utilize the diffuse intercepted radiation fraction more efficiently; thus, attributed to the widespread increase of final crop RUE value (Richards 2000). The increased radiation penetration within the crop canopy also reduced the leaf-level light saturation and facilitated the effective utilization of intercepted radiation to enhance crop RUE value under elevated CO_2 environment (Smart et al. 1994; De Costa et al. 2006).

Increased radiation penetration through 17% reduction in extinction coefficient (*k*), with ~30% increase in wheat canopy LAI indicated the modification of canopy architecture grown under elevated CO_2 exposure (Sims et al. 1999). Changes in leaf angle distribution under atmospheric CO_2 environment might play a significant role in the observed increase in crop RUE and canopy LAI simultaneously, without any significant change in canopy radiation interception fractions. Under sufficient N availability, elevated CO_2 exposure (+200 ppm in FACE system) reduced wheat leaf tip angle distribution by 4° with improved canopy light capturing ability, enhanced canopy level net CO_2 exchange rate and green plant area index (Brooks et al. 2000). Mean canopy leaf angles are related to the canopy light extinction coefficients (Wheeler et al. 1995). The observed modification in leaf angle distribution resulted the significant reduction in canopy light extinction coefficients (*k)* in wheat (−17.1%; Smart et al. 1994), pigeon pea (−7.5%; Saha et al. 2012), chickpea (−21.3%; Saha et al. 2014a, b) under elevated CO_2 exposure treatments. However, such elevated CO_2 induced modification was absent for cauliflower (Wheeler et al. 1995). Diurnal variation of RUE was low at noon and high in the morning or afternoon for the elevated CO_2 grown crop canopy that leads to the significantly higher value of cumulative RUE under elevated CO_2 (Hui et al. 2001). Therefore, the use of a constant multiplier of RUE to model effects of increased atmospheric CO_2 concentrations on crop growth is questionable. Our present elevated CO_2 research should be focused on the growth stage-specific daily leaf C gain dynamics, identification of phenology-associated gene and their role in controlling phonological plasticity and crop growth specific RUE values for different crop species under variable soil N availability. In addition, recent advancement of next-generation sequencing technologies (QTL identifications, RNA interference, etc.) may play their inevitable role in characterizing the genetic loci for the observed variability in the location-specific research outcome. Indirectly, similar studies will increase the efficiency of crop simulation models for better future prediction of agricultural productivity under variable degree of input availability in the projected scenario of climate change.

6.2.6.3 Water Use Efficiency

Increasing atmospheric CO_2 level from the accelerated degree of anthropogenic climate change phenomenon has envisaged the periodic water use dynamics (evapotranspiration) and water use efficiency (WUE) of majority of the crop species

(Hunsaker et al. 2000; Thomas 2008). Alike RUE, WUE is defined as the ration of accumulated aboveground biomass (includes dead-leaf mass) per unit of cumulative crop water use (i.e. evapotranspiration-ET)/consumed by the standing crop species over the entire/ any specific crop growth period under non-stressed environmental conditions. A significant decrease in water consumption (ET), combined with the obvious increase in aboveground biomass production from enhanced photosynthesis under elevated CO_2 was expected to raise the average crop WUE values. Increases in plant growth under elevated CO_2 might cause a rapid depletion of other limiting resources (Koch and Mooney 1996; Pospíšilová and Čatský 1999). But, conversely there was overwhelming evidence that elevated CO_2 reduces stomatal conductance and that had the potential to increase water use efficiency in different cultivated crop species viz. rice (Kumar et al. 2019), wheat (Hunsaker et al. 2000; O'Leary et al. 2015; Manderscheid et al. 2018), sorghum (Conley et al. 2001), soybean (Madhu and Hatfield 2014), pigeon pea (Saha et al. 2011), field pea (Parvin et al. 2019), etc. Growth-chamber experiment shows that water use efficiency in terms of shoot biomass and grain yield were increased under elevated CO_2 because the magnitude of the increase in shoot dry weight and grain yield was greater than that of the total consumption of water under elevated CO_2 conditions (Wu et al. 2004). Under high soil moisture, small reduction in ET in wheat grown under well-watered and high soil N conditions increased crop WUE under elevated CO_2 (Hunsaker et al. 2000). Increased root growth and faster canopy closure may lead to higher root water uptake under elevated CO_2 (Polley 2002; Saha et al. 2011, 2016). Under long-term elevated CO_2 exposure, the net impact may get nullified towards water savings at the end of experiment (Kammann et al. 2005). In FACE experiment, cotton ET measured using three independent approaches: soil water balance (Hunsaker et al. 1994), sap flow gauges (Dugas et al. 1994) and energy balance (Kimball et al. 1994), showed no significant change with increased CO_2 to 550 μmol mol^{-1} level. Schapendonk et al. (1997) reported that, though the average water use efficiency was increased at elevated (doubled) CO_2, but the higher water use efficiency was fully compensated for by a higher leaf area index, as they found total transpiration on a canopy basis was equal for the both ambient and elevated CO_2 concentrations. The elevated CO_2 induced stomatal closure increased soil moisture ameliorated the impact of water deficit stress and increased the plant's efficiency for soil moisture uptake (Widodo et al. 2003; Zavaleta et al. 2003; Li et al. 2004; Sarker and Hara 2009). Our present crop breeding approach should be focused for achieving higher water use efficiency under elevated CO_2 environment (Condon et al. 2004).

6.2.7 Yield Component and Harvest Index

Harvest index is defined as the ratio of economic grain yield to the total dry matter yield at harvest. It is an effective primary tool for screening crop varieties under elevated CO_2 exposure. The net impact of elevated CO_2 accounted for the obvious rise in net aboveground dry matter yield as well as economic grain yield. In absence of external abiotic stress factors, the relative proportion of increase for these two factors depends on changes in the resource conversion efficiency of elevated CO_2 grown crop species. The crop species with positive response in the HI values will be advantageous to grow under the future projected elevated CO_2 world.

The observed obvious trend of increased crop dry matter accumulation under elevated CO_2 may not always result in decreased harvest index; preferably due to inconsistent behaviour of different crop species towards the economic grain yield under atmospheric CO_2 enrichment. Cultivar specificity of the elevated CO_2 induced seed yield enhanced factor was evident for soybean (Ziska et al. 2001), spring wheat (Manderscheid and Weigel 1997), *Brassica napus* L. (Frenck et al. 2011), etc. The stimulative effect of elevated CO_2 on grain yield for rice (Kim et al. 2003; Lieffering et al. 2004; Liu et al. 2008), wheat (Wu et al. 2004; Lam et al. 2012a; Weigel and Manderscheid 2012), soybean (Cure et al. 1988; Ziska et al. 2001), pigeon pea (Vanaja et al. 2007), potato (Craigon et al. 2002; Högy and Fangmeier 2008), barley and sugar beet (Weigel and Manderscheid 2012). Grain yield was reported to remain unaltered for wheat and barley (Sæbø and Mortensen 2002), soybean (Rogers et al. 1986; Ferris et al. 1999), with varying levels of atmospheric CO_2 enrichment. The conversion ability of accumulated dry matter into the economic seed yield differs from one crop species to other with a large variable and erratic response crop harvest index values under elevated CO_2 enrichment (Table 6.3).

The rise in grain yield is evident for majority of the experiments. However, the origin of the increase varied from one experiment to another. Elevated CO_2 significantly increased wheat seed yield due to increased tiller number and seed mass, but with decreasing the number of seeds per head resulted from a sustained increase in canopy quantum yield with no change in harvest index (Monje and Bugbee 1998). In contrast, the increase in the number of wheat grains per plant (Wu et al. 2004) with the faster rate of grain filling (Li et al. 2000) attributed the increase in grain yield under elevated CO_2 treatment. Bunce (2008) reported about the change in the number of pods produced by *Phaseolus vulgaris* L, grown under elevated CO_2, was the primary determinant of the response of harvested seed yield rather than variation in photosynthetic response. $\delta^{13}C$ study that revealed no significant effect of elevated CO_2 exposure on wheat biomass production and grain filling (Aranjuelo et al. 2011). Expansion of grain ripening period (Imai et al. 1985), more partitioning of photosynthetic assimilates towards increased grain growth and seed yield (Wheeler et al. 1996) gave the natural evolutionarily advantage for those annual crop species to make full use of extra carbon assimilates for increasing plant fitness, by allocating the carbon assimilates (Wu and Wang 2000). Under optimal resource availability and absence of abiotic stress factors, the degree of net response varied even from one variety to another for any specific crop species. The probability of achieving the net positive response is low for C4 crop species. Significant CO_2 × cultivar interaction also existed for the higher productivity under elevated CO_2, a large sink, that is a prerequisite that improves carbon allocation by increasing grain setting resulting in the increased yield response to elevated CO_2 (Hasegawa et al. 2013). Lack of plant's capacity to utilize the more abundant photosynthetic assimilates from the reported photosynthetic stimulation under elevated CO_2 environment depressed

Table 6.3 Observed summary of grain yield (GY) and harvest index (HI) response for different crop species under elevated CO_2 environment

Crop species	Cultivar	CO_2 concentration in ppm (ambient/elevated)	Facility used	GY (% change)	HI (% change)	References
Rice	*Oryza sativa* L. cv. Nipponbare	350/700	Glasshouse experiment	+71.30	+15.38	Imai et al. (1985)
	O. sativa L., cv. IR-30	330/660	Controlled-environment chamber	+59.70	+21.43	Baker et al. (1992)
	O. sativa L., cv.IR-36	360/660	Greenhouse experiment	+65.00	+41.01	Ziska and Teramura (1992)
	O. sativa L., cv. Fujiyama-5	360/660	Greenhouse experiment	No change	No change	Ziska and Teramura 1992
	O. sativa L., cv. IR-30	330/(500–900)	Soil–plant–atmosphere research (SPAR) chambers	+2.92	+4.55	Baker et al. (1996)
	O. sativa L. cv. IR 72	360/560	Open-top chamber	+15 to +27	No change	Ziska et al. (1997)
	O. sativa L. cv. IR 72	370/570	Open-top chamber	+12.5 to +52.9	−5.6	Moya et al. (1998)
	O. sativa L. cv. Azucena, IRAT 104, IR 28, IR 30, IR 36, IR 72, IR 74, ITA 186, KinandangPatong, OS4, Salumpikit, YRL-39	373/664	Glass house experiment	+32.74	−1.85 to −35.71	Ziska et al. (1996)
	O. sativa L. cv. IAC 165, IR 46, IR 64, MGL-2, N 22	373/664	Glass house experiment	+344.77	+7.14 to +71.4	Ziska et al. (1996)
	O. sativa L. cv. Pusa Basmati 1	385/(575–620)	Open-top chamber	+38.60	−5.2	Uprety et al. (2003)
	O. sativa L. cv. Pusa 677	385/(575–620)	Open-top chamber	+24.10	+12.4	Uprety et al. (2003)
	O. sativa L. cv. BG300	(363 ± 16)/(567 ± 28)	Open-top chamber	+24 to +39	No change	De Costa et al. (2006)
	O. sativa L. cv. Wuxiangjing 14; Japonica	380/580	Free-air CO_2 enrichment	+12.60	−2.60	Yang et al. (2006)

(continued)

Table 6.3 (continued)

Crop species	Cultivar	CO_2 concentration in ppm (ambient/elevated)	Facility used	GY (% change)	HI (% change)	References
Rice	*O. sativa* L. cv. Akitakomachi	365/560	Free-air CO_2 enrichment	+15.90	+5.7	Ziska et al. (1996)
	O. sativa L. cv. BRRIdhan 39	360/570	Open-top chamber	+11.03	−8.67	Razzaque et al. (2009)
	O. sativa L. cv. Khaskani	360/571	Open-top chamber	+43.27	+9.44	Razzaque et al. (2009)
	O. sativa L. cv. Shakkorkhora	360/572	Open-top chamber	+42.63	+24.84	Razzaque et al. (2009)
	O. sativa L. cv. Rajshree, Rajendra bhagwati, Swarna sub 1, MTU 7029	380/480	Open-top chamber	+23.2 to +32.2	+1 to +5.9	Singh et al. (2013)
	O. sativa L. cv. Koshihikari	386/560	Free-air CO_2 enrichment	+6.7 to +16.3	+2	Zhang et al. (2013)
	O. sativa L. cv. Naveen	394/550	Open-top chamber	+16.3 to +27.4	+4	Bhattacharyya et al. (2013)
	O. sativa L. cv. Akita 63, Koshihikari, Takanari	385/560	Free-air CO_2 enrichment	+6.6 to +21.2	No change	Zhang et al. (2015)
	O. sativa L. cv. Changyou 5	390/550	Free-air CO_2 enrichment	+5.1 to +7.5	No change	Cai et al. (2016)
	O. sativa L.Subsp. japonica cv. Wuyoudao no. 4	390/(450–550)	CO_2 gradient tunnel	25	+12.4 to +20.5	Li et al. (2017)
	O. sativa L. cv. NL 44, Pusa 1121	385/580	Open-top chamber	+15.3 to +23.6	+1.8 to +8	Chaturvedi et al. (2017b)
	O. sativa L. cv. Pusa 44	395/550	Free-air CO_2 enrichment	+16.9 to +26.1	No change	Raj et al. (2019)
Wheat	*Triticum aestivum* L. cv. GWO 1809	300/1000	Controlled-environment growth chamber	+62	No change	Sionit et al. (1980)
	T. aestivum L. cv. Massey and Saluda	350/500	Open-top chamber	+14.6 to +26	+5.1 to +9.2	Rudorff et al. (1996)
	T. aestivum L. cv. Minaret	360/520	Open-top chamber	+23.2 to +27.7	No change	Fangmeier et al. (1996)

(continued)

Table 6.3 (continued)

Crop species	Cultivar	CO_2 concentration in ppm (ambient/elevated)	Facility used	GY (% change)	HI (% change)	References
Wheat	*T. aestivum* L. cv. Hereward	380/684	Temperature gradient tunnel	+15 to +55	+1.18	Wheeler et al. (1996)
	T. aestivum L. cv. HeinesKolben, JanetzkisFriiher, Adler, Rimpaus Langensteiner, Turbo, Nandu	379/689	Open-top chamber	+26 to +46	No change	Manderscheid and Weigel (1997)
	T. aestivum L. cv. Veery 10	330/1200	Controlled environment chamber	+13.01	No change	Monje and Bugbee (1998)
	T. aestivum L. cv. Minaret	350/550–680	Open-top chamber	+30	No change	Mulholland et al. (1998)
	T. aestivum L. cv. Polkka	350/700	Open-top chamber	+6.1 to +24.6	+3.22	Hakala (1998)
	T. aestivum L. cv. Malviya 23	360/600	Open-top chamber	+30.5	+16.2	Deepak and Agrawal (1999)
	T. aestivum L. cv. Dragon	350/680	Open-top chamber	+7.1 to +21.2	No change	Pleijel et al. (2000)
	T. aestivum L. cv. Minaret	395/675	Open-top chamber	+4.8 to +12.5	No change	Manderscheid et al. (2003)
	T. monococcum	385/550	Free-air CO_2 enrichment	+13.25	+5.41	Uprety et al. (2009)
	T. durum	385/550	Free-air CO_2 enrichment	+15.9	+10.58	Uprety et al. (2009))
	T. aestivum L. cv. PBW-373	385/550	Free-air CO_2 enrichment	+22.19	+14.89	Uprety et al. (2009)
	T. aestivum L. cv. Yitpi	365/550	Free-air CO_2 enrichment	+22.1 to +30.4	No change	O'Leary et al. (2015)
	T. aestivum L. cv. Yangmai 14	390/480	Free-air CO_2 enrichment	+4.6 to +6.3	No change	Cai et al. (2016)
	T. aestivum L. cv. Yitpi	390/550	Free-air CO_2 enrichment	+18.03 to +33.6	No change	Walker et al. (2017)
	T. aestivum L. cv. Yitpi	400/700	Glasshouse experiment	+28 to +71	No change	Uddin et al. (2018)

(continued)

Table 6.3 (continued)

Crop species	Cultivar	CO_2 concentration in ppm (ambient/ elevated)	Facility used	GY (% change)	HI (% change)	References
Wheat	*T. aestivum* L. cv. Yitpi	390/550	Free-air CO_2 enrichment	+27 to +33	−2	Houshmandfar et al. (2016)
	T. aestivum L. cv. Scout	390/550	Free-air CO_2 enrichment	0 to +16	+2.5 to +3.16	Houshmandfar et al. (2016)
	T. aestivum L. cv. Lianmai6	400/800	Glasshouse experiment	+9.9	No change	Li et al. (2019)
Barley	*Hordeum vulgare* L. cv. Jol621	400/700	Glasshouse experiment	+14.4	No change	Kleemola et al. (1994)
	Hordeum vulgare L. cv. Alexis	366/650	Open-top chamber	+44.7	+2.2	Fangmeier et al. (2000)
	Hordeum vulgare L. cv. Theresa	375/550	Free-air CO_2 enrichment	+8 to +17	No change	Manderscheid et al. (2009)
Maize	*Zea mays* L. cv. Pioneer 3714	350/500	Open-top chamber	+36.90	No change	Rudorff et al. (1996)
	Z. mays L. cv. DHM-117, Varun and Harsha	390/550	Open-top chamber	+46 to +127	+11 to +68	Vanaja et al. (2015a)
	Z. mays L., cv. Romario	378/550	Free-air CO_2 enrichment	No change	No change	Manderscheid et al. (2014)
	Z. mays L. cv. PEHM 5	400/550	Open-top chamber	+53.7	+2	Abebe et al. (2016)
Jowar	*Sorghum bicolor* L. cv. DeKalb 28E	370/570	Free-air CO_2 enrichment	−4.84	−7.6	Conley et al. (2001)
	S. bicolor L. cv. DeKalb 28E	350/700	Soil–plant–atmosphere research (SPAR) chamber	+26	−5 to −19	Prasad et al. (2006)
	S. bicolor L. cv. BRS 330	400/800	Open-top chamber	No change	−15.7	de Souza et al. (2015)
Mustard	*Brassica juncea* cv. Bio!072!81	350/600	Open-top chamber	+47.4 to +48.2	+26.7 to +28.9	Uprety and Mahalaxmi (2000)

(continued)

Table 6.3 (continued)

Crop species	Cultivar	CO_2 concentration in ppm (ambient/elevated)	Facility used	GY (% change)	HI (% change)	References
Groundnut	*Arachis hypogaea* L.cv Kadiri-3	350/700	Controlled-environment glasshouses	+25	+5.5 to +14.2	Clifford et al. (1993)
	A. hypogaea L. cv. Georgia Red	400/800	Controlled-environment chamber	+55.8	+18.7	Stanciel et al. (2000)
	A. hypogaea L. cv. Georgia Green	350/700	Controlled-environment chamber	+30	No change	Prasad et al. (2003)
	A. hypogaea L. cv. Pronto	400/700	Plant growth chamber	−24.4	−53.6	Bannayan et al. (2009)
	A. hypogaea L. cv. Georgia Green	400/700	Plant growth chamber	−53.2	−61.2	Bannayan et al. (2009)
Soybean	*Glycine max* L. Merr cv. Pana and Pioneer 93B15	370/550	Free-air CO_2 enrichment	+0.15	−3	Morgan et al. (2005)
	G. max L Merr cv. A3127, Clark, Dwight, HS93-4118, IA3010, LN97-15076, Loda, NE3399 and Pana;	385/550	Free-air CO_2 enrichment	+12 to +24	−3.5 to +20.5	Bourgault et al. (2016)
Field pea	*Pisum sativum* L. cv. PBA Hayman, Bohatyr, Kaspa and Sturt	390/550	Free-air CO_2 enrichment	+26	No change	Bourgault et al. (2016)
Pigeon pea	*Cajanus cajan* L. cv. Pusa-992, PS-2009	380/580	Open-top chamber	+12.1 to +33	−19.1 to −37.4	Saha et al. (2012)
	C. cajan L. cv. ICPL 15011	390/550	Open-top chamber	+39.7 to +42.7	+3.9 to +5.25	Sreeharsha et al. (2015)
	C. cajan L. cv. ICPL-88039 and AKP-1, GT-1	390/550	Open-top chamber	+3.29 to +23.04	+95 to +132	Vanaja et al. (2015b)
Chickpea	*Cicer arietinum* L. cv. Pusa-1105	385/580	Open-top chamber	+9.6 to +12.6	No change	Saha et al. (2015)

(continued)

Table 6.3 (continued)

Crop species	Cultivar	CO_2 concentration in ppm (ambient/ elevated)	Facility used	GY (% change)	HI (% change)	References
Sunflower	*Helianthus annus* L. cv DRSH1, DRSF 113	(370 ± 20)/ (550 ± 50)	Open-top chamber	+35.2 to +46.1	−13.1 to −16.1	Pal et al. (2014)
	H. annus L. cv. Hybrid KBSH-1	380/ (550–700)	Open-top chamber	+21.1 to +45.9	+1.9 to +3.8	Jyothi Lakshmi et al. (2017)

crop HI values (Rogers et al. 1986; Ziska et al. 1997; Kim et al. 2001; Saha et al. 2012). The cultivars with stable HI values under the atmospheric elevated CO_2 exposure have the greater resiliency to grow as 'no loss–no gain' situation in the elevated CO_2 environment (Manderscheid and Weigel 1997; Monje and Bugbee 1998; De Costa et al. 2006). Selective breeding approaches for these potentially positive responded or stable HI cultivars have the potential to pave the prospect of our future crop improvement research towards enhanced agricultural crop production and attending the global food security in the projected elevated CO_2 world.

References

Abebe A, Pathak H, Singh SD et al (2016) Growth, yield and quality of maize with elevated atmospheric carbon dioxide and temperature in north-west India. Agric Ecosyst Environ 218:66–72. https://doi.org/10.1016/j.agee.2015.11.014

Acock B, Reddy VR, Hodges HF et al (1985) Photosynthetic response of soybean canopies to full-season carbon dioxide enrichment. Agron J 77:942. https://doi.org/10.2134/agronj1985.00021962007700060025x

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol 165:351–372. https://doi.org/10.1111/j.1469-8137.2004.01224.x

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. Plant Cell Environ 30:258–270. https://doi.org/10.1111/j.1365-3040.2007.01641.x

Ainsworth EA, Rogers A, Nelson R, Long SP (2004) Testing the "source–sink" hypothesis of down-regulation of photosynthesis in elevated [CO_2] in the field with single gene substitutions in Glycine max. Agric For Meteorol 122:85–94. https://doi.org/10.1016/j.agrformet.2003.09.002

Allen LH, Kakani VG, Vu JCV, Boote KJ (2011) Elevated CO_2 increases water use efficiency by sustaining photosynthesis of water-limited maize and sorghum. J Plant Physiol 168:1909–1918. https://doi.org/10.1016/j.jplph.2011.05.005

Alonso A, Pérez P, Martínez-Carrasco R (2009) Growth in elevated CO_2 enhances temperature response of photosynthesis in wheat. Physiol Plant 135:109–120. https://doi.org/10.1111/j.1399-3054.2008.01177.x

Al-Rawahy SH, Sulaiman H, Farooq SA et al (2013) Effect of O_3 and CO_2 levels on growth, biochemical and nutrient parameters of Alfalfa (*Medicago sativa*). APCBEE Procedia 5:288–295. https://doi.org/10.1016/j.apcbee.2013.05.050

Andrews TJ, Lorimer GH (1987) Rubisco: structure, mechanisms and prospects for improvement. In: The biochemistry of plants, vol. 10

Anten NPR, Hirose T, Onoda Y et al (2004) Elevated CO_2 and nitrogen availability have interactive effects on canopy carbon gain in rice. New Phytol 161:459–471. https://doi.org/10.1046/j.1469-8137.2003.00943.x

Aranjuelo I, Perez P, Hernandez L et al (2005) The response of nodulated alfalfa to water supply, temperature and elevated CO_2: photosynthetic downregulation. Physiol Plant 123:348–358. https://doi.org/10.1111/j.1399-3054.2005.00459.x

Aranjuelo I, Cabrera-Bosquet L, Morcuende R et al (2011) Does ear C sink strength contribute to overcoming photosynthetic acclimation of wheat plants exposed to elevated CO_2? J Exp Bot 62:3957–3969. https://doi.org/10.1093/jxb/err095

Arnone JA, Körner C (1995) Soil and biomass carbon pools in model communities of tropical plants under elevated CO_2. Oecologia 104:61–71. https://doi.org/10.1007/BF00365563

Asseng S, Martre P, Maiorano A et al (2019) Climate change impact and adaptation for wheat protein. Glob Chang Biol 25:155–173. https://doi.org/10.1111/gcb.14481

Awasthi JP, Paraste KS, Rathore M et al (2018) Effect of elevated CO_2 on Vigna radiata and two weed species: yield, physiology and crop–weed interaction. Crop Pasture Sci 69:617. https://doi.org/10.1071/cp17192

Baker JT, Allen LH, Boote KJ (1992) Response of rice to carbon dioxide and temperature. Agric For Meteorol 60:153–166. https://doi.org/10.1016/0168-1923(92)90035-3

Baker JT, Allen LH Jr, Boote KJ, Pickering NB (1996) Assessment of rice response to global climate change: CO2 and temperature. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic, San Diego, pp 265–282

Bannayan M, Tojo Soler CM, Garcia y. Garcia A et al (2009) Interactive effects of elevated [CO_2] and temperature on growth and development of a short- and long-season peanut cultivar. Clim Change 93:389–406. https://doi.org/10.1007/s10584-008-9510-1

Bettarini I, Vaccari FP, Miglietta F (1998) Elevated CO_2 concentrations and stomatal density: observations from 17 plant species growing in a CO_2 spring in central Italy. Glob Chang Biol 4:17–22. https://doi.org/10.1046/j.1365-2486.1998.00098.x

Bhatt RK, Baig MJ, Tiwari HS (2007) Growth, biomass production, and assimilatory characters in Cenchrus ciliaris L. under elevated CO_2 condition. Photosynthetica 45:296–298. https://doi.org/10.1007/s11099-007-0048-7

Bhattacharya NC, Biswas PK, Battacharya S et al (1985) Growth and yield response of sweet potato to atmospheric CO_2 enrichment. Crop Sci 25:975. https://doi.org/10.2135/cropsci1985.0011183X002500060019x

Bhattacharyya P, Roy KS, Neogi S et al (2013) Impact of elevated CO_2 and temperature on soil C and N dynamics in relation to CH4 and N2O emissions from tropical flooded rice (*Oryza sativa* L.). Sci Total Environ 461–462:601–611. https://doi.org/10.1016/j.scitotenv.2013.05.035

Bloom AJ, Rubio Asensio JS, Randall L et al (2012) CO_2 enrichment inhibits shoot nitrate assimilation in C 3 but not C 4 plants and slows growth under nitrate in C 3 plants. Ecology 93:355–367. https://doi.org/10.1890/11-0485.1

Bourgault M, Brand J, Tausz M, Fitzgerald GJ (2016) Yield, growth and grain nitrogen response to elevated CO_2 of five field pea (*Pisum sativum* L.) cultivars in a low rainfall environment. Field Crop Res 196:1–9. https://doi.org/10.1016/j.fcr.2016.04.011

Bowes G (1991) Growth at elevated CO_2: photosynthetic responses mediated through Rubisco. Plant Cell Environ 14:795–806. https://doi.org/10.1111/j.1365-3040.1991.tb01443.x

Breda NJJ (2003) Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. J Exp Bot 54:2403–2417. https://doi.org/10.1093/jxb/erg263

Brooks A, Farquhar GD (1985) Effect of temperature on the CO_2/O_2 specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. Planta 165:397–406. https://doi.org/10.1007/BF00392238

Brooks TJ, Wall GW, Pinter PJ et al (2000) Acclimation response of spring wheat in a free-air CO_2 enrichment (FACE) atmosphere with variable soil nitrogen regimes. 3. Canopy architecture and gas exchange. Photosynth Res 66:97–108. https://doi.org/10.1023/A:1010634521467

Bunce J (1992) Stomatal conductance, photosynthesis and respiration of temperate deciduous tree seedlings grown outdoors at an elevated concentration of carbon dioxide. Plant Cell Environ 15:541–549. https://doi.org/10.1111/j.1365-3040.1992.tb01487.x

Bunce JA (2004) Carbon dioxide effects on stomatal responses to the environment and water use by crops under field conditions. Oecologia 140:1–10. https://doi.org/10.1007/s00442-003-1401-6

Bunce JA (2008) Contrasting responses of seed yield to elevated carbon dioxide under field conditions within Phaseolus vulgaris. Agric Ecosyst Environ 128:219–224. https://doi.org/10.1016/j.agee.2008.06.003

Cai C, Yin X, He S et al (2016) Responses of wheat and rice to factorial combinations of ambient and elevated CO_2 and temperature in FACE experiments. Glob Chang Biol 22:856–874. https://doi.org/10.1111/gcb.13065

Calfapietra C, De Angelis P, Gielen B et al (2007) Increased nitrogen-use efficiency of a short-rotation poplar plantation in elevated CO_2 concentration. Tree Physiol 27:1153–1163. https://doi.org/10.1093/treephys/27.8.1153

Centritto M, Lucas ME, Jarvis PG (2002) Gas exchange, biomass, whole-plant water-use efficiency and water uptake of peach (*Prunus persica*) seedlings in response to elevated carbon dioxide concentration and water availability. Tree Physiol 22:699–706. https://doi.org/10.1093/treephys/22.10.699

Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric CO_2 on woody plants. New Phytol 127:425–446. https://doi.org/10.1111/j.1469-8137.1994.tb03961.x

Charles-Edwards DA, Doley D, Rimmington GM (1986) Modelling plant growth and development. Academic, Sydney

Chater C, Peng K, Movahedi M et al (2015) Elevated CO_2-induced responses in stomata require ABA and ABA signaling. Curr Biol 25:2709–2716. https://doi.org/10.1016/j.cub.2015.09.013

Chaturvedi AK, Bahuguna RN, Pal M et al (2017a) Elevated CO2 and heat stress interactions affect grain yield, quality and mineral nutrient composition in rice under field conditions. Field Crop Res 206:149–157. https://doi.org/10.1016/j.fcr.2017.02.018

Chaturvedi AK, Bahuguna RN, Shah D et al (2017b) High temperature stress during flowering and grain filling offsets beneficial impact of elevated CO2 on assimilate partitioning and sink-strength in rice. Sci Rep 7:8227. https://doi.org/10.1038/s41598-017-07464-6

Clifford SC, Stronach IM, Mohamed AD et al (1993) The effects of elevated atmospheric carbon dioxide and water stress on light interception, dry matter production and yield in stands of groundnut (*Arachis hypogaea* L.). J Exp Bot 44:1763–1770

Clifford SC, Stronach IM, Mohamed AD et al (2007) The effects of elevated atmospheric carbon dioxide and water stress on Ligth interception, dry matter production and yield in stands of groundnut (*Arachis hypogaea* L.). J Exp Bot 44:1763–1770. https://doi.org/10.1093/jxb/44.12.1763

Coleman JS, McConnaughay KDM, Bazzaz FA (1993) Elevated CO_2 and plant nitrogen-use: is reduced tissue nitrogen concentration size-dependent? Oecologia 93:195–200. https://doi.org/10.1007/BF00317671

Condon AG, Richards RA, Rebetzke GJ, Farquhar GD (2004) Breeding for high water-use efficiency. J Exp Bot 55:2447–2460. https://doi.org/10.1093/jxb/erh277

Conley MM, Kimball BA, Brooks TJ et al (2001) CO_2 enrichment increases water-use efficiency in sorghum. New Phytol 151:407–412. https://doi.org/10.1046/j.1469-8137.2001.00184.x

Cotrufo MF, Ineson P, Scott A (1998) Elevated CO_2 reduces the nitrogen concentration of plant tissues. Glob Chang Biol 4:43–54. https://doi.org/10.1046/j.1365-2486.1998.00101.x

Craigon J, Fangmeier A, Jones M et al (2002) Growth and marketable-yield responses of potato to increased CO_2 and ozone. Eur J Agron 17:273–289. https://doi.org/10.1016/S1161-0301(02)00066-7

Craufurd PQ, Wheeler TR (2009) Climate change and the flowering time of annual crops. J Exp Bot 60:2529–2539. https://doi.org/10.1093/jxb/erp196

Crespo HM, Frean M, Cresswell CF, Tew J (1979) The occurrence of both C3 and C4 photosynthetic characteristics in a single *Zea mays* plant. Planta 147:257–263. https://doi.org/10.1007/BF00388748

Cui M, Miller PM, Nobel PS (1993) CO_2 exchange and growth of the Crassulacean acid metabolism plant Opuntia ficus-indica under elevated CO_2 in open-top chambers. Plant Physiol 103:519–524. https://doi.org/10.1104/pp.103.2.519

Cure JD, Israel DW, Rufty TW (1988) Nitrogen stress effects on growth and seed yield of Nonnodulated soybean exposed to elevated carbon dioxide. Crop Sci 28:671. https://doi.org/10.2135/cropsci1988.0011183X002800040023x

Davey PA, Olcer H, Zakhleniuk O et al (2006) Can fast-growing plantation trees escape biochemical down-regulation of photosynthesis when grown throughout their complete production cycle in the open air under elevated carbon dioxide? Plant Cell Environ 29:1235–1244. https://doi.org/10.1111/j.1365-3040.2006.01503.x

De Costa WAJM, Weerakoon WMW, Herath HMLK et al (2006) Physiology of yield determination of rice under elevated carbon dioxide at high temperatures in a subhumid tropical climate. Field Crop Res 96:336–347. https://doi.org/10.1016/j.fcr.2005.08.002

de Souza AP, Cocuron J-C, Garcia AC et al (2015) Changes in whole-plant metabolism during grain-filling stage in *Sorghum bicolor* l. (moench) grown under elevated CO_2 and drought. Plant Physiol 169(3):1755–1765. https://doi.org/10.1104/pp.15.01054

Deepak S, Agrawal M (1999) Growth and yield responses of wheat plants to elevated levels of CO_2 and SO_2, singly and in combination. Environ Pollut 104:411–419. https://doi.org/10.1016/S0269-7491(98)00171-7

Delgado E, Mitchell RAC, Parry MAJ et al (1994) Interacting effects of CO_2 concentration, temperature and nitrogen supply on the photosynthesis and composition of winter wheat leaves. Plant Cell Environ 17:1205–1213. https://doi.org/10.1111/j.1365-3040.1994.tb02018.x

Delucia EH, Sasek TW, Strain BR (1985) Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. Photosynth Res 7:175–184. https://doi.org/10.1007/BF00037008

DeLucia EH, George K, Hamilton JG (2002) Radiation-use efficiency of a forest exposed to elevated concentrations of atmospheric carbon dioxide. Tree Physiol 22:1003–1010. https://doi.org/10.1093/treephys/22.14.1003

Dermody O, Long SP, DeLucia EH (2006) How does elevated CO_2 or ozone affect the leaf-area index of soybean when applied independently? New Phytol 169:145–155. https://doi.org/10.1111/j.1469-8137.2005.01565.x

Dermody O, Long SP, McConnaughay K, DeLucia EH (2008) How do elevated CO_2 and O_3 affect the interception and utilization of radiation by a soybean canopy? Glob Chang Biol 14:556–564. https://doi.org/10.1111/j.1365-2486.2007.01502.x

Dey SK, Chakrabarti B, Prasanna R et al (2016) Productivity of mungbean (*Vigna radiata*) with elevated carbon dioxideat various phosphorus levels and cyanobacteria inoculation. Legum Res 40:497–505. https://doi.org/10.18805/lr.v0iOF.3765

Dey SK, Chakrabarti B, Prasanna R et al (2017) Elevated carbon dioxide level along with phosphorus application and cyanobacterial inoculation enhances nitrogen fixation and uptake in cowpea crop. Arch Agron Soil Sci 63:1927–1937. https://doi.org/10.1080/03650340.2017.1315105

Dier M, Sickora J, Erbs M et al (2018) Decreased wheat grain yield stimulation by free air CO_2 enrichment under N deficiency is strongly related to decreased radiation use efficiency enhancement. Eur J Agron 101:38–48. https://doi.org/10.1016/j.eja.2018.08.007

Dlugokencky E, Miller J, Staehelin J (2010) The global atmosphere watch: a history of contributing to climate monitoring. World Meteorol Organ Bull 59:35

Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? Annu Rev Plant Physiol Plant Mol Biol 48:609–639. https://doi.org/10.1146/annurev.arplant.48.1.609

Drennan PM, Nobel PS (2000) Responses of CAM species to increasing atmospheric CO_2 concentrations. Plant Cell Environ 23:767–781. https://doi.org/10.1046/j.1365-3040.2000.00588.x

Dugas WA, Heuer ML, Hunsaker D et al (1994) Sap flow measurements of transpiration from cotton grown under ambient and enriched CO_2 concentrations. Agric For Meteorol 70:231–245. https://doi.org/10.1016/0168-1923(94)90060-4

Dugas WA, Prior SA, Rogers HH (1997) Transpiration from sorghum and soybean growing under ambient and elevated CO_2 concentrations. Agric For Meteorol 83:37–48. https://doi.org/10.1016/S0168-1923(96)02353-2

Dwyer SA, Ghannoum O, Nicotra A, Von Caemmerer S (2007) High temperature acclimation of C4 photosynthesis is linked to changes in photosynthetic biochemistry. Plant Cell Environ 30:53–66. https://doi.org/10.1111/j.1365-3040.2006.01605.x

Eamus D, Berryman C, Duff G (1993) Assimilation, Stomatal conductance, specific leaf area and chlorophyll responses to elevated CO_2 of *Maranthes corymbosa*, a tropical monsoon rain Forest species. Funct Plant Biol 20:741. https://doi.org/10.1071/PP9930741

Edwards EJ, Mccaffery S, Evans JR (2005) Phosphorus status determines biomass response to elevated CO_2 in a legume: C4 grass community. Glob Chang Biol 11:1968–1981. https://doi.org/10.1111/j.1365-2486.2005.1049.x

Ellsworth DS, Reich PB, Naumburg ES et al (2004) Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO_2 across four free-air CO_2 enrichment experiments in forest, grassland and desert. Glob Chang Biol 10:2121–2138. https://doi.org/10.1111/j.1365-2486.2004.00867.x

Erbs M, Manderscheid R, Jansen G et al (2010) Effects of free-air CO_2 enrichment and nitrogen supply on grain quality parameters and elemental composition of wheat and barley grown in a crop rotation. Agric Ecosyst Environ 136:59–68. https://doi.org/10.1016/j.agee.2009.11.009

Estiarte M, Peñuelas J, Kimball BA et al (1994) Elevated CO_2 effects on stomatal density of wheat and sour orange trees. J Exp Bot 45:1665–1668. https://doi.org/10.1093/jxb/45.11.1665

Ewert F (2004) Modelling plant responses to elevated CO_2: how important is leaf area index? Ann Bot 93:619–627. https://doi.org/10.1093/aob/mch101

Fangmeier A, Grüters U, Hertstein U et al (1996) Effects of elevated CO_2 nitrogen supply and tropospheric ozone on spring wheat. I. Growth and yield. Environ Pollut 91:381–390. https://doi.org/10.1016/0269-7491(95)00042-9

Fangmeier A, Chrost B, Högy P, Krupinska K (2000) CO_2 enrichment enhances flag leaf senescence in barley due to greater grain nitrogen sink capacity. Environ Exp Bot 44:151–164. https://doi.org/10.1016/S0098-8472(00)00067-8

Feng Z, Rütting T, Pleijel H et al (2015) Constraints to nitrogen acquisition of terrestrial plants under elevated CO_2. Glob Chang Biol 21:3152–3168. https://doi.org/10.1111/gcb.12938

Ferris R, Wheeler TR, Ellis RH, Hadley P (1999) Seed yield after environmental stress in soybean grown under elevated CO_2. Crop Sci 39:710. https://doi.org/10.2135/cropsci1999.0011183X003900030018x

Field CB, Jackson RB, Mooney HA (1995) Stomatal responses to increased CO_2: implications from the plant to the global scale. Plant Cell Environ 18:1214–1225. https://doi.org/10.1111/j.1365-3040.1995.tb00630.x

Field CB, Lobell DB, Peters HA, Chiariello NR (2007) Feedbacks of terrestrial ecosystems to climate change. Annu Rev Environ Resour 32:1–29. https://doi.org/10.1146/annurev.energy.32.053006.141119

Franklin O, Ågren GI (2002) Leaf senescence and resorption as mechanisms of maximizing photosynthetic production during canopy development at N limitation. Funct Ecol 16:727–733. https://doi.org/10.1046/j.1365-2435.2002.00674.x

Franzaring J, Högy P, Fangmeier A (2008) Effects of free-air CO_2 enrichment on the growth of summer oilseed rape (*Brassica napus* cv. Campino). Agric Ecosyst Environ 128:127–134. https://doi.org/10.1016/j.agee.2008.05.011

Franzaring J, Weller S, Schmid I, Fangmeier A (2011) Growth, senescence and water use efficiency of spring oilseed rape (*Brassica napus* L. cv. Mozart) grown in a factorial combination of nitrogen supply and elevated CO_2. Environ Exp Bot 72:284–296. https://doi.org/10.1016/j.envexpbot.2011.04.003

Frenck G, van der Linden L, Mikkelsen TN et al (2011) Increased [CO_2] does not compensate for negative effects on yield caused by higher temperature and [O_3] in Brassica napus L. Eur J Agron 35:127–134. https://doi.org/10.1016/j.eja.2011.05.004

Fujita T, Noguchi K, Terashima I (2013) Apoplastic mesophyll signals induce rapid stomatal responses to CO_2 in *Commelina communis*. New Phytol 199:395–406. https://doi.org/10.1111/nph.12261

Furbank RT, Jenkins CLD, Hatch MD (2008) CO_2 concentrating mechanism of C4 photosynthesis: permeability of isolated bundle sheath cells to inorganic carbon. Plant Physiol 91:1364–1371. https://doi.org/10.1104/pp.91.4.1364

Gadpayle KA, Bhattacharyya R, Pal M, Fulekar MH (2018) Additional N supply improves grain yield in Triticale (× Triticosecale sp.) better than wheat (*Triticum aestivum* L) under elevated CO_2 environment. Indian J Plant Physiol 23:521–528. https://doi.org/10.1007/s40502-018-0401-9

Gao J, Han X, Seneweera S et al (2015) Leaf photosynthesis and yield components of mung bean under fully open-air elevated [CO_2]. J Integr Agric 14:977–983. https://doi.org/10.1016/S2095-3119(14)60941-2

Garcia RL, Long SP, Wall GW et al (1998) Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air atmospheric CO_2 enrichment. Plant Cell Environ 21:659–669. https://doi.org/10.1046/j.1365-3040.1998.00320.x

Geiger M, Haake V, Ludewig F et al (1999) The nitrate and ammonium nitrate supply have a major influence on the response of photosynthesis, carbon metabolism, nitrogen metabolism and growth to elevated carbon dioxide in tobacco. Plant Cell Environ 22:1177–1199. https://doi.org/10.1046/j.1365-3040.1999.00466.x

Ghannoum O, Von Caemmerer S, Ziska LH, Conroy JP (2000) The growth response of C4 plants to rising atmospheric CO_2 partial pressure: a reassessment. Plant Cell Environ 23:931–942. https://doi.org/10.1046/j.1365-3040.2000.00609.x

Ghannoum O, Von Caemmerer S, Conroy JP (2002) Plant water use efficiency of 17 Australian NAD-ME and NADP-ME C4 grasses at ambient and elevated CO_2 partial pressure. Funct Plant Biol 28:1207. https://doi.org/10.1071/pp01056

Griffin KL, Luo Y (1999) Sensitivity and acclimation of *Glycine max* (L.) Merr. leaf gas exchange to CO_2 partial pressure. Environ Exp Bot 42:141–153. https://doi.org/10.1016/S0098-8472(99)00028-3

Gunderson CA, Wullschleger SD (1994) Photosynthetic acclimation in trees to rising atmospheric CO_2: a broader perspective. Photosynth Res 39:369–388. https://doi.org/10.1007/BF00014592

Hakala K (1998) Growth and yield potential of spring wheat in a simulated changed climate with increased CO_2 and higher temperature. Eur J Agron 9:41–52. https://doi.org/10.1016/S1161-0301(98)00025-2

Han X, Tsunekawa A, Tsubo M, Shao H (2013) Responses of plant-soil properties to increasing N deposition and implications for large-scale eco-restoration in the semiarid grassland of the northern Loess Plateau, China. Ecol Eng 60:1–9. https://doi.org/10.1016/j.ecoleng.2013.07.053

Hao X, Li P, Han X et al (2016) Effects of free-air CO_2 enrichment (FACE) on N, P and K uptake of soybean in northern China. Agric For Meteorol 218–219:261–266. https://doi.org/10.1016/j.agrformet.2015.12.061

Hartz-Rubin JS, DeLucia EH (2001) Canopy development of a model herbaceous community exposed to elevated atmospheric CO_2 and soil nutrients. Physiol Plant 113:258–266. https://doi.org/10.1034/j.1399-3054.2001.1130214.x

Hasegawa T, Sakai H, Tokida T et al (2013) Rice cultivar responses to elevated CO_2 at two free-air CO_2 enrichment (FACE) sites in Japan. Funct Plant Biol 40:148. https://doi.org/10.1071/FP12357

Haworth M, Killi D, Materassi A, Raschi A (2015) Coordination of stomatal physiological behavior and morphology with carbon dioxide determines stomatal control. Am J Bot 102:677–688. https://doi.org/10.3732/ajb.1400508

Högy P, Fangmeier A (2008) Effects of elevated atmospheric CO_2 on grain quality of wheat. J Cereal Sci 48:580–591. https://doi.org/10.1016/j.jcs.2008.01.006

Högy P, Fangmeier A (2009) Atmospheric CO_2 enrichment affects potatoes: 1. Aboveground biomass production and tuber yield. Eur J Agron 30:78–84. https://doi.org/10.1016/j.eja.2008.07.007

Högy P, Keck M, Niehaus K et al (2010) Effects of atmospheric CO_2 enrichment on biomass, yield and low molecular weight metabolites in wheat grain. J Cereal Sci 52:215–220. https://doi.org/10.1016/j.jcs.2010.05.009

Houshmandfar A, Fitzgerald GJ, Macabuhay AA et al (2016) Trade-offs between water-use related traits, yield components and mineral nutrition of wheat under free-air CO_2 enrichment (FACE). Eur J Agron 76:66–74. https://doi.org/10.1016/j.eja.2016.01.018

Hui D, Luo Y, Cheng W et al (2001) Canopy radiation- and water-use efficiencies as affected by elevated [CO_2]. Glob Chang Biol 7:75–91. https://doi.org/10.1046/j.1365-2486.2001.00391.x

Hunsaker DJ, Hendrey GR, Kimball BA et al (1994) Cotton evapotranspiration under field conditions with CO_2 enrichment and variable soil moisture regimes. Agric For Meteorol 70:247–258. https://doi.org/10.1016/0168-1923(94)90061-2

Hunsaker DJ, Kimball BA, Pinter PJ et al (2000) CO_2 enrichment and soil nitrogen effects on wheat evapotranspiration and water use efficiency. Agric For Meteorol 104:85–105. https://doi.org/10.1016/S0168-1923(00)00157-X

Hussain MZ, VanLoocke A, Siebers MH et al (2013) Future carbon dioxide concentration decreases canopy evapotranspiration and soil water depletion by field-grown maize. Glob Chang Biol 19:1572–1584. https://doi.org/10.1111/gcb.12155

Idso SB, Kimball BA, Wall GW et al (1994) Effects of free-air CO2 enrichment on the light response curve of net photosynthesis in cotton leaves. Agric For Meteorol 70:183–188. https://doi.org/10.1016/0168-1923(94)90057-4

Imai K, Coleman DF, Yanagisawa T (1985) Increase in atmospheric partial pressure of carbon dioxide and growth and yield of rice (*Oryza sativa* L.). Japan J Crop Sci 54:413–418

IPCC (2007) Climate change 2007, the physical science basis, contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Jablonski LM, Wang X, Curtis PS (2002) Plant reproduction under elevated CO_2 conditions: a meta-analysis of reports on 79 crop and wild species. New Phytol 156:9–26. https://doi.org/10.1046/j.1469-8137.2002.00494.x

Jackson RB, Sala OE, Field CB, Mooney HA (1994) CO_2 alters water use, carbon gain, and yield for the dominant species in a natural grassland. Oecologia 98:257–262. https://doi.org/10.1007/BF00324212

Jagadish SVK, Bahuguna RN, Djanaguiraman M et al (2016) Implications of high temperature and elevated CO_2 on flowering time in plants. Front Plant Sci 7:1–11. https://doi.org/10.3389/fpls.2016.00913

Jin Z, Ainsworth EA, Leakey ADB, Lobell DB (2018) Increasing drought and diminishing benefits of elevated carbon dioxide for soybean yields across the US Midwest. Glob Chang Biol 24:e522–e533. https://doi.org/10.1111/gcb.13946

Jyothi Lakshmi N, Vanaja M, Yadav SK et al (2017) Effect of CO_2 on growth, seed yield and nitrogen uptake in sunflower. J Agrometeorol 19:195–199

Kakani VG, Vu JCV, Allen LH, Boote KJ (2011) Leaf photosynthesis and carbohydrates of CO_2-enriched maize and grain sorghum exposed to a short period of soil water deficit during vegetative development. J Plant Physiol 168:2169–2176. https://doi.org/10.1016/j.jplph.2011.07.003

Kammann C, Grünhage L, Grüters U et al (2005) Response of aboveground grassland biomass and soil moisture to moderate long-term CO_2 enrichment. Basic Appl Ecol 6:351–365. https://doi.org/10.1016/j.baae.2005.01.011

Kanemoto K, Yamashita Y, Ozawa T et al (2009) Photosynthetic acclimation to elevated CO_2 is dependent on N partitioning and transpiration in soybean. Plant Sci 177:398–403. https://doi.org/10.1016/j.plantsci.2009.06.017

Kang SZ, Zhang FC, Hu XT, Zhang JH (2002) Benefits of CO_2 enrichment on crop plants are modified by soil water status. Plant Soil 238:69–77. https://doi.org/10.1023/A:1014244413067

Katny MAC, Hoffmann-Thoma G, Schrier AA et al (2005) Increase of photosynthesis and starch in potato under elevated CO_2 is dependent on leaf age. J Plant Physiol 162:429–438. https://doi.org/10.1016/j.jplph.2004.07.005

Kellomäki S, Wang K-Y (1997) Effects of elevated O_3 and CO_2 concentrations on photosynthesis and stomatal conductance in scots pine. Plant Cell Environ 20:995–1006. https://doi.org/10.1111/j.1365-3040.1997.tb00676.x

Kim HY, Lieffering M, Miura S et al (2001) Growth and nitrogen uptake of CO_2-enriched rice under field conditions. New Phytol 150:223–229. https://doi.org/10.1046/j.1469-8137.2001.00111.x

Kim HY, Lieffering M, Kobayashi K et al (2003) Seasonal changes in the effects of elevated CO_2 on rice at three levels of nitrogen supply: a free air CO_2 enrichment (FACE) experiment. Glob Chang Biol 9:826–837. https://doi.org/10.1046/j.1365-2486.2003.00641.x

Kim S-H, Sicher RC, Bae H et al (2006) Canopy photosynthesis, evapotranspiration, leaf nitrogen, and transcription profiles of maize in response to CO_2 enrichment. Glob Chang Biol 12:588–600. https://doi.org/10.1111/j.1365-2486.2006.01110.x

Kim SH, Gitz DC, Sicher RC et al (2007) Temperature dependence of growth, development, and photosynthesis in maize under elevated CO_2. Environ Exp Bot 61:224–236. https://doi.org/10.1016/j.envexpbot.2007.06.005

Kimball BA, LaMorte RL, Seay RS et al (1994) Effects of free-air CO_2 enrichment on energy balance and evapotranspiration of cotton. Agric For Meteorol 70:259–278. https://doi.org/10.1016/0168-1923(94)90062-0

Kimball BA, Kobayashi K, Bindi M (2002) Responses of agricultural crops to free-air CO2 enrichment. Adv Agron 77:293–368

Kleemola J, Peltonen J, Peltonen-Sainio P (1994) Apical development and growth of barley under different CO_2 and nitrogen regimes. J Agron Crop Sci 173:79–92. https://doi.org/10.1111/j.1439-037X.1994.tb00541.x

Koch GW, Mooney HA (1996) Response of terrestrial ecosystems to elevated CO_2: a synthesis and summary. In: Carbon dioxide and terrestrial ecosystems. Academic, Cambridge, pp 415–429

Körner C, Morgan J, Norby R (2007) CO2 fertilization: when, where, how much? In: Terrestrial ecosystems in a changing world. Springer, Berlin, pp 9–21

Kumar S, Chaitanya BSK, Ghatty S, Reddy AR (2014) Growth, reproductive phenology and yield responses of a potential biofuel plant, Jatropha curcas grown under projected 2050 levels of elevated CO_2. Physiol Plant 152:501–519. https://doi.org/10.1111/ppl.12195

Kumar A, Nayak AK, Das BS et al (2019) Effects of water deficit stress on agronomic and physiological responses of rice and greenhouse gas emission from rice soil under elevated atmospheric CO_2. Sci Total Environ 650:2032–2050. https://doi.org/10.1016/j.scitotenv.2018.09.332

Lam SK, Han X, Lin E et al (2012a) Does elevated atmospheric carbon dioxide concentration increase wheat nitrogen demand and recovery of nitrogen applied at stem elongation? Agric Ecosyst Environ 155:142–146. https://doi.org/10.1016/j.agee.2012.04.012

Lam SK, Hao X, Lin E et al (2012b) Effect of elevated carbon dioxide on growth and nitrogen fixation of two soybean cultivars in northern China. Biol Fertil Soils 48:603–606. https://doi.org/10.1007/s00374-011-0648-z

Lammertsma EI, de Boer HJ, Dekker SC et al (2011) Global CO_2 rise leads to reduced maximum stomatal conductance in Florida vegetation. Proc Natl Acad Sci U S A 108:4035–4040. https://doi.org/10.1073/pnas.1100371108

Lawlor DW, Mitchell RAC (2000) Crop ecosystem responses to climatic change: wheat. In: Reddy KR, Hodges HF (eds) Climate change and global crop productivity. CAB International, Wallingford, pp 57–80

Lawson T, Simkin AJ, Kelly G, Granot D (2014) Mesophyll photosynthesis and guard cell metabolism impacts on stomatal behaviour. New Phytol 203:1064–1081. https://doi.org/10.1111/nph.12945

Leakey ADB, Bernacchi CJ, Dohleman FG et al (2004) Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future [CO_2] rich atmospheres? An analysis of diurnal courses of CO2 uptake under free-air concentration enrichment (FACE). Glob Chang Biol 10:951–962. https://doi.org/10.1111/j.1529-8817.2003.00767.x

Leakey ADB, Bernacchi CJ, Ort DR, Long SP (2006) Long-term growth of soybean at elevated [CO_2] does not cause acclimation of stomatal conductance under fully open-air conditions. Plant Cell Environ 29:1794–1800. https://doi.org/10.1111/j.1365-3040.2006.01556.x

Leakey ADB, Ainsworth EA, Bernacchi CJ et al (2009) Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. J Exp Bot 60:2859–2876. https://doi.org/10.1093/jxb/erp096

Li A-G, Hou Y-S, Wall GW et al (2000) Free-air CO enrichment and drought stress effects on grain filling rate and duration in spring wheat. Crop Sci 40:1263. https://doi.org/10.2135/cropsci2000.4051263x

Li C, Williams MM, Loh Y-T et al (2002) Resistance of cultivated tomato to cell content-feeding herbivores is regulated by the octadecanoid-signaling pathway. Plant Physiol 130:494–503. https://doi.org/10.1104/pp.005314

Li F, Kang S, Zhang J, Cohen S (2003) Effects of atmospheric CO_2 enrichment, water status and applied nitrogen on water- and nitrogen-use efficiencies of wheat. Plant Soil 254:279–289. https://doi.org/10.1023/A:1025521701732

Li F, Kang S, Zhang J (2004) Interactive effects of elevated CO_2, nitrogen and drought on leaf area, stomatal conductance, and evapotranspiration of wheat. Agric Water Manag 67:221–233. https://doi.org/10.1016/j.agwat.2004.01.005

Li Y, Yu Z, Liu X, et al (2017) Elevated CO2 increases nitrogen fixation at the reproductive phase contributing to various yield responses of soybean cultivars. Front Plant Sci 8. https://doi.org/10.3389/fpls.2017.01546

Li X, Khan A, Lv Z et al (2019) Effect of multigenerational exposure to elevated atmospheric CO 2 concentration on grain quality in wheat. Environ Exp Bot 157:310–319. https://doi.org/10.1016/j.envexpbot.2018.10.028

Lieffering M, Kim HY, Kobayashi K, Okada M (2004) The impact of elevated CO_2 on the elemental concentrations of field-grown rice grains. Field Crop Res 88:279–286. https://doi.org/10.1016/j.fcr.2004.01.004

Liu H, Yang L, Wang Y et al (2008) Yield formation of CO_2-enriched hybrid rice cultivar Shanyou 63 under fully open-air field conditions. Field Crop Res 108:93–100. https://doi.org/10.1016/j.fcr.2008.03.007

Long SP, Drake BG (1991) Effect of the long-term elevation of CO_2 concentration in the field on the quantum yield of photosynthesis of the C3 sedge, Scirpus olneyi. Plant Physiol 96:221–226. https://doi.org/10.1104/pp.96.1.221

Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide: plants FACE the future. Annu Rev Plant Biol 55:591–628. https://doi.org/10.1146/annurev.arplant.55.031903.141610

Madhu M, Hatfield JL (2014) Interaction of carbon dioxide enrichment and soil moisture on photosynthesis, transpiration, and water use efficiency of soybean. Agric Sci 5:410–429. https://doi.org/10.4236/as.2014.55043

Maherali H, Reid CD, Polley HW et al (2002) Stomatal acclimation over a subambient to elevated CO_2 gradient in a C_3/C_4 grassland. Plant Cell Environ 25:557–566. https://doi.org/10.1046/j.1365-3040.2002.00832.x

Manderscheid R, Weigel HJ (1997) Photosynthetic and growth responses of old and modern spring wheat cultivars to atmospheric CO_2 enrichment. Agric Ecosyst Environ 64:65–73. https://doi.org/10.1016/S0167-8809(97)00020-0

Manderscheid R, Bender J, Schenk U, Weigel HJ (1997) Response of biomass and nitrogen yield of white clover to radiation and atmospheric CO_2 concentration. Environ Exp Bot 38:131–143. https://doi.org/10.1016/S0098-8472(97)00007-5

Manderscheid R, Burkart S, Bramm A, Weigel H-J (2003) Effect of CO_2 enrichment on growth and daily radiation use efficiency of wheat in relation to temperature and growth stage. Eur J Agron 19:411–425. https://doi.org/10.1016/S1161-0301(02)00133-8

Manderscheid R, Pacholski A, Frühauf C, Weigel HJ (2009) Effects of free air carbon dioxide enrichment and nitrogen supply on growth and yield of winter barley cultivated in a crop rotation. Field Crop Res 110:185–196. https://doi.org/10.1016/j.fcr.2008.08.002

Manderscheid R, Pacholski A, Weigel H-J (2010) Effect of free air carbon dioxide enrichment combined with two nitrogen levels on growth, yield and yield quality of sugar beet: evidence for a sink limitation of beet growth under elevated CO_2. Eur J Agron 32:228–239. https://doi.org/10.1016/j.eja.2009.12.002

Manderscheid R, Erbs M, Weigel HJ (2014) Interactive effects of free-air CO_2 enrichment and drought stress on maize growth. Eur J Agron 52:11–21. https://doi.org/10.1016/j.eja.2011.12.007

Manderscheid R, Dier M, Erbs M et al (2018) Nitrogen supply—a determinant in water use efficiency of winter wheat grown under free air CO_2 enrichment. Agric Water Manag 210:70–77. https://doi.org/10.1016/j.agwat.2018.07.034

Markelz RJC, Strellner RS, Leakey ADB (2011) Impairment of C_4 photosynthesis by drought is exacerbated by limiting nitrogen and ameliorated by elevated [CO_2] in maize. J Exp Bot 62:3235–3246. https://doi.org/10.1093/jxb/err056

Maroco JP, Edwards GE, Ku MS (1999) Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. Planta 210:115–125

McCarthy HR, Oren R, Finzi AC et al (2007) Temporal dynamics and spatial variability in the enhancement of canopy leaf area under elevated atmospheric CO_2. Glob Chang Biol 13:2479–2497. https://doi.org/10.1111/j.1365-2486.2007.01455.x

Medlyn BE, Barton CVM, Broadmeadow MSJ et al (2001) Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis. New Phytol 149:247–264. https://doi.org/10.1046/j.1469-8137.2001.00028.x

Meng F, Zhang J, Yao F, Hao C (2014) Interactive effects of elevated CO_2 concentration and irrigation on photosynthetic parameters and yield of maize in Northeast China. PLoS One 9:e98318. https://doi.org/10.1371/journal.pone.0098318

Monje O, Bugbee B (1998) Adaptation to high CO_2 concentration in an optimal environment. Plant Cell Environ 21:315

Monteith JL (1981) Does light limit crop production? Proceedings of the University of Nottingham Easter School in Agricultural Science. Nottingham University Press, Loughborough

Morgan PB, Bollero GA, Nelson RL et al (2005) Smaller than predicted increase in aboveground net primary production and yield of field-grown soybean under fully open-air [CO_2] elevation. Glob Chang Biol 11:1856–1865. https://doi.org/10.1111/j.1365-2486.2005.001017.x

Morison J, Gifford R (1984) Plant growth and water use with limited water supply in high CO_2 concentrations. I. Leaf area, water use and transpiration. Funct Plant Biol 11:361. https://doi.org/10.1071/PP9840361

Moya TB, Ziska LH, Namuco OS, Olszyk D (1998) Growth dynamics and genotypic variation in tropical, field-grown paddy rice (*Oryza sativa* L.) in response to increasing carbon dioxide and temperature. Glob Chang Biol 4:645–656. https://doi.org/10.1046/j.1365-2486.1998.00180.x

Muhaidat R, Sage RF, Dengler NG (2007) Diversity of Kranz anatomy and biochemistry in C_4 eudicots. Am J Bot 94:362–381. https://doi.org/10.3732/ajb.94.3.362

Mulholland BJ, Craigon J, Black CR et al (1998) Growth, light interception and yield responses of spring wheat (Triticum aestivum L.) grown under elevated CO_2 and O_3 in open-top chambers. Glob Chang Biol 4:121–130. https://doi.org/10.1046/j.1365-2486.1998.00112.x

Mulholland BJ, Craigon J, Black CR et al (2007) Effects of elevated carbon dioxide and ozone on the growth and yield of spring wheat (*Triticum aestivum* L.). J Exp Bot 48:113–122. https://doi.org/10.1093/jxb/48.1.113

Myers SS, Zanobetti A, Kloog I et al (2014) Increasing CO_2 threatens human nutrition. Nature 510:139–142. https://doi.org/10.1038/nature13179

Nabity PD, Hillstrom ML, Lindroth RL, DeLucia EH (2012) Elevated CO_2 interacts with herbivory to alter chlorophyll fluorescence and leaf temperature in *Betula papyrifera* and *Populus tremuloides*. Oecologia 169:905–913. https://doi.org/10.1007/s00442-012-2261-8

Nakano H, Makino A, Mae T (1997) The effect of elevated patial pressures of CO_2 on the relationship between photosynthetic capacity and nitrogen content in rice leaves. Plant Physiol 115:191–198

Nijs I, Impens I, Behaeghe T (1989) Leaf and canopy responses of *Lolium perenne* to long-term elevated atmospheric carbon-dioxide concentration. Planta 177:312–320. https://doi.org/10.1007/BF00403588

Nobel PS, Israel AA (1994) Cladode development, environmental responses of CO_2 uptake, and productivity for Opuntia ficus-indica under elevated CO_2. J Exp Bot 45:295–303. https://doi.org/10.1093/jxb/45.3.295

Norby RJ, Sholtis JD, Gunderson CA, Jawdy SS (2003) Leaf dynamics of a deciduous forest canopy: no response to elevated CO_2. Oecologia 136:574–584. https://doi.org/10.1007/s00442-003-1296-2

O'Leary GJ, Christy B, Nuttall J et al (2015) Response of wheat growth, grain yield and water use to elevated CO_2 under a free-air CO_2 enrichment (FACE) experiment and modelling in a semi-arid environment. Glob Chang Biol 21:2670–2686. https://doi.org/10.1111/gcb.12830

Ollerton J, Lack A (1998) Relationships between flowering phenology, plant size and reproductive success in *Lotus corniculatus* (Fabaceae). Plant Ecol 139:35–47. https://doi.org/10.1023/A:1009798320049

Osborne CP, La Roche J, Garcia RL et al (1998) Does leaf position within a canopy affect acclimation of photosynthesis to elevated CO_2? Plant Physiol 117:1037–1045. https://doi.org/10.1104/pp.117.3.1037

Osmond CB (2003) Crassulacean acid metabolism: a curiosity in context. Annu Rev Plant Physiol 29:379–414. https://doi.org/10.1146/annurev.pp.29.060178.002115

Ottman MJ, Kimball BA, Pinter PJ et al (2001) Elevated CO_2 increases sorghum biomass under drought conditions. New Phytol 150:261–273. https://doi.org/10.1046/j.1469-8137.2001.00110.x

Pacholski A, Manderscheid R, Weigel HJ (2015) Effects of free air CO_2 enrichment on root growth of barley, sugar beet and wheat grown in a rotation under different nitrogen supply. Eur J Agron 63:36–46. https://doi.org/10.1016/j.eja.2014.10.005

Pal M, Karthikeyapandian V, Jain V et al (2004) Biomass production and nutritional levels of berseem (*Trifolium alexandrium*) grown under elevated CO_2. Agric Ecosyst Environ 101:31–38. https://doi.org/10.1016/S0167-8809(03)00202-0

Pal M, Rao LS, Jain V, Srivastava AC, Pandey R, Raj A, Singh KP (2005) Effects of elevated CO_2 and nitrogen on wheat growth and photosynthesis. Biol Plant 49(3):467–470

Pal M, Talawar S, Deshmukh PS et al (2008) Growth and yield of chickpea under elevated carbon dioxide concentration. Indian J Plant Physiol 13:367–374

Pal M, Chaturvedi AK, Pandey SK et al (2014) Rising atmospheric CO_2 may affect oil quality and seed yield of sunflower (*Helianthus annus* L.). Acta Physiol Plant 36:2853–2861. https://doi.org/10.1007/s11738-014-1651-4

Parvin S, Uddin S, Fitzgerald GJ et al (2019) Free air CO_2 enrichment (FACE) improves water use efficiency and moderates drought effect on N_2 fixation of *Pisum sativum* L. Plant Soil 436:587–606. https://doi.org/10.1007/s11104-019-03949-7

Pathare VS, Crous KY, Cooke J et al (2017) Water availability affects seasonal CO_2-induced photosynthetic enhancement in herbaceous species in a periodically dry woodland. Glob Chang Biol 23:5164–5178. https://doi.org/10.1111/gcb.13778

Peterson AG, Ball JT, Luo Y et al (1999) Quantifying the response of photosynthesis to changes in leaf nitrogen content and leaf mass per area in plants grown under atmospheric CO_2 enrichment. Plant Cell Environ 22:1109–1119. https://doi.org/10.1046/j.1365-3040.1999.00489.x

Pinter PJ, Kimball BA, Mauncy JR et al (1994) Effects of free-air carbon dioxide enrichment on PAR absorption and conversion efficiency by cotton. Agric For Meteorol 70:209–230. https://doi.org/10.1016/0168-1923(94)90059-0

Pinter PJ, Kimball BA, Garcia RL, Wall GW, Hunsacker DJ, Lamorte RL (1996) Free-air CO2 enrichment—responses of cotton and wheat crops. In: Koch G, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic, San Diego, pp 215–249

Pleijel H, Gelang J, Sild E et al (2000) Effects of elevated carbon dioxide, ozone and water availability on spring wheat growth and yield. Physiol Plant 108:61–70. https://doi.org/10.1034/j.1399-3054.2000.108001061.x

Polley HW (2002) Implications of atmospheric and climatic change for crop yield and water use efficiency. Crop Sci 42:131–140

Pons TL, Flexas J, Von Caemmerer S et al (2009) Estimating mesophyll conductance to CO_2: methodology, potential errors, and recommendations. J Exp Bot 60:2217–2234. https://doi.org/10.1093/jxb/erp081

Poorter H, Navas ML (2003) Plant growth and competition at elevated CO_2: on winners, losers and functional groups. New Phytol 157:175–198. https://doi.org/10.1046/j.1469-8137.2003.00680.x

Porteaus F, Hill J, Ball AS et al (2009) Effect of free air carbon dioxide enrichment (FACE) on the chemical composition and nutritive value of wheat grain and straw. Anim Feed Sci Technol 149:322–332. https://doi.org/10.1016/j.anifeedsci.2008.07.003

Pospíšilová J, Čatský J (1999) Development of water stress under increased atmospheric CO_2 concentration. Biol Plant 42:1–24. https://doi.org/10.1023/A:1002102405980

Prasad PVV, Boote KJ, Allen LH, Thomas JMG (2003) Super-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L.) reproductive processes and yield at both ambient and elevated carbon dioxide. Glob Chang Biol 9:1775–1787. https://doi.org/10.1046/j.1365-2486.2003.00708.x

Prasad PVV, Boote KJ, Allen LH (2006) Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain-sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to higher tissue temperatures. Agric For Meteorol 139:237–251. https://doi.org/10.1016/j.agrformet.2006.07.003

Prasad PVV, Vu JCV, Boote KJ, Allen LH (2009) Enhancement in leaf photosynthesis and upregulation of Rubisco in the C_4 sorghum plant at elevated growth carbon dioxide and temperature occur at early stages of leaf ontogeny. Funct Plant Biol 36:761. https://doi.org/10.1071/fp09043

Prior SA, Runion GB, Rogers HH et al (2005) Elevated atmospheric CO_2 effects on biomass production and soil carbon in conventional and conservation cropping systems. Glob Chang Biol 11:657–665. https://doi.org/10.1111/j.1365-2486.2005.00935.x

Pritchard SG, Prior SA, Rogers HH et al (2006) Effects of elevated atmospheric CO_2 on root dynamics and productivity of sorghum grown under conventional and conservation agricultural management practices. Agric Ecosyst Environ 113:175–183. https://doi.org/10.1016/j.agee.2005.09.010

Raj A, Chakrabarti B, Pathak H et al (2019) Growth, yield and nitrogen uptake in rice crop grown under elevated carbon dioxide and different doses of nitrogen fertilizer. Indian J Exp Biol 57:181–187

Razzaque M, Haque M, Hamid M et al (2009) Effects of nitrogen fertilizer and elevated CO_2 on dry matter production and yield of rice cultivars. Bangladesh J Agric Res 34:313–322. https://doi.org/10.3329/bjar.v34i2.5804

Reich PB, Hobbie SE, Lee TD, Pastore MA (2018) Response to comment on “unexpected reversal of C_3 versus C_4 grass response to elevated CO_2 during a 20-year field experiment”. Science 361:eaau8982. https://doi.org/10.1126/science.aau8982

Richards RA (2000) Selectable traits to increase crop photosynthesis and yield of grain crops. J Exp Bot 51:447–458. https://doi.org/10.1093/jexbot/51.suppl_1.447

Rogers HH, Cure JD, Smith JM (1986) Soybean growth and yield response to elevated carbon dioxide. Agric Ecosyst Environ 16:113–128. https://doi.org/10.1016/0167-8809(86)90098-8

Roux F, Touzet P, Cuguen J, Le Corre V (2006) How to be early flowering: an evolutionary perspective. Trends Plant Sci 11:375–381. https://doi.org/10.1016/j.tplants.2006.06.006

Roy KS, Bhattacharyya P, Neogi S et al (2012) Combined effect of elevated CO_2 and temperature on dry matter production, net assimilation rate, C and N allocations in tropical rice (*Oryza sativa* L.). Field Crop Res 139:71–79. https://doi.org/10.1016/j.fcr.2012.10.011

Rudorff BFT, Mulchi CL, Daughtry CST, Lee EH (1996) Growth, radiation use efficiency, and canopy reflectance of wheat and corn grown under elevated ozone and carbon dioxide atmospheres. Remote Sens Environ 55:163–173. https://doi.org/10.1016/0034-4257(95)00208-1

Ruhil K, Sheeba, Ahmad A et al (2015) Photosynthesis and growth responses of mustard (*Brassica juncea* L. cv Pusa Bold) plants to free air carbon dioxide enrichment (FACE). Protoplasma 252:935–946. https://doi.org/10.1007/s00709-014-0723-z

Ruiz-Vera UM, De Souza AP, Long SP, Ort DR (2017) The role of sink strength and nitrogen availability in the down-regulation of photosynthetic capacity in Field-grown *Nicotiana tabacum* L. at elevated CO_2 concentration. Front Plant Sci 8:1–12. https://doi.org/10.3389/fpls.2017.00998

Sæbø A, Mortensen LM (2002) Growth, morphology and yield of wheat, barley and oats grown at elevated atmospheric CO_2 concentration in a cool, maritime climate. Agric Ecosyst Environ 57:9–15. https://doi.org/10.1016/0167-8809(95)01009-2

Sage RF, Coleman JR (2001) Effects of low atmospheric CO_2 on plants: more than a thing of the past. Trends Plant Sci 6:18–24. https://doi.org/10.1016/S1360-1385(00)01813-6

Saha S, Chakraborty D, Lata et al (2011) Impact of elevated CO2 on utilization of soil moisture and associated soil biophysical parameters in pigeon pea (*Cajanus cajan* L.). Agric Ecosyst Environ 142:213–221. https://doi.org/10.1016/j.agee.2011.05.008

Saha S, Sehgal VK, Nagarajan S, Pal M (2012) Impact of elevated atmospheric CO_2 on radiation utilization and related plant biophysical properties in pigeon pea (*Cajanus cajan* L.). Agric For Meteorol 158–159:63–70. https://doi.org/10.1016/j.agrformet.2012.02.003

Saha S, Sehgal VK, Chakraborty D, Pal M (2013) Growth behavior of kabuli chickpea under elevated atmospheric. J Agric Phys 13:55–61

Saha S, Sehgal VK, Chakraborty D, Pal M (2014a) Atmospheric carbon dioxide enrichment induced modifications in canopy radiation utilization, growth and yield of chickpea [*Cicer arietinum* L.]. Agric For Meteorol 202:102–111. https://doi.org/10.1016/j.agrformet.2014.12.004

Saha S, Sehgal VK, Pal M (2014b) Elevated CO_2 promotes plant Scenscence in kabuli chickpea—a ground-based remote sensing study. J Agric Phys 14:167–171

Saha S, Chakraborty D, Sehgal VK, Pal M (2015) Potential impact of rising atmospheric CO2 on quality of grains in chickpea (*Cicer arietinum* L.). Food Chem 187:431–436. https://doi.org/10.1016/j.foodchem.2015.04.116

Saha S, Chakraborty D, Sehgal VK et al (2016) Long-term atmospheric CO_2 enrichment impact on soil biophysical properties and root nodule biophysics in chickpea (*Cicer arietinum* L.). Eur J Agron 75:1–11. https://doi.org/10.1016/j.eja.2015.12.005

Sanz-Sáez Á, Erice G, Aranjuelo I et al (2010) Photosynthetic down-regulation under elevated CO_2 exposure can be prevented by nitrogen supply in nodulated alfalfa. J Plant Physiol 167:1558–1565. https://doi.org/10.1016/j.jplph.2010.06.015

Sarker BC, Hara M (2009) Effects of elevated CO_2 and water stress on root structure and hydraulic conductance of solanum melongena L. Bangladesh J Bot 38:55–63

Schapendonk AHCM, Dijkstra P, Groenwold J et al (1997) Carbon balance and water use efficiency of frequently cut Lolium perenne L. swards at elevated carbon dioxide. Glob Chang Biol 3:207–216. https://doi.org/10.1046/j.1365-2486.1997.00099.x

Seneweera S, Makino A, Hirotsu N et al (2011) New insight into photosynthetic acclimation to elevated CO_2: the role of leaf nitrogen and ribulose-1,5-bisphosphate carboxylase/oxygenase content in rice leaves. Environ Exp Bot 71:128–136. https://doi.org/10.1016/j.envexpbot.2010.11.002

Sharma-Natu P, Ghildiyal MC (1994) Diurnal changes in photosynthesis in relation to ribulose-1, 5,-biphosphate carboxylase activity and saccharides content in wheat leaves. Photosynthetica 45(3):334–339

Shi K, Li X, Zhang H et al (2015) Guard cell hydrogen peroxide and nitric oxide mediate elevated CO_2-induced stomatal movement in tomato. New Phytol 208:342–353. https://doi.org/10.1111/nph.13621

Shimono H, Okada M, Yamakawa Y et al (2009) Genotypic variation in rice yield enhancement by elevated CO_2 relates to growth before heading, and not to maturity group. J Exp Bot 60:523–532. https://doi.org/10.1093/jxb/ern288

Sicher RC (2010) Daily changes of amino acids in soybean leaflets are modified by CO_2 enrichment. Int J Plant Biol 1:18. https://doi.org/10.4081/pb.2010.e18

Sicher RC (2011) Photosynthetic acclimation and decreased chlorophyll (A + B) concentrations occur in nitrogen-sufficient tobacco leaves in response to carbon dioxide enrichment. J Plant Nutr 34:1995–2005. https://doi.org/10.1080/01904167.2011.610486

Sicher RC, Bunce JA (1997) Relationship of photosynthetic acclimation to changes of Rubisco activity in field-grown winter wheat and barley during growth in elevated carbon dioxide. Photosynth Res 52:27–38. https://doi.org/10.1023/A:1005874932233

Siebke K, Ghannoum O, Conroy JP, Von Caemmerer S (2002) Elevated CO_2 increases the leaf temperature of two glasshouse-grown C4 grasses. Funct Plant Biol 29:1377–1385. https://doi.org/10.1071/FP02075

Sims DA, Cheng W, Luo Y, Seemann JR (1999) Photosynthetic acclimation to elevated CO_2 in a sunflower canopy. J Exp Bot 50:645–653. https://doi.org/10.1093/jxb/50.334.645

Singh SS, Mukherjee J, Kumar S, Idris M (2013) Effect of elevated CO_2 on growth and yield of rice crop in open top chamber in sub humid climate of eastern India. J Agrometeorol 15:1–10

Sionit N, Hellmers H, Strain BR (1980) Growth and yield of wheat under CO_2 enrichment and water Stress1. Crop Sci 20:687. https://doi.org/10.2135/cropsci1980.0011183X002000060003x

Skinner RH, Nelson CJ (1994) Effect of tiller trimming on Phyllochron and Tillering regulation during tall fescue development. Crop Sci 34:1267. https://doi.org/10.2135/cropsci1994.0011183X003400050024x

Slattery RA, Ainsworth EA, Ort DR (2013) A meta-analysis of responses of canopy photosynthetic conversion efficiency to environmental factors reveals major causes of yield gap. J Exp Bot 64:3723–3733. https://doi.org/10.1093/jxb/ert207

Smart DR, Chatterton NJ, Bugbee B (1994) The influence of elevated CO_2 on non-structural carbohydrate distribution and fructan accumulation in wheat canopies. Plant Cell Environ 17:435–442. https://doi.org/10.1111/j.1365-3040.1994.tb00312.x

Spencer W, Bowes G (1986) Photosynthesis and growth of water hyacinth under CO_2 enrichment. Plant Physiol 82:528–533. https://doi.org/10.1104/pp.82.2.528

Springer C, Ward J (2007) Flowering time and elevated CO_2. New Phytol 176:243–255

Sreeharsha RV, Sekhar KM, Reddy AR (2015) Delayed flowering is associated with lack of photosynthetic acclimation in pigeon pea (*Cajanus cajan* L.) grown under elevated CO_2. Plant Sci 231:82–93. https://doi.org/10.1016/j.plantsci.2014.11.012

Stanciel K, Mortley DG, Hileman DR et al (2000) Growth, pod, and seed yield, and gas exchange of hydroponically grown peanut in response to CO_2 enrichment. HortScience 35:49–52

Stitt M, Krapp A (1999) The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. Plant Cell Environ 22:583–621. https://doi.org/10.1046/j.1365-3040.1999.00386.x

Streit K, Siegwolf RTW, Hagedorn F et al (2014) Lack of photosynthetic or stomatal regulation after 9 years of elevated [CO_2] and 4 years of soil warming in two conifer species at the alpine treeline. Plant Cell Environ 37:315–326. https://doi.org/10.1111/pce.12197

Szarek SR, Holthe PA, Ting IP (1987) Minor physiological response to elevated CO_2 by the CAM plant Agave vilmoriniana. Plant Physiol 83:938–940. https://doi.org/10.1104/pp.83.4.938

Taub DR, Miller B, Allen H (2008) Effects of elevated CO_2 on the protein concentration of food crops: a meta-analysis. Glob Chang Biol 14:565–575. https://doi.org/10.1111/j.1365-2486.2007.01511.x

Tausz M, Norton RM, Tausz-Posch S et al (2017) Can additional N fertiliser ameliorate the elevated CO_2-induced depression in grain and tissue N concentrations of wheat on a high soil N background? J Agron Crop Sci 203:574–583. https://doi.org/10.1111/jac.12209

Tausz-Posch S, Seneweera S, Norton RM et al (2012) Can a wheat cultivar with high transpiration efficiency maintain its yield advantage over a near-isogenic cultivar under elevated CO_2? Field Crop Res 133:160–166. https://doi.org/10.1016/j.fcr.2012.04.007

Teng N, Jin B, Wang Q et al (2009) No detectable maternal effects of elevated CO_2 on Arabidopsis thaliana over 15 generations. PLoS One 4:e6035. https://doi.org/10.1371/journal.pone.0006035

Terashima I, Hanba YT, Tholen D, Niinemets U (2011) Leaf functional anatomy in relation to photosynthesis. Plant Physiol 155:108–116. https://doi.org/10.1104/pp.110.165472

Thomas A (2008) Development and properties of 0.25-degree gridded evapotranspiration data fields of China for hydrological studies. J Hydrol 358:145–158. https://doi.org/10.1016/j.jhydrol.2008.05.034

Ting IP (1994) CO_2 and Crassulacean acid metabolism plants: a review. In: Tolbert NE, Preiss J (eds) Regulation of atmospheric CO_2 and O_2 by photosynthetic carbon metabolism. Oxford University Press, New York, pp 176–183

Tissue DT, Thomas RB, Strain BR (1997) Atmospheric CO_2 enrichment increases growth and photosynthesis of Pinus taeda: a 4 year experiment in the field. Plant Cell Environ 20:1123–1134. https://doi.org/10.1046/j.1365-3040.1997.d01-140.x

Torbert HA, Prior SA, Rogers HH, Runion GB (2004) Elevated atmospheric CO_2 effects on N fertilization in grain sorghum and soybean. Field Crop Res 88:57–67. https://doi.org/10.1016/j.fcr.2003.11.011

Tuba Z, Szente K, Koch J (1994) Response of photosynthesis, stomatal conductance, water use efficiency and production to Long-term elevated CO_2 in winter wheat. J Plant Physiol 144:661–668. https://doi.org/10.1016/S0176-1617(11)80657-7

Uddin S, Löw M, Parvin S et al (2018) Water use and growth responses of dryland wheat grown under elevated [CO_2] are associated with root length in deeper, but not upper soil layer. Field Crop Res 224:170–181. https://doi.org/10.1016/j.fcr.2018.05.014

Uddling J, Hogg AJ, Teclaw RM et al (2010) Stomatal uptake of O_3 in aspen and aspen-birch forests under free-air CO_2 and O_3 enrichment. Environ Pollut 158:2023–2031. https://doi.org/10.1016/j.envpol.2009.12.001

Ulman P, Čatský J, Pospíšilová J (2000) Photosynthetic traits in wheat grown under decreased and increased CO_2 concentration, and after transfer to natural CO_2 concentration. Biol Plant 43:227–237. https://doi.org/10.1023/A:1002752210237

Uprety D, Mahalaxmi V (2000) Effect of elevated CO_2 and nitrogen nutrition on photosynthesis, growth and carbon-nitrogen balance in Brassica juncea. J Agron Crop Sci 184:271–276. https://doi.org/10.1046/j.1439-037x.2000.00392.x

Uprety D, Dwivedi N, Jain R et al (2003) Responses of rice cultivars to the elevated CO_2. Biol Plant 46:35–39. https://doi.org/10.1023/A:1022349814670

Uprety DC, Dwivedi N, Raj A et al (2009) Study on the response of diploid, tetraploid and hexaploid species of wheat to the elevated CO_2. Physiol Mol Biol Plants 15:161–168. https://doi.org/10.1007/s12298-009-0018-6

Usuda H (2006) Effects of elevated CO_2 on the capacity for photosynthesis of a single leaf and a whole plant, and on growth in a radish. Plant Cell Physiol 47:262–269. https://doi.org/10.1093/pcp/pci244

Van Oosten J-J, Besford RT (1995) Some relationships between the gas exchange, biochemistry and molecular biology of photosynthesis during leaf development of tomato plants after transfer to different carbon dioxide concentrations. Plant Cell Environ 18:1253–1266. https://doi.org/10.1111/j.1365-3040.1995.tb00185.x

Vanaja M, Raghuram Reddy P, Jyothi Lakshmi N et al (2007) Effect of elevated atmospheric CO_2 concentrations on growth and yield of blackgram (*Vigna mungo* L. Hepper)-a rainfed pulse crop. Plant Soil Environ 53:81–88

Vanaja M, Maheswari M, Jyothi Lakshmi N et al (2015a) Variability in growth and yield response of maize genotypes at elevated CO_2 concentration. Adv Plants Agric Res 2:2–5. https://doi.org/10.15406/apar.2015.02.00042

Vanaja M, Maheswari M, Sathish P et al (2015b) Variability in phenology, physiology and yield response of different maturity duration pigeon pea genotypes at elevated CO_2. Clim Chang Environ Sustain 3:131. https://doi.org/10.5958/2320-642x.2015.00014.9

von Caemmerer S, Quick WP (2000) Rubisco: physiology in vivo. In: Photosynthesis. Springer, pp 85–113

Vu JCV, Gesch RW, Pennanen AH et al (2001) Soybean photosynthesis, rubisco, and carbohydrate enzymes function at supraoptimal temperatures in elevated CO_2. J Plant Physiol 158:295–307. https://doi.org/10.1078/0176-1617-00290

Wahl V, Ponnu J, Schlereth A et al (2013) Regulation of flowering by Trehalose-6-phosphate signaling in Arabidopsis thaliana. Science 339:704–707. https://doi.org/10.1126/science.1230406

Walker C, Armstrong R, Panozzo J et al (2017) Can nitrogen fertiliser maintain wheat (*Triticum aestivum*) grain protein concentration in an elevated CO_2 environment? Soil Res 55:518–523. https://doi.org/10.1071/SR17049

Wall GW, Garcia RL, Wechsung F, Kimball BA (2011) Elevated atmospheric CO_2 and drought effects on leaf gas exchange properties of barley. Agric Ecosyst Environ 144:390–404. https://doi.org/10.1016/j.agee.2011.07.006

Wand SJE, Midgley GF, Jones MH, Curtis PS (1999) Responses of wild C_4 and C_3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. Glob Chang Biol 5:723–741. https://doi.org/10.1046/j.1365-2486.1999.00265.x

Wang H, Xiao W, Niu Y et al (2013) Nitric oxide enhances development of lateral roots in tomato (*Solanum lycopersicum* L.) under elevated carbon dioxide. Planta 237:137–144. https://doi.org/10.1007/s00425-012-1763-2

Wang M, Xie B, Fu Y et al (2015) Effects of different elevated CO_2 concentrations on chlorophyll contents, gas exchange, water use efficiency, and PSII activity on C_3 and C_4 cereal crops in a closed artificial ecosystem. Photosynth Res 126:351–362. https://doi.org/10.1007/s11120-015-0134-9

Weerakoon WMW, Ingram KT, Moss DN (2000) Atmospheric carbon dioxide and fertilizer nitrogen effects on radiation interception by rice. Plant Soil 220:99–106

Weigel H-J, Manderscheid R (2012) Crop growth responses to free air CO_2 enrichment and nitrogen fertilization: rotating barley, ryegrass, sugar beet and wheat. Eur J Agron 43:97–107. https://doi.org/10.1016/j.eja.2012.05.011

Wheeler TR, Ellis RH, Hadley P, Morison JIL (1995) Effects of CO_2, temperature and their interaction on the growth, development and yield of cauliflower (*Brassica oleracea* L. botrytis). Sci Hortic (Amsterdam) 60:181–197. https://doi.org/10.1016/0304-4238(94)00725-U

Wheeler TR, Hong TD, Ellis RH et al (1996) The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO_2. J Exp Bot 47:623–630. https://doi.org/10.1093/jxb/47.5.623

Widodo W, Vu JCV, Boote KJ et al (2003) Elevated growth CO_2 delays drought stress and accelerates recovery of rice leaf photosynthesis. Environ Exp Bot 49:259–272. https://doi.org/10.1016/S0098-8472(02)00091-6

Woodward FI (1987) Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. Nature 327:617–618. https://doi.org/10.1038/327617a0

Woodward FI, Bazzaz FA (1988) The responses of Stomatal density to CO_2 partial pressure. J Exp Bot 39:1771–1781. https://doi.org/10.1093/jxb/39.12.1771

Wu DX, Wang GX (2000) Interaction of CO_2 enrichment and drought on growth, water use, and yield of broad bean (*Vicia faba*). Environ Exp Bot 43:131–139. https://doi.org/10.1016/S0098-8472(99)00053-2

Wu D-X, Wang G-X, Bai Y-F, Liao J-X (2004) Effects of elevated CO_2 concentration on growth, water use, yield and grain quality of wheat under two soil water levels. Agric Ecosyst Environ 104:493–507. https://doi.org/10.1016/j.agee.2004.01.018

Wullschleger SD, Norby RJ (2001) Sap velocity and canopy transpiration in a sweetgum stand exposed to free-air CO_2 enrichment (FACE). New Phytol 150:489–498. https://doi.org/10.1046/j.1469-8137.2001.00094.x

Wullschleger SD, Norby RJ, Hendrix DL (1992) Carbon exchange rates, chlorophyll content, and carbohydrate status of two forest tree species exposed to carbon dioxide enrichment. Tree Physiol 10:21–31. https://doi.org/10.1093/treephys/10.1.21

Wullschleger SD, Gunderson CA, Hanson PJ et al (2002a) Sensitivity of stomatal and canopy conductance to elevated CO_2 concentration—interacting variables and perspectives of scale. New Phytol 153:485–496. https://doi.org/10.1046/j.0028-646X.2001.00333.x

Wullschleger SD, Tschaplinski TJ, Norby RJ (2002b) Plant water relations at elevated CO_2-implications for water-limited environments. Plant Cell Environ 25:319–331. https://doi.org/10.1046/j.1365-3040.2002.00796.x

Xiao G, Zhang Q, Wang R, Xiong Y (2009) Effects of elevated CO_2 concentration, supplemental irrigation and nitrogenous fertilizer application on rain-fed spring wheat yield. Acta Ecol Sin 29:205–210. https://doi.org/10.1016/j.chnaes.2009.08.002

Xu Z, Jiang Y, Jia B, Zhou G (2016) Elevated- CO_2 response of stomata and its dependence on environmental factors. Front Plant Sci 7:657. https://doi.org/10.3389/fpls.2016.00657

Yang L, Huang J, Yang H et al (2006) The impact of free-air CO_2 enrichment (FACE) and N supply on yield formation of rice crops with large panicle. Field Crop Res 98:141–150. https://doi.org/10.1016/j.fcr.2005.12.014

Yang L, Wang Y, Dong G et al (2007) The impact of free-air CO_2 enrichment (FACE) and nitrogen supply on grain quality of rice. Field Crop Res 102:128–140. https://doi.org/10.1016/j.fcr.2007.03.006

Yoshimoto M, Oue H, Kobayashi K (2005) Energy balance and water use efficiency of rice canopies under free-air CO2 enrichment. Agric For Meteorol 133:226–246. https://doi.org/10.1016/j.agrformet.2005.09.010

Zavaleta ES, Shaw MR, Chiariello NR et al (2003) Additive effects of simulated climate changes, elevated CO2, and nitrogen deposition on grassland diversity. Proc Natl Acad Sci U S A 100:7650–7654. https://doi.org/10.1073/pnas.0932734100

Zeng Q, Liu B, Gilna B et al (2011) Elevated CO_2 effects on nutrient competition between a C_3 crop (Oryza sativa L.) and a C_4 weed (*Echinochloa crusgalli* L.). Nutr Cycl Agroecosyst 89:93–104. https://doi.org/10.1007/s10705-010-9379-z

Zhang DY, Chen GY, Gong ZY et al (2008) Ribulose-1,5-bisphosphate regeneration limitation in rice leaf photosynthetic acclimation to elevated CO_2. Plant Sci 175:348–355. https://doi.org/10.1016/j.plantsci.2008.05.008

Zhang G, Sakai H, Tokida T et al (2013) The effects of free-air CO_2 enrichment (FACE) on carbon and nitrogen accumulation in grains of rice (*Oryza sativa* L.). J Exp Bot 64:3179–3188. https://doi.org/10.1093/jxb/ert154

Zhang G, Sakai H, Usui Y et al (2015) Grain growth of different rice cultivars under elevated CO_2 concentrations affects yield and quality. Field Crop Res 179:72–80. https://doi.org/10.1016/j.fcr.2015.04.006

Zhu J, Talbott LD, Jin X, Zeiger E (1998) The stomatal response to CO_2 is linked to changes in guard cell zeaxanthin. Plant Cell Environ 21:813–820. https://doi.org/10.1046/j.1365-3040.1998.00323.x

Zhu J, Goldstein G, Bartholomew DP (1999) Gas exchange and carbon isotope composition of Ananas comosus in response to elevated CO_2 and temperature. Plant Cell Environ 22:999–1007. https://doi.org/10.1046/j.1365-3040.1999.00451.x

Ziska LH (2000) The impact of elevated CO_2 on yield loss from a C_3 and C_4 weed in field-grown soybean. Glob Chang Biol 6:899–905. https://doi.org/10.1046/j.1365-2486.2000.00364.x

Ziska LH, Bunce JA (1997) Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C_4 crops and weeds. Photosynth Res 54:199–208. https://doi.org/10.1023/A:1005947802161

Ziska LH, Teramura AH (1992) Intraspecific variation in the response of rice (*Oryza sativa*) to increased CO_2–photosynthetic, biomass and reproductive characteristics. Physiol Plant 84:269–274. https://doi.org/10.1111/j.1399-3054.1992.tb04664.x

Ziska LH, Manalo PA, Ordonez RA (1996) Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO_2 and temperature: growth and yield response of 17 cultivars. J Exp Bot 47:1353–1359. https://doi.org/10.1093/jxb/47.9.1353

Ziska LH, Namuco O, Moya T, Quilang J (1997) Growth and yield response of field-grown tropical rice to increasing carbon dioxide and air temperature. Agron J 89:45. https://doi.org/10.2134/agronj1997.00021962008900010007x

Ziska LH, Bunce JA, Caulfield FA (2001) Rising atmospheric carbon dioxide and seed yield of soybean genotypes. Crop Sci 41:385. https://doi.org/10.2135/cropsci2001.412385x

Chapter 7
Coping with Saline Environment: Learning from Halophytes

Amal Ahmed Morsy, Karima Hamid A. Salama, and Mohammed Magdy F. Mansour

Contents

Abstract Salt stress is a crucial barrier to crop growth, development, and production and hence negatively affects food security globally. In addition, the current trends of climate change increase the frequencies and severities of drought and heat which accelerate and spread the processes of salt mobilization and accumulation within the upper horizons of arid and semiarid soil. Elevated salinization in arid and semiarid regions necessitates development of economic and environmentally friendly saline agriculture to be comparable with world population increase. As salt stress is a multi-factorial phenomenon caused by various factors or a combination of factors leading to a complex tolerance mechanism, the utilization of suited

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halophytes as niche crops is one of the most promising approaches in this regard. Halophytes have the capability to combat various abiotic factors which occur in their surroundings, and they follow different mechanisms to stress adverse effects. Therefore, investigating halophyte can be useful as the processes by which halophytes thrive and sustain productivity in saline water when understood help in modulating adaptation in crop plants. Further, exploring more halophytes to identify additional salt-responsive genes may also lead to the development of transgenic crops with high adaptation to salinity, which are suitable for sustainable salt soil agriculture. This review thus discusses an ecological integrative approach of halophytes, which implies ecological observations in the field that are associated with halophyte development, physiology, and biochemistry. Halophyte utilization in remediation of polluted soils through their sequestration of absorbed harmful ions into their vacuoles as well as other mechanisms of salt resistance is reviewed.

There are also recommendations for current progress and future work on the use of halophytes to enhance crop quality on marginal and irrigated land.

Keywords Anatomy · Bioremediation · Ecophysiology · Halophytes · Mineral nutrition · Salinity stress · Tolerance mechanisms · Water relations

Abbreviations

AKT	K^+ in channels
EC	Electrical conductivity
HKT	High-affinity K^+ transporters
Ksat	Saturated hydraulic conductivity
KUP/HAK/KT	High-affinity K^+-H^+ symporters
NSCC	Nonselective cation channels
PDD	Predawn disequilibrium
PM	Plasma membrane
ROS	Reactive oxygen species
SOS	Salt overly sensitive
TDS	Total dissolved solids
TSA	Total soluble anions
TSC	Total soluble cations
USEPA	United States Environmental Protection Agency
WUE	Water-use efficiency

7.1 Introduction

The world population has doubled in less than 50 years which put a great pressure on world food reserves, fuel, soil, and biological and water resources. The United Nations (2001) predicts about 9.4 billion people worldwide by 2050. Furthermore, the World Health Organization reports 3.7 billion people are undernourished, and the problem of malnourished will be further increasing in the future. Also, food production since 1984 has been declining per capita because of elevating people number, energy shortage in crop production, and freshwater depletion (Pimentel and Pimentel 2008). It is reported that the problem of water supplies for humankind is one of the major threats that we currently have and appears to be more worse in the future (Cosgrove and Loucks 2015). Saline conditions not only reduce most crop production but also affect soil properties and the ecological balance (Hu and Schmidhalter 2002). The salinity effects also include reduced agricultural productivity, low economic yields, and soil erosion. Moreover, soils with low agricultural potential are often saline in the hot and dry regions of the world.

In these regions, most crops are grown under traditional irrigation which exacerbates the problem since this insufficient management of irrigation contributes to secondary salinization in 20% of irrigated land worldwide (Glick et al. 2007). Consequently, both salinity abundance and freshwater depletion are serious environmental problems affecting the food needs of the world's population, and in turn this urges a need to create new productive areas from saline habitats. This situation necessitates development of economically and environmentally sustainable saline farming, which favors the utilization of suited halophytes as niche crops.

Plants that can withstand increased salinity are called halophytes, whereas agricultural crops have a wide range of responses to salt stress. Halophytes follow different mechanisms to adjust to salinity adverse effects by the accumulation of salts in the vacuoles away from the chloroplast and cytosol, osmolyte biosynthesis, ion homeostasis, and ROS scavenging systems (Flowers and Colmer 2015). Different halophytic species have different strategies for dealing with high salinity. Tolerance to salinity in halophytes is due not only to physiological traits and their genetic modification (Vasquez et al. 2006) but also to compound ecological features in the plant rhizosphere and phyllosphere (Ruppel et al. 2013). Both latter strategies are ascribed to microorganisms inhabiting halophyte roots and leaves, which contribute significantly to halophyte salinity tolerance.

It is also established that inauguration of these mechanisms via short-term treatment with low concentration of salts can enhance salt tolerance of plants (Meng et al. 2018), a process called salt acclimatization. In the current contribution, our goal is to suggest an ecological integrative approach of halophytes, which involves an attempt to correlate ecological observations gathered in the field with halophyte growth, anatomy, and physiological and biochemical data. Also, some halophytes have been shown to have the ability to remove soil pollutants, a strategy termed phytoremediation of contaminated soils (Manousaki and Kalogerakis 2011). We intend therefore in this contribution to get a comprehensive report of the relationships between halophytes and corresponding environmental factors. Learning from halophyte mechanism to cope with high salt for the purpose of crop plants to withstand high soil salinity is also discussed.

7.2 Causes of Soil Salinity

The causes of soil salinity may be natural (primary salinization) or man-made (secondary salinization).

7.2.1 Primary Salinization

Primary salinization is a natural process in arid areas which refers to the deposition of salts as a result of lithological heritage or topography (Tanji 2002). Climatic effects and water management can also induce salinization. For example, evapotranspiration mainly contributes to the pedogenesis of saline and sodic soils in arid and semiarid areas. In addition, arid tropical countries are susceptible to high vaporization which is higher than rainfall, and this leads to the rise of H_2O to the surface soil where solutes accumulate and salinity happens (Smith et al. 1995). Another

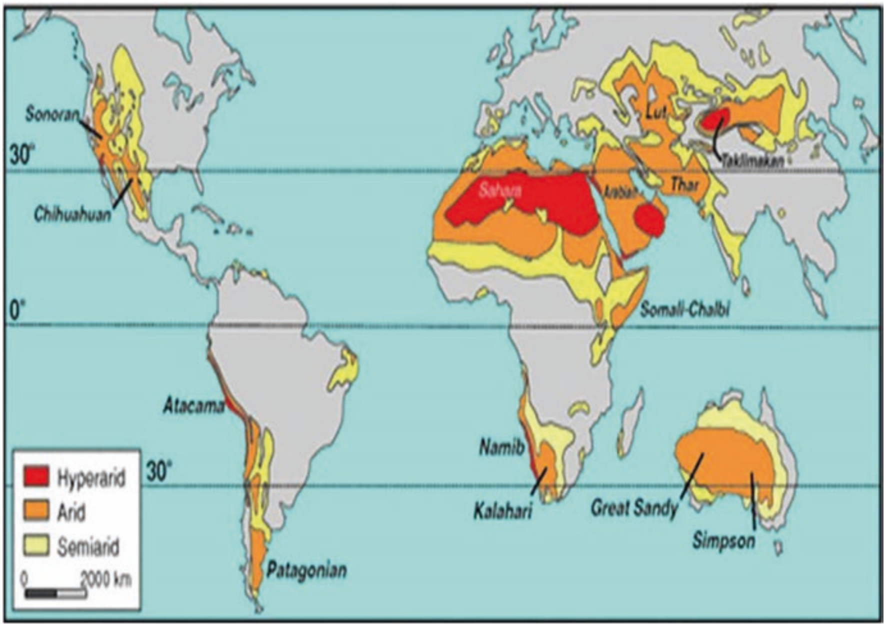

Fig. 7.1 World map of arid and semiarid regions

form of salinity occurs in marshes where the main cause is the intrusion of saline water into rivers or aquifers (Howard and Mullings 1996). Another natural source of soil salinity may include oceanic salt deposition in the coastal areas.

7.2.2 *Secondary Salinization*

Secondary salinization is the term used to distinguish human-induced salinization from naturally salt-affected soils. This type of salinization is mostly found in the semiarid and arid areas where the mean annual precipitation is 25–500 mm (Pla-Sentis 2005). Most of the arid areas globally range from 15 to 30° north and south of the equator (Fig. 7.1, Ustin et al. 2009). The secondary salinity of water and soils in arid regions is rising as a result of growth in mining, industry, and agriculture as well as water resource re-use. Irrigated agriculture is not only participating in the deterioration of water quality, but also it is a key player in the observed water quality deterioration of many rivers. Utilization of such impaired water quality is a future threat for soils with insufficient leaching (FAO 2009). Leaching of mineral salt from the local geology after rainfall and also mining and industrial contamination is considered an important cause for secondary salinization (Stark et al. 2000). FAO (2009) indicated that "although soil salinity is easy to detect, most soil maps, particularly at small scales, show primary salinity because of its association with geological or geomorphological features, which facilitates mapping at such small scales. The mapping of secondary salinization is, however, more complicated because of high spatial and temporal variability and therefore reliable figures are hard to obtain."

7.3 Salinity Composition and Measurement

Soluble salts are those inorganic chemicals that are more soluble than gypsum ($CaSO_4.2H_2O$), which has a solubility of 0.241 g per 100 mL of water at 0 °C (Essington 2005). Most soluble salt in saline soil are composed of cations (Na_+, Ca^{2+}, Mg^{2+}) and anions (CI^-, $SO_4{}^{2-}$, HCO_3). Usually smaller quantities of potassium (K^+), ammonium ($NH_4{}^+$), nitrate ($NO_3{}^-$), and carbonate ($CO_3{}^{2-}$) are also found as do many other ions. Among all these salts, the dominant anions are chloride (CI^-) and sulfate ($SO_4{}^{2-}$), and the dominant cations are Na^+, Ca^{2+}, and Mg^{2+} (Vargas et al. 2018).

Electrical conductivity (EC) is one of the measurements used to measure soil salinity. Electrical conductivity is reported as decisiemens/m ($dS\ m^{-1}$) or millisiemens/cm ($mS\ cm^{-1}$); the latter is equivalent to mmhos/cm. Second, total dissolved solids (TDS) are defined as mg/L or g/L, and multiplying the EC by 640 approximated it for solutions up to approximately 5 $dS\ m^{-1}$. Meanwhile for high salty water and soil solutions, EC is multiplied by 800. Also, salinity could be measured through total soluble cations (TSC) and total soluble anions (TSA). Both TSC and TSA are recorded as charge/L or meq/L. Osmotic potential in MPa can be calculated by taking the product of EC multiplied by 0.00364. Further, if EC is multiplied by 0.0127, ionic strength in ML^{-1} can be calculated (Tanji 2002). For plant response to salt stress, the USDA National Resources Conservation Service characterizes plant salinity tolerance as none (0–2 dS m^{-1}), low (2.1–4 dS m^{-1}), medium (4.1–8 dS m^{-1}), and high (greater than 8 dS m^{-1}) when plant growth is reduced by no more than 10% when plant presents in soil of the indicated soil salinity range.

7.4 Halophytes

Halophytes are specialized plants which have been developed over a long period to tolerate salinity in their substrate than glycophytes can do (Flowers and Muscolo 2015). They can also complete their life cycle under high salinity which is usually toxic to other plant species and causes damage to almost 99% of their population (Flowers and Colmer 2008). Halophytes are highly evolved organisms that can maintain their morphological, anatomical, and physiological characteristics even under high saline conditions (Flowers et al. 1977; Flowers and Colmer 2008).

The term halophyte derives from halophilous (salt-loving), which describes plant species that grow well under saline conditions like salt marches (Yense 2000). Although over 1400 genes are known to be involved in salt tolerance mechanism in

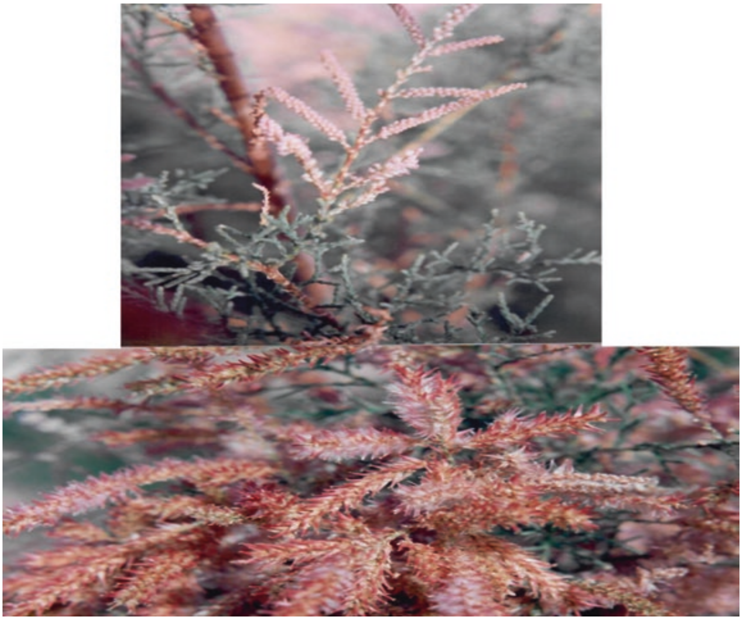

Fig. 7.2 True close up views showing *Tamarix passerinoides* Del

Fig. 7.3 Upper photo showing *Suaeda vermiculata* Forssk., the lower one of *Sevada schimperi* Moq.

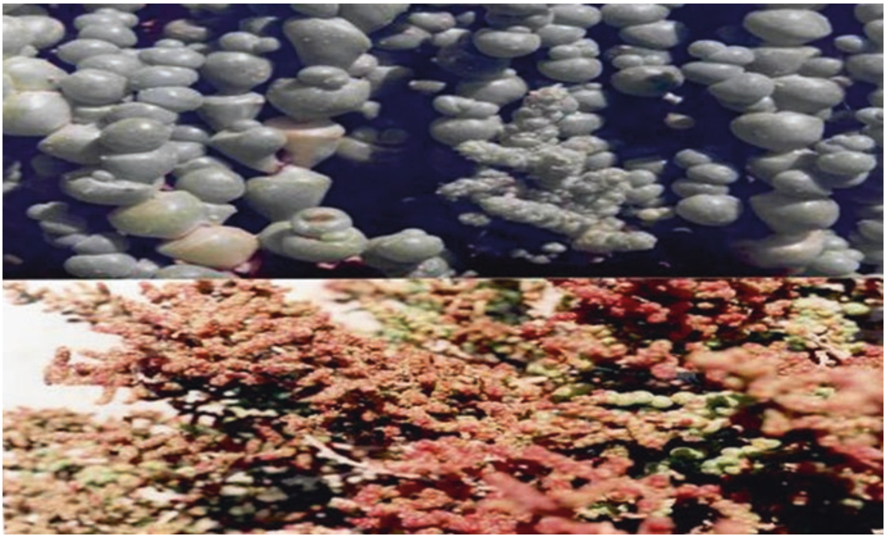

Fig. 7.4 Early flowering *Halopeplis perfoliata* (Forssk.) Bge. ex Schweinf

some halophytes, the exact mechanism whereby wild plants cope with saline environments is not very well understood despite the new genetic engineering approaches (Yancey et al. 1982). Such genes and other enzyme systems as well most likely operate in concert not in a solo, and each halophytic species supposedly has its own orchestra to match its tolerance mechanism requirements (Flowers and Muscolo 2015). Halophytes (Figs. 7.2, 7.3, and 7.4) mainly belong to the Tamaricaceae (*Tamarix* spp.), Aizoaceae (total 52 species; *Mesembryanthemum*), Avicenniaceae (total 19 species; *Avicennia*), Brassicaceae (total 19 species; *Thellungiella*), Chenopodiaceae (total 281 species; *Atriplex*, *Halopeplis*, *Sevada*, *Suaeda*), Plumbaginaceae (total 60 species; *Limonium*), Poaceae (total 143 species; *Distichlis*, *Leptochloa*, *Puccinellia*, *Thinopyrum*, *Spartina*, *Hordeum marinum*), Rhizophoraceae (total 31 species; *Rhizophora*), and Zosteraceae (total 18 species; *Zostera*) families (Aronson 1989; Flowers and Colmer 2008).

7.4.1 Classification of Halophytes

Halophyte classification depends on many factors such as ecological behavior, distribution, growth, and salt intake (Waisel 1972). Based on the interaction between salt and plant in different environments, Steiner (1934) classified halophytes to (a) salt-regulating types, which include managing by increasing succulence and diluting the concentration of salt in the cell sap (e.g., *Haloxylon recurvum*, *Salsola baryosma*, *Sesuvium sesuviodes*, *Trianthema triquetra*, *Zygophyllum simplex*); (b) salt excretion, which occurs through the salt glands in the desalting halophytes (e.g., *Aeluropus lagopoides*, *Chloris virgata*, *Cressa cretica*, *Sporobolus helvolus*, *Tamarix* spp.); and (c) regulation absent, which occurs in those leading to a constant but slow increase in the salt concentration during the vegetative periods (e.g., *Juncus* sp.). Another system of classification depending on the internal salt of the halophyte species where Ashraf et al. (2006) classified halophytes into (a) excluders: where salt concentration in the above ground plant parts are constantly low under various soil concentrations, and (b) includers: where salts are concentrated in above ground plant parts from low or high soil levels and (c) includers: where salts are concentrated in the shoots either in low or high soil salt contents. Furthermore, Walter (1961) classified the halophytes into (a) facultative halophytes, plants that grow and develop in natural soils (i.e., lacking salts) but can withstand certain levels of soil salinity (Cyperaceae, Juncaceae, and Gramineae), and (b) euhalophytes, plants that show optimum growth with certain salt levels but do not grow in a vigorous way (Mangroves). One more system of halophytes classification is adopted by Weber (2009) where halophytes are classified into (a) excretive (excretive plant species possess an excretive option called glandular cells which enable plants to excrete excess salt from their body in the form of salt crystals), and (b) succulents (in succulent halophytic plants, leaf surfaces have salt bladder which enable the plant to have high water content and thus avoid salt injurious impacts). Most of succulent halophytes inhabiting deserts belong to this category. Depending on the different habitat of halophytic plants, Youssef (2009) classified halophytes into (a) hydro-halophytes (they are those which can grow in both aquatic and wet soils, such as salt marsh species and mangroves that inhabit costal lines), and (b) xero-halophytes (they are mostly succulent plants where the soil is saline with low water content due to evaporation).

7.4.2 Ecophysiological Characteristics of Halophytes

7.4.2.1 Plant Growth, Morphology, and Anatomy

In the tropical and subtropical areas, a large number of halophytes are shrubs. However, a small percentage of them are annuals like *Acanthus ilicifolius*. As a result of their cymosely branching, most of halophytic shrubs have a dome-shaped appearance. The majority of species examined had most biomass increase under low salinity conditions, while their growth was slow down by high seawater concentration (Kelly et al. 1982; Glenn and O'Leary 1984; Gorham 1996). Other works report this growth trend of halophytes: as the salt concentration in the growth milieu increases above a critical threshold, depending on halophytic species, the growth decreases gradually in most species (Harrouni et al. 1999, 2001; Daoud et al. 2001). One important indicator that reflects the effect of the growing conditions in the root system is the growth parameter root/shoot ratio. Under moderate drought stress conditions, the growth of the root system increases in order to enable the plant to increase its capacity for water uptake from the growing medium (Harrouni 1989). In saline environments up to a specific limit, the impact of the salinity on root system growth can be matched to that of water stress as salt behaves more like an osmoticum rather than a toxic substance. Increased large root system would therefore seem to be of adaptive significant for plants and their yields as such root system is capable to penetrate more soil layers and thus can absorb greater amount of water and nutrients (Vamerali et al. 2003; Franco et al. 2011). Conversely, another study has demonstrated that halophytic species with other root characteristics, e.g., small roots, can be highly beneficial for greater shoot growth and development as few roots in moist soil can easily uptake enough water independent of the root number (Ma et al. 2010). A consequent response is the root hydraulic conductance in plants irrigated with poor-quality water decreases because the root length and surface area are reduced by such low water quality (Ma et al. 2010).

In mangrove species, root proliferation varies with species and growth conditions such as soil compaction, water capacity, wind speed, and wave direction, which have impacts on the tree stability (Mickovski and Ennos 2003; Ong et al. 2004; Alongi 2009).

To avoid such deleterious conditions, some mangrove species modify to aerial roots, stilt roots/prop roots, and buttress roots instead of tap root systems (Ong et al. 2004; Duke 2011). Such root modifications improve the mangrove tree stability in poor mud along shorelines, which supports them to withstand tides and winds.

For example, *Rhizophora mangle* has prop roots and trunk originated flying buttresses, and both adaptations protect the trees against storm waves (Bayas et al. 2011; Ohira et al. 2013; Mendez-Alonzo and Moctezuma 2015). Besides the supporting function of buttress roots, they act as a conducting system for the transport of water, nutrients, and metabolites for long distances (Tomlinson 1986; Day et al. 2010). Also, the root shape tends to become more oval in weaker soils, which helps them to spread horizontally and ultimately cover a large area of the soil and in turn collect more nutrients from the soil surface (Nicoll and Ray 1996; Clair et al. 2003; Dupuy et al. 2005; Mendez-Alonzo and Moctezuma 2015). However, Srikanth et al. (2015) indicate that other species of mangrove trees that grow in drier soils do not need such root adaptations for their support.

Concerning stem growth in halophytes, several halophytes have been shown to develop succulent stems, which is associated with plant salt tolerance, and the succulence degree is a good indicator of the plant ability to live in saline conditions (Repp et al. 1959). For instance, *Salicornia herbacea* and *Suaeda maritima* are familiar examples for succulence feature where their succulence is developed after ion accumulation in their organs is elevated above a threshold (Joseph et al. 2013). It is noteworthy that salinity stress has been shown to enhance conditions which are suited for succulence: salts inhibit cell division and cell elongation which are typical features for succulence. On the contrary, submerged marine angiosperms are of few halophytes that do not develop succulence, and temperate halophytes are herbaceous, while the tropical halophytes are mostly bushy and exhibit heavily cymosis (Khan and Qaiser 2006). As for the halophyte leaves, they are mostly small, succulent, thick, entire, and glassy in appearance, whereas some species have no leaves (Parida et al. 2016). Additional mode of adaptation is found in aerohalophytes where there stems and leaves are heavily covered with trichomes (Parida et al. 2016). Furthermore, submerged marine halophyte leaves are thin, with green epidermis, and their vascular system is not well developed, and hence they can directly absorb water and nutrients from their growth medium directly (Srikanth et al. 2015).

Other adaptive mechanisms and features in the morpho-anatomy have been developed in plants inhabiting coastal areas to help them to survive under unfavorable conditions (Grigore and Toma 2007; Hameed et al. 2009; Ashraf and Harris 2013). For example, salinity increases the epidermal thickness to improve the plant water-use efficiency (WUE) and provide more space for Na^+ sequestration in the leaf epidermis as well (Shabala et al. 2012). At high salinity (750 mM NaCl), however, the thickness of the epidermis decreased to the value observed in the leaves treated with 250 mM NaCl, which was attributed to the decline in cell division as well as growth under high saline condition (Carcamo et al. 2012). Also, at 250 mM NaCl, the thickness of palisade tissue of *Salvadora persica* leaves raised; meanwhile, at 500 mM NaCl, it declined to the control level and disappeared when plants were treated with 750 mM NaCl (Parida et al. 2016). The significance of palisade tissue decline at high salinity might be of an adaptive value to this halophyte to reduce the use of photosynthetic energy under extreme salinity. In contrast, in semi-mangrove *Myoporum bontioides*, a rise in the palisade tissue thickness was observed under high salinity (Xu et al. 2014). Furthermore, in *Spartina species*, the spongy tissue thickness also elevated with increasing salinity which might help in leaf water content, succulence, and turgor maintenance under high salt stress (Maricle et al. 2009). The study of Maricle et al. (2009) also illustrated that the stomatal density and stomatal aperture diameter declined on lower and upper leaf surfaces by salinity. The decrement in the stomatal number under saline conditions has been similarly indicated in other halophytes such as *Bruguiera parviflora* (Parida et al. 2004), *Nitraria retusa* and *Atriplex halimus* (Boughalleb and Denden 2011), and *Chenopodium quinoa* (Shabala et al. 2012, 2013). Conversely, stomatal index in *Salvadora persica* did not change significantly under saline conditions, which was interpreted to be due to elevated both leaf succulence and pavement cell size, thus improving its WUE and offering extra space for sequestration of Na^+ in the leaf epidermis (Shabala et al. 2012, 2013; Adolf et al. 2013). Based on the above results, it seems that these changes are fundamental mechanisms to enable halophytic species to survive and cope with saline conditions.

Salinity also induces significant alternations in the stem anatomy of halophytes. In *S. persica*, anatomical alterations have been reported: in response to high salinity, the epidermal cells' diameter and thickness of cortex were lowered, whereas thickness of hypodermal layer, diameter of hypodermal cell, pith area, and pith cell diameter were raised (Parida et al. 2016). Also, salt stress impacts root anatomy where an increase in epidermal thickness and a decrease in the epidermal cell diameters and conducting tissues were observed, which may have an adaptive significance under salinity (Parida et al. 2016). This decrease in cortical cell thickness was also demonstrated in several halophytes mainly due to degradation of the cortical cells, the feature that might be adaptive to conserve essential energy for survival in response to severe salinity (Alam et al. 2015; Nawaz et al. 2016). Although xylem vessel diameters in the stem of *S. persica* did not significantly change, they were declined in many other plants which results in a reduction in water and mineral absorption under high salinity (Sandalio et al. 2001; Ortega et al. 2006; Rewald et al. 2012; Atabayeva et al. 2013). It is therefore proposed that in *S. persica* this response may be an adaptive mechanism to maintain continuous water and mineral ion absorption and transport to the shoot.

As plant roots are the first structure directly faced with soil salinity, they may have a dual mechanism acting as the first line of defense or damage (Rewald et al. 2012). Opposite to the shoot system, the root vascular bundle diameter reduced with salinity, an adaptation to decrease the hydraulic conductivity in order to protect the vessel with considerable conductivity during the stress period (Junghans et al. 2006). It appears that the reduction in the root vessel diameter leads to water uptake declining and consequently decreases plant growth and metabolism under high salinity. Also, a decrease in the size of the vascular cylinder of *Prosopis tamarugo* was reported by Serrato-Vlenti et al. (1991), while Hajibagher et al. (1985) found an increase in the root stelar diameter of the halophyte *Suaeda maritima* in response to salinity. The reduced conducting tissues might explain the decrease in the total growth in several species with increasing salinity (de Villiers 1993). Abd Elhalim et al. (2016) reported that the woody tissues of the old root of halophytes are placed and surrounded by lignified cells for support and to protect water columns from embolism and balance the high osmotic pressure that the halophytes facing in their rhizosphere (Grigore and Toma 2007). Similarly, Jacobsen et al. (2005) indicate that presence of much lignified cells in the old root is crucial for providing rigidity and also contributes to cavitation resistance. Another root adaptive response is provided by the fact that an increase in the root cortical cells and epidermal thickness was found in crynohalophyte shrubs *Nitraria retusa* and *Atriplex halimus* under saline conditions (Boughalleb et al. 2009), suggestive of participation in ion diffusion reduction into the roots. Furthermore, the phellem which is the outer part of the root could slow down the water absorption, and hence the salts pass with difficulty in the root, but when they penetrate within the root, they spread in it and become diluted and cause less damage to the plants (Grigore and Toma 2007). Such leaf, stem, and root modifications in response to salt stress are primarily adaptive in order to enable the halophytes to withstand the stress conditions, and some of these changes appear to be species specific.

7.4.3 Water Relations and Mineral Nutrition

Saline habitats have been conducted on natural systems inhabited by plants that can withstand low soil water potential, adapt to the adverse effects of Na^+ ions, and thus tolerate their high concentration (Munns 2002; Richards et al. 2005; Bazihizina et al. 2012). Salt-stressed plants have been found to upregulate their xylem sap Na^+ concentration to maximize hydraulic ability (Munns 1985; López-Portillo et al. 2005, 2014), although no references demonstrated the negative effect of salinity on xylem hydraulics in leaves. However, it is supposed that the effect of salt level of xylem sap on hydraulic efficiency is through its impact on membrane permeability (Zwieniecki et al. 2001; Nardini et al. 2011; van Doorn et al. 2011; Santiago et al. 2013). Another important parameter in water relations of halophytes is predawn disequilibrium (PDD) in water balance between water potential of the soil (Ψw) and plant. Predawn plant Ψw is used to indicate the abundance of soil moisture to plants and hence is utilized to express an array of ecophysiological measurements like ultimate stomatal conductance and transpiration (Reich and Hinckley 1989; AmeÂglio and Archer 1996; Mediavilla and Escudero 2003), plant growth (Mitchell et al. 1993), and differences in root proliferation, adaptation to stress, and habitat sharing between different species (Davis and Mooney 1986; Donovan and Ehleringer 1994; Peuke et al. 2002; Filella and Penuelas 2003). For many halophytes, even at night time and well-watered soils, water loss from the root and shoot is reduced, and PDD can still be of importance (0.2–1.6 MPa) (Donovan et al. 2001, 2003). These authors proposed an explanation that may participate to the significant PDD in halophytes as due to the high solute content in the leaf apoplast. It is noteworthy that water relation studies point to the notion that in absence of low apoplastic Ψs, predawn turgor pressure may reach a level that otherwise induces cell damage (Ritchie and Hinckley 1975; Passioura 1991; Boyer 1995). It is therefore suggested that low predawn apoplastic Ψs could be an effective strategy to modulate Ψs in plants that have high solute levels or when they are grown in soils with fluctuating water availability (James et al. 2005). Furthermore, inconsistences present in PDD among halophytes: although Slatyer (1967) indicates that predawn plant Ψw will balance with soil Ψw, a lot of evidence propose that predawn plant Ψw can be markedly lower (i.e., more negative) than Ψw of the rooting zone in various plant species (Ourcival and Berger 1995; Donovan et al. 2001, 2003; Bucci et al. 2004; James et al. 2005). Explanations for absence of plant and soil Ψw equilibration at night have been indicated. They include low hydraulic conductance, night loss of water by the canopy or root system, high capacitance, and diversity in the soil moisture (Blake and Ferrell 1977; Richards and Caldwell 1987; Ourcival and Berger 1995; Sellin 1999). Further, Donovan et al. (2001, 2003) proposed a mechanism that may play role in the large PDD in halophytes which is high level of osmotica in the leaf apoplast, which is documented by the fact that high solute level in the leaf apoplast has been shown during daily transpiration in both glycophytes and halophytes (Meinzer and Moore 1988; Canny 1993). It is obvious that further research is needed to better understand the strategies driving PDD and unmask the adaptive significance and ecophysiological importance of PDD.

It is established that both cations (Ca^{2+}, Na^+, Mg^{2+}) and anions (Cl^-, SO_4^{2-}, HCO_3^-, CO_3) are available in saline soil but vary in concentration, and usually the proportion of sodium ion cannot exceed the available cations. Meanwhile, if the concentration of Mg^{2+} increased in the soil, it may be toxic because the elevated concentration will be accompanied by decreased absorption of Ca^{2+} and K^+ (Gil et al. 2014). Such effect could be decreased through the presence of high concentration of Ca^{2+}. However, Anosheh et al. (2016) suggested that the relation between calcium accumulation in plants and salinity level is inversely proportion. For mineral relations, many studies measured ion and osmolyte contents in different halophytes growing in the same conditions and thus make it possible to compare between the responses of different species at the same habitat (Albert and Popp 1977; Gorham et al. 1980; Briens and Larher 1982; Popp and Polania 1989; Tipirdamaz et al. 2006). In monocot halophytes, mechanism of salt tolerance depends on Na^+ and Cl^- exclusion from the plant green parts and at the same time maintains cellular K^+/Na^+ ratios relative to dicot halophytes (Flowers and Colmer 2008). In such case, compatible solutes are accumulated in the cytosol for osmotic balance (Albert and Popp 1977; Gorham et al. 1980; Briens and Larher 1982; Rozema 1991; Gil et al. 2014). On the contrary, the dicot halophytes are mainly accumulating Na^+ and Cl^- ions in the plant aerial parts and hence decreasing K^+/Na^+ ratios (Acosta-Motos et al. 2017). However, in dicots it is also crucial to minimize Na^+ content in the cytosol and cellular organelles (Flowers and Colmer 2008). Therefore, the salt tolerance mechanism is apparently based on sequestration of toxic ions into the vacuole to avoid toxicity of the cytoplasm. Adjustment of osmotic balance between the cytoplasm and vacuole depends on gradual gathering of innocent osmotic molecules in the cytoplasm to prevent dehydration of the cytoplasm (Gorham et al. 1980; Briens and Larher 1982; Tipirdamaz et al. 2006; Gil et al. 2014).

High concentrations of cytosolic K^+ are needed to adjust the plant metabolism (Leigh and Wyn Jones 1984) because K^+ has an essential role in plant growth, reproduction, photosynthesis, stress resistance, stomatal movement, osmoregulation, enzyme activation, nitrogen uptake, and protein synthesis (Prajapati and Modi 2012). It is also reported that chloroplasts and mitochondria contain high potassium concentrations (Flowers and Colmer 2008). Despite the key roles of K^+, halophytic species such as *Atriplex mannifera* (Temel and Surmen 2018), *Suaeda maritima* (Clipson 1987), *Salicornia europaea* (Ushakova et al. 2005), *Rhizophora mangle*, and *Laguncularia racemosa* (Medina et al. 1995) showed K^+ content decline in response to salt stress. In addition to K^+, calcium plays a crucial role in retaining plasma membrane integrity (Mansour 1995) and thus regulates selective transport of K^+ under high salt, which enable a plant to be more salt tolerant (Epstein 1998). Despite exogenous supplying of Ca^{2+}, salt stress declined its content in *Aegiceras corniculatum* (Shindle and Bhosale 1985), *Rhizophora mucronata*, *Avicennia officinalis* (Bhosale and Malik 1991), *Allenrolfea occidentalis* (Bilquees et al. 2000), and *Atriplex griffithii* (Khan and Ungar 2000), but no change has been found in Ca^{2+} content in *Suaeda nudiflora* (Joshi and Iyengar 1987). It is obvious that ion homeostasis is a crucial trait for stress resistance under high salinity, and some studies however showed that it is species specific.

7.5 Using Halophytes as Bioremediators

Sustainment of crop productivity needs good strategies to cultivate the unused and marginal lands. One of the most important struggles is the desalination and saline soil recovery. Over the past two decades, improvement of the conditions of both saline and sodic soils was performed through using chemical amendments. Because of over-demands of these amendments by developed countries, the costs are continuing to increase (Qadir et al. 2007). The disadvantage of using chemical amendments for the treatment of saline soils necessitates using phytoremediation techniques which has been proven to be an effective improvement strategy (Qadir et al. 1996). Phytoremediation using halophytic species is a promising approach to reduce salt contents in the saline soils. Phytoremediation is a strategy in which living plants are utilized to cleanse contaminated soil, air, and water from dangerous contaminants that otherwise damage plant life (Salt et al. 1998). For instance, Akhter et al. (2003) indicate that salt-tolerant species are an effective means to address both climate and amendment costs. The authors demonstrate the phytoremediation ability of *Leptochloa fusca* (kallar grass, salt-tolerant species) as this species has the potentiality to leach salts from surface (0–20 cm) to lower depths (>100 cm) resulting in decrement of soil salinity, sodicity, and pH. The soil pH was declined by both release of CO_2 and solubilization of $CaCO_3$ by kallar grass roots. Additionally, it is important to note that in the first 3 years, kallar grass showed an improvement in soil chemical environment, and further grass growth up to 5 years restored and maintained soil fertility, highlighting the contention that growing salt-tolerant plants can avoid depletion of saline barren lands. Recently, using phytoremediation as a low-cost, solar energy-driven cleanup approach to manage the salinity problem has been introduced (Kumar 2017). In support, several reports indicate that reclamation of salt-affected soils was operated by cultivated halophytic species (Chaudhri et al. 1964; Ravindran et al. 2007). In addition, the possibility of using halophytic species as oil seed crops and as forage has also been reported (Glenn et al. 1999). Evidence confirming the beneficial usage of halophytic species as bioremediators comes from the following findings. In Pakistan, Chaudhri et al. (1964) working on *Suaeda fruticosa* showed the ability of this species to accumulate sodium and other salts in their leaves. Also, Ravindran et al. (2007) found that both *Suaeda maritima* and *Sesuvium portulacastrum* have the ability to accumulate salts in their tissue and reduce salts from saline soil. Both halophytes have the ability to eliminate 504 and 474 kg of NaCl, respectively, from 1 ha of the saline soil in a 4-month period. Moreover, due to using the phytoremediation technique to remove salts from saline soils, the farmers' economy will not only increase from salt-affected land treatment, but also they get industrial raw material, food, fodder, and fuel wood. The advantages of utilizing the phytoremediation approach may include the following: (1) we will not need to pay for chemical amendments, (2) we will not only improve the land with halophytes, but also we will get money as a result, (3) amelioration of physical properties of soil (stability, macropores) as well as rapid increasing number of roots, (4) availability of nutrient in soil after phytoremediation, (5) improvement of soil profile, and (6) environmental issues as far as carbon sequestration is concerned in the post-amelioration lands (Hasanuzzaman et al. 2014).

Further evidence for using halophytes as phytoremediators is given in this section. For example, Boyko (1966) demonstrated that both saline soil and water could be desalinated using halophytes. Also, Zahran and Abdel Wahid (1982) used *Juncus rigidus* and *Juncus acutus* to reclaim badly drained soils in Egypt. The authors report that the EC of soil had a 50% saturation decrease in a single growth period. Further, Helalia et al. (1992) showed that saline-sodic soil could be remediated using *Echinochloa stagnina* through reducing sodium level at the soil surface layer. Another study indicated approximately 20 tons of dry weight per hectare have 3–4 tons of salt produced by *Suaeda salsa* (Ke-Fu 1991). Interestingly, *Portulaca oleracea* had salt uptake of 497 kg ha^{-1} accompanied with 3948 kg ha^{-1} biomass production (Hamidov et al. 2007). Rabhi et al. (2010) consistently report that *Arthrocnemum indicum*, *Suaeda fruticosa*, and *Sesuvium portulacastrum* seedlings grown in salty soil greatly decreased the soil salinity and EC via up taking Na$^+$ ions. The authors also observed that *Sesuvium portulacastrum* accumulate almost 30% of Na$^+$ content in the shoots over 170 days. Similarly, when three salt accumulator halophytes, namely, *Tamarix aphylla*, *Atriplex nummularia*, and *Atriplex halimus*, were used to remediate saline-sodic soil in Jordan Valley, a remarkable decrease in soil salinity was recorded (Al Nasir et al. 2010). Based on the above evidence, it is obvious that salinity problem could be resolved by environmentally safe and clean technique such as introducing salt-accumulating plants in order to regulate salinity and conserve farmland sustainability.

Several researchers similarly indicate that hyperaccumulating plants tend to accumulate enormous salt quantities from saline soils in their aboveground biomass (Purakayastha et al. 2017; Suska-Malawska et al. 2019). These authors indicate that one of the environmental and economic solutions in phytoremediation is the use of salt-accumulating halophytes which own a multifunction role in the remediation of saline soils, animal fodder, and organic composts. The ability of halophytic species to remove salts is therefore very crucial particularly when no enough precipitation in arid and semi-arid regions to leach the high salt concentration in the root area. It is noteworthy that cleaning up contaminated soils and underground water at large scale utilizing phytoremediation approaches needs plants with greater rate of salt uptake, tolerance to more than one environmental threat, as well as large biomass. De Souza et al. (2012) studied growth patterns and anatomical changes in *Atriplex nummularia* Lindl and found that this species is a promising halophyte that assists under different conditions such as water deficit, sodic, or saline soil, and hence this halophyte has an important role in managing soil and water quality in semiarid regions. Despite the large evidence presented in this regard, the effectiveness of phytoremediation has some restrictions that should be solved to have a common usage. First, it takes several growing seasons to decrease the level of soil contamination, and therefore it can be time-consuming. Second, it works only in certain soil depths that are associated to rooting zone. Third, remediation of high salinity soil is not easy task since salinity greatly inhibits the germination and growth of several plant species, and therefore selecting suitable plant species for remediation is very crucial. Forth, the plant species must also have a deep and robust root growth as well as enough aerial biomass production for exploring and accumulating more salts (Pajević et al. 2009). Accordingly, it is recommended that halophytes with higher biomass of shoots and root roots should be mainly chosen for remediation. Highly salt-tolerant, food, and fodder plant species are very useful in this connection. Despite the obvious discussed evidence, it seems that using halophytes for soil reclamation needs more research for good utilization of these precious species.

7.6 Mechanisms of Salt Tolerance

High levels of Na^+ in the cells cause salt toxicity which impacts enzymes and impairs cellular metabolism (Hasegawa et al. 2000). High salinity also disturbs K^+ absorption and content, despite the fact that K^+/Na^+ ratio has been reported as a key determinant of plant salt tolerance (Hasegawa et al. 2000). Maintenance of cytosolic Na^+ and Cl^- ions in a low concentration with adequate K^+ is a key tolerance feature in halophytes, and thus ion homeostasis is an urgent mechanism. Halophytes complete their life cycle at external salts more than 200 mM and accumulate more than 500 mM in their shoot (Flowers et al. 2015; Zhang et al. 2015; Santos et al. 2016). Understanding the mechanism of Na^+ transport in halophytes and how they deal with high Na^+ content at cellular and molecular levels is thus needed. It is reported that halophytes have distinct integration of different adaptive mechanisms mainly physiological rather than morphological or anatomical (Shabala 2011). Halophytes tolerate high concentration of salt via strategies working at cellular level which results in evolved defense mechanisms (Flowers and Colmer 2008).

These mechanisms include osmotic adjustment (tissue tolerance), ion homeostasis involving PM and vacuolar membrane transport systems, antioxidant defense systems either enzymatic or nonenzymatic, and alterations of the membrane components (Mansour and Salama 2019). Ion homeostasis mainly includes ion compartmentation in includer halophytes and ion exclusion in excluder halophytes (Hasanuzzaman et al. 2014). Understanding these strategies greatly facilitates developing tolerant plant species/cultivars to saline conditions, which allows utilization of salt and marginal lands (Hasanuzzaman et al. 2014).

7.6.1 Tissue Tolerance

Tissue tolerance is the plant capability to maintain tissue activity through accumulating high Na^+ in older leaves, rather than in younger leaves, where leaf senescence appears first. In addition, salinity induces osmotic action which affects plant growth due to lowered water potential in the surrounding medium. In order to keep continuous water absorption, the cellular water potential needs to be reduced, relative to that of the soil solution, in order to provide water potential gradient between the soil and plant. This water potential gradient drives water entrance to the plant that helps in maintaining the cell turgor and elongation, which eventually promotes growth. Halophytes decline their cellular water potential through absorption and storage of toxic ions (Na^+ and Cl^-) in the vacuole to avoid cytoplasmic toxicity; compartmentation of ions in the vacuole is regarded as one mechanism of tissue tolerance (Munns and Tester 2008). The solute potential of the cytosol is adjusted and balanced to that of the vacuole by elevation of K^+ and compatible osmolytes or innocent solutes in the cytoplasm (Mansour and Salama 2019). It is well established that halophytes synthesized and accumulate compatible osmolytes, such as proline, glycine betaine, polyphenols, and soluble sugars, under saline conditions (Bartels and Dinakar 2013); this accumulation of organic solutes is also one facet of tissue tolerance. Accumulation of inorganic ions and organic innocent solutes in response to high salinity counterbalances the osmotic action of salinity as such mechanism keeps water absorption going on. In addition to their involvement in osmotic adjustment, these compatible solutes also participate in the protection of cellular macromolecules, ROS scavenging, nitrogen and carbon storage, and chaperones (Munns and Tester 2008; Mansour et al. 2015; Mansour and Salama 2019).

7.6.2 Salt Includers and Excluders

Transport of ions in halophytes can clarify the way by which plants avert the injurious impacts of salt on cellular metabolism. It is worth mentioning that halophytes can tolerate high levels of salts in their cytoplasm. The mechanisms or strategies by which plants get rid of toxic ions are crucial for better plant performance under high salinity. Halophytes that accumulate large amounts of Na^+ ions (i.e., includers) pump Na^+ into the vacuoles by specific transporters (detailed below) in order to avert accumulation of ions in the cytoplasm which is illustrated to be a cellular adaptation response leading to tissue tolerance in halophytes (Munns and Tester 2008). It is important to note that the vacuoles of the halophytes are proposed to remodel the composition of their membrane lipids to avoid Na^+ flow back into the cytoplasm (Bartels and Dinakar 2013). Another strategy to keep a reasonable cytosolic concentration of Na^+ is found in recretrohalophytes; this type of halophytes excludes Na^+ out through special structures (Yuan et al. 2016). Also, some other types of halophytes prevent intracellular Na^+ ion accumulation (i.e., excluders) through maintaining Na^+ in their roots and prevent its transport to the aerial green shoot or retrieve it from the shoot to the roots through xylem (Bartels and Dinakar 2013). Flowers et al. (2010) confirm the regulation of ion transport from root to shoot as a vital strategy for halophytes to cope with adverse effects of salinity. In a recent review by Flowers et al. (2019), the transport of toxic ions via transport protein (channels and transporters) and vesicles (exo- and endocytosis) is shown in Fig. 7.5 and discussed below.

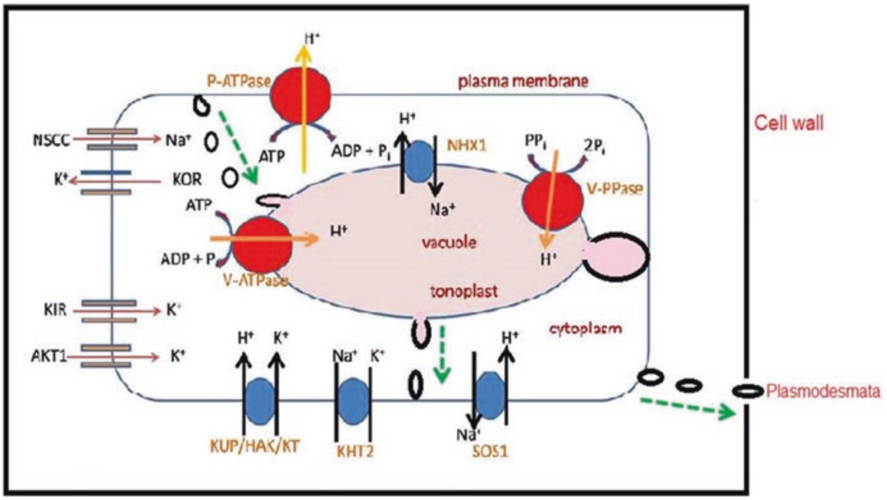

Fig. 7.5 The plasma and vacuolar membrane transport proteins as well as Na^+ vesicular transport participating in ion homeostasis and salt tolerance. (Adapted from Mansour and Salama (2019) and Flowers et al. (2019) with modifications)

7.6.3 PM and Vacuolar Transport Proteins

As no Na^+ pumps have been characterized in plant, uptake of the toxic ions takes place passively via using secondary active transport (Pedersen and Palmgren 2017). PM transport systems operate to either include or exclude Na^+ ions into the cytoplasm, whereas tonoplast transport systems sequester Na^+ in the vacuoles. For secondary transport systems (ion channels and transporters) to work, plasma and vacuolar membrane proton pump activity is required to establish and maintains the electrochemical potential gradient (the proton gradient and membrane potential) across the membrane (Mansour 2014). Membrane channels and transporters involved in the secondary active transport can couple this electrochemical potential gradient to movement of ions against their concentration gradients (Flowers et al. 2010; Mansour 2014). A detailed review by Mansour (2014) presents evidence for the involvement of high-affinity K^+ transporter, AKT1-type channel, and Na^+/H^+ antiporter in the regulation of Na^+ uptake and exclusion under salt stress. Increased activity and expression of PM H^+-ATPase in different halophytes and tolerant glycophytes under high salinity points to the important of this pump in salt tolerance (Bose et al. 2014). In addition, the crucial role of vacuolar ATPase and pyrophosphatase in plant resistance to salt stress is reported by Mansour and Salama (2019). In support to the involvement of plasma and vacuolar transport systems in salt resistance is the finding that expression and activity of plasma membrane and vacuolar membrane H^+-ATPase significantly increased in *Suaeda salsa* in response to NaCl treatment (Chen et al. 2010; Yang et al. 2010).

Halophytes control the cytosolic concentration of Na^+ within 100–200 mM via Na^+/H^+ antiporters or ion channels of PM and vacuole to keep the crucial high ratio of K^+/Na^+ in the cytosol (Flowers et al. 2019). Transporting Na^+, Cl^-, and K^+ into the halophyte cells is proposed to involve 18 or more transporters (Flowers and Colmer 2008). These transporters include low-affinity cation transporter 1 (LCT1), AKT-type ion channels, K^+ transporters from the KUP/HAK/KT family, members of the HKT1 and HKT2 classes of transporters, as well as nonselective cation channels that possibly participate in Na^+ transport across the PM (Wang et al. 2007; Almeida et al. 2013; Wu 2018). So far, the only characterized antiporter that dumps Na^+ from the cytosol to outside the cells is SOS1, and it is located at the PM (Wu 2018). Inhibition of SOS1 activity increased salt sensitivity in the halophytic *Arabidopsis*; the finding confirms the important role of the SOS1 Na^+/H^+ antiporter in plant salt tolerance. In addition, during Na^+ compartmentalization, vacuolar Na^+/H^+ exchangers (NHX) play also crucial roles in Na^+ and K^+ transport and homeostasis: vacuolar Na^+/H^+ antiporter overexpression has been illustrated to enhance tolerance to high salinity in various plant species (Silva and Gerós 2009). It is noteworthy that although membrane ATPase and ion transporters have been reported to have a prime role in salt tolerance of halophytes, the specific mechanism whereby Na^+ and Cl^- enter and leave the cells needs further elucidation (Meng et al. 2018).

7.6.4 Vesicular Transport

Vesicular transport of ions is widespread among eukaryotes with the mechanism of exo- and endocytosis being conserved (Cucu et al. 2017). Recently, Flowers et al. (2019) reviewed the mechanism of ion transport via vesicles which participate in exporting ions into salt glands. In endocytosis, vesicles formed by the Golgi apparatus are combined with the PM, surround the ion, and export it to salt glands. Vesicle-mediated transport systems may also be produced from the vacuole to the PM in order to carry solutes from the vacuole through tonoplast vesicles into apoplast. Exocytosis acts to the recovery of membrane material from the PM. Ion transport through vesicle is different from that by transporters or ion channels (Flowers et al. 2019) where vesicular ion transport depends on ion concentration near forming vesicle and electrical charge of vesicular membrane, whereas transport via intrinsic proteins is determined by its structure. Vesicular traffic of Na^+ and Cl^- is considered as a part of salt resistance in halophytes (Flowers et al. 2019). Further investigations at the molecular, cellular, and whole plant are needed to prove the role and the way of vesicular transport in halophytes.

Specialized salt glands are well-known tolerance trait in several halophytes to control toxic ion levels under high salt stress (Flowers and Colmer 2015; Yuan et al. 2016; Santos et al. 2016). Recretohalophytes are the groups that have a specific salt execratory structure originating from the epidermis (Yuan et al. 2016). The salt exclusion mechanisms differ among recretohalophytes species according to the structure of salt excluder. In Aizoaceae and Amaranthaceae, toxic ions are deposited in bladder cell vacuole and thus accumulated in the bladders (Agarie et al. 2007; Park et al. 2009). The bladder cells are next ruptured and ions are accumulated on the surface of the epidermis. Such mechanism to compartmentalize salts in the vacuoles of the bladder cells is similar to that utilized by several halophytes and glycophytes where salt is sequestered in the vacuoles of the mesophyll cells of the succulent leaves (Park et al. 2009). Agarie et al. (2007) indicated that toxic ions are sequestered into the epidermal bladder cells of the common ice plant (*Mesembryanthemum crystallinum*) maintaining ion homeostasis suitable for green active tissues and thus contributing to plant tolerance to saline conditions.

Other species of halophytes exclude Na^+ via bicellular salt gland as chloridoid grasses (Amarasinghe and Watson 1988). However, multicellular glands were also found in *Limonium bicolor* (Feng et al. 2014) and in *Aeluropus littoralis* (Barhoumi et al. 2008). Multicellular glands are composed of basal accumulating cells and secretory cells (Thomson et al. 1988). The collecting cells are supposedly to maintain a downhill gradient to accumulate ions from surrounding mesophyll cells and then transport them to the secretory cells (Faraday and Thomson 1986). Tan et al. (2013) report that for the secretory cells to prevent leakage of ions back to the surrounding cells, they are surrounded by a cuticle except the connection between them and the basal collecting cells. The basal collecting cells may partially be connected with plasmodesmata; thus, salt is most likely transported actively from the collecting cells into the secretory cells and eventually to outside the cell through the pores in the cuticle (Faraday and Thomson 1986). It is obvious that understanding the mechanism of salt secretion via the salt gland performance can enable us to develop salt-tolerant crops which makes it possible to cultivate non-used saline lands.

7.6.5 Antioxidant Defense Systems

High salinity induced the formation of reactive oxygen species (ROS) which are produced from the electron or energy transfer in the mitochondria and chloroplasts and hence cause oxidative stress in plants (Das and Kumar 2016; Meng et al. 2018). The ROS cause oxidation and damage of cellular macromolecules such as protein, membrane lipid, and nucleic acids leading to impairing their functions (Mansour and Ali 2017). To detoxify ROS, plant increases the activity, expression, and biosynthesis of antioxidant systems to protect cells from oxidative damage (Mansour and Salama 2019). It is therefore crucial that the plant cell produces antioxidant defense systems to combat the deleterious impacts of ROS. The antioxidant defense systems include either enzymatic or nonenzymatic species, targeted as tissue tolerance mechanism. In several halophytes, antioxidant enzymes have been identified to play crucial roles in the protection against ROS damage, such as glutathione transferases from *Salicornia brachiata* (Jha et al. 2011), ascorbate peroxidases from *Suaeda salsa* and *Populus tomentosa* (Li et al. 2012; Cao et al. 2017), superoxide dismutases from *Tamarix* (Wang et al. 2010), and monodehydroascorbate reductase from *Avicennia marina* (Kavitha et al. 2010). Consistently, when *Salicornia brachiata* metallothionein gene *sbMT-2* is overexpressed in tobacco, transgenic plants showed enhance salt tolerance with elevated superoxide dismutase expression, peroxidase, and ascorbate peroxidases, confirming antioxidant enzymes' role in ROS detoxification and eventually salt resistance (Chaturvedi et al. 2014). Together with antioxidant enzymes, increased contents of nonenzymatic antioxidants including ascorbic acid, glutathione, polyphenols, tocopherols, and flavonoids have been illustrated in several halophytes under high salinity and have been found to greatly participate in their salt resistance (Ben Amor et al. 2006; Ivan and Oprică 2013). In agreement with that, the importance of nonenzymatic antioxidants in halophyte salt tolerance is emphasized as a powerful system acting against the damaging effects of hydroxyl radicals on cellular macromolecules (Bose et al. 2014).

7.6.6 Membrane Lipid Modeling

Alteration in the membrane structure and composition is an evolved strategy in salt tolerance mechanism (Mansour and Salama 2019). The structure and composition of PM highly affect the fluidity, permeability, stability of membrane, and membrane transport system activities (Mansour 2013; Mansour et al. 2015; Meng et al. 2018; Mansour and Salama 2019). The pivotal roles of the PM constituents in plant adaptation to high salinity and the relationship between PM lipid modulations and tolerance to saline conditions are detailed in a recent review by Mansour et al. (2015). The membrane changes in halophytes were always in the positive and sustainable direction to retain membrane integrity and transport system activity, and therefore these changes are correlated with salt tolerance under saline conditions. For example, membrane lipid alterations have shown to relate with type of salt accumulation and resistance in ten wild halophytes (Rozentsvet et al. 2014). In the halophyte *Thellungiella halophile*, Sui and Han (2014) found high phosphatidylglycerol content as well as greater unsaturated fatty acids under high salt stress. The study revealed that these alterations enhanced the resistance of photosystem II to high salinity. In addition, PM different lipid and phospholipid species were altered in *Zygophyllum album* and *Zygophyllum coccineum* as a result of soil pollution with the increase in saturation/unsaturation ratio of both species (Morsy et al. 2010), which also contributed to stress tolerance. In the same trend, PM lipid changes in salt marsh grass (*Spartina patens*) under saline environments were found to be correlated with salt resistance (Wu et al. 2005). In agreement with these findings, introducing the *Suaeda salsa* gene encoding enzyme catalyzed phosphatidylglycerol synthesis in *Arabidopsis* resulted in transgenic plants with enhanced resistance to high salinity (Sui et al. 2017). Additionally, increased unsaturated fatty acid contents in membrane lipids preserve photosystems I and II which improves salt resistance in *Suaeda salsa* and tomato (Sun et al. 2010; Sui et al. 2010). Also, when Leach et al. (1990) studied isolated vacuoles from the halophyte *Suaeda maritime*, it turns out that the vacuolar membrane lipids as well as the degree of fatty acid saturation have a key role in NaCl compartmentation in the vacuole. Similarly, PM high sterol content and high unsaturated fatty acids are related to salt resistance in the halophyte *Cakile maritime* (Chalbi et al. 2015). The importance of modeling of membrane lipids under high salinity comes from the fact that this modeling ensures presence of certain lipid species required for maintenance of membrane integrity as well as for proper functioning of membrane transport proteins involved in ion homeostasis under high salinity (Chalbi et al. 2015; Mansour et al. 2015). Further, the role of membrane lipids as intracellular mediators in signaling pathways in plant environmental responses is documented (Ruelland et al. 2015). Despite the clear association between membrane lipid remodeling and salt resistance, more research is needed at the molecular level to further examine and document the role of certain lipid classes in salt tolerance mechanism.

7.7 Future Perspectives

Increasing population will bring certainly increased demands for food all over the world. There is every reason to believe that challenge to produce more and better food at lower cost will be met. Therefore, long-term studies are urgently needed to demonstrate the viability of halophyte crop production and its economic prospects for potential farmers.

Real benefits can be achieved if concerted efforts are made to investigate species-specific regulation during abiotic stress, expand genetic capital, and exploit mechanisms of stress tolerance in crops.

In this regard, several studies have shown that the genes cloned from halophytes promote stress tolerance when expressed in glycophytes.

Future research should also work on identifying additional salt-responsive genes by exploring more suitable halophytes that help us better understand the mechanisms of salt tolerance and apply the findings to the production of high salinity transgenic crops. Moreover, halophytic crops should undergo the same process undergone by conventional agricultural crops such as breeding to improve their agricultural traits, and thus during short time spans, economically profitable and consumer-acceptable products can be attained. For example, halophytic crops have been indicated to possess economic importance, such as vegetable, forage, and oilseed crops, and also can be used as resource for the future to reduce the water crisis (Koyro et al. 2011).

More use of halophytes is supported by the notion that halophytes are an important plant species with high soil salinity and saline water irrigation, thus having the potential for desalination (phytoremediation) and saline soil restoration. As for long term, a promising issue will be raised and can be a must by then which is the halophyte biofuel production costs will be lower than other alternative energy resources and advancing halophyte cultivation will be an ultimate goal.

References

Abd Elhalim ME, Abo-Alatta OK, Habib SA, Abd Elbar OH (2016) The anatomical features of the desert halophytes *Zygophyllum album* L.F. and *Nitraria retusa* (Forssk.) Asch. Ann Agric Sci 61:97–104

Acosta-Motos JR, Ortuno MF, Bernal-Vicente A, Diaz-Vivancos P, Sanchez-Blanco MJ, Hernandez JA (2017) Plant responses to salt stress: adaptive mechanisms. Agronomy 7:1–38

Adolf VI, Jacobsen SE, Shabala S (2013) Salt tolerance mechanisms in quinoa (*Chenopodium quinoa* Willd.). Environ Exp Bot 92:43–54

Agarie S, Shimoda T, Shimizu Y, Baumann K, Sunagawa H, Kondo A (2007) Salt tolerance, salt accumulation, and ionic homeostasis in an epidermal bladder-cell-less mutant of the common ice plant *Mesembryanthemum crystallinum*. J Exp Bot 58:1957–1967

Akhter J, Mahmood K, Malik KA, Ahmed S, Murray R (2003) Amelioration of a saline sodic soil through cultivation of a salt-tolerant grass *Leptochloa fusca*. Environ Conserv 30:168–174

Al Nasir F, Batarseh M, Abdel-ghani A, Jiries A (2010) Free amino acids content in some halophytes under salinity stress in arid environment, Jordan. Clean Soil Air Water 38:592–600

Alam MA, Juraimi AS, Rafii MY, Hamid AA (2015) Effect of salinity on biomass yield and physiological and stem-root anatomical characteristics of Purslane (*Portulaca oleracea* L.) accessions. Biomed Res Int 2015:105695

Albert R, Popp M (1977) Chemical composition of halophytes from the Neusiedler Lake region in Austria. Oecologia 27:157–170

Almeida P, Katschnig D, de Boer AH (2013) HKT transporters—state of the art. Int J Mol Sci 14:20359–20385

Alongi DM (2009) The energetics of mangrove forests. Springer, New York

Amarasinghe V, Watson L (1988) Comparative ultrastructure of microhairs in grasses. Bot J Linn Soc 98:303–319

AmeÂglio T, Archer P (1996) Repreâsentativiteâdupotentiel de basesur sols aáhumiditeâheâteâro-geáne. Agronomie 16:493–503

Anosheh HP, Ranjbar G, Pakniyat H, Emam Y (2016) Physiological mechanisms of salt stress tolerance in plants: an overview. In: Azooz MM, Ahmad P (eds) Plant-environment interaction: responses and approaches to mitigate stress. Wiley, New Jersey, pp 141–160

Aronson J (1989) Halophytes. A database of salt tolerant plant of the world. Office of Arid Lands Studies, Univ. Arizona, Tucson

Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: an overview. Photosynthetica 51:163–190

Ashraf M, Hameed M, Arshad M, Ashraf Y, Akhtar K (2006) Salt tolerance of some potential forage grasses from Cholistan desert of Pakistan. In: Khan MA, Weber DJ (eds) Ecophysiology of high salinity tolerance plants. Springer, Dordrecht, pp 31–54

Atabayeva S, Nurmahanova A, Minocha S, Ahmetova A, Kenzhebayeva S, Aidosov S (2013) The effect of salinity on growth and anatomical attributes of barley seedling (*Hordeum vulgare* L.). Afr J Biotechnol 12:2366–2377

Barhoumi Z, Djebali W, Abdelly C, Chaïbi W, Smaoui A (2008) Ultrastructure of Aeluropus littoralis leaf salt glands under NaCl stress. Protoplasma 233:195–202

Bartels B, Dinakar C (2013) Balancing salinity stress responses in halophytes and non-halophytes: a comparison between Thellungiella and Arabidopsis thaliana. Funct Plant Biol 40:819–831

Bayas JCL, Marohn C, Dercon G, Dewi S, Piepho PH, Joshi L, Noordwijk M, Cadisch G (2011) Influence of coastal vegetation on the 2004 tsunami wave impact in west Aceh. PNAS 108:18612–18617

Bazihizina N, Barret-Lennard EG, Colmer TD (2012) Plant growth and physiology under heterogeneous salinity. Plant Soil 354:1–19

Ben Amor N, Jimenez A, Megdiche W, Lundqvist M, Sevilla F, Abdelly C (2006) Response of antioxidant systems to NaCl stress in the halophyte *Cakile maritima*. Physiol Plant 126:446–457

Bhosale LJ, Malik NG (1991) Strategies of seed germination in mangroves. In: Proc. in turn seed symposium, pp 201–205

Bilquees G, Weber DJ, Khan MA (2000) Effect of salinity and planting density and physiological responses of *Allenrolfea occidentalis*. West North Am Nat 60:188–197

Blake J, Ferrell WK (1977) Association between soil and xylem water potential, leaf resistance, and abscisic acid content in Leaf apoplastic solutes and water relations. Physiol Plant 39:106–109

Bose J, Rodrigo-Moreno A, Shabala S (2014) ROS homeostasis in halophytes in the context of salinity stress tolerance. J Exp Bot 65:1241–1257

Boughalleb F, Denden M (2011) Physiological and biochemical changes of two halophytes, *Nitraria retusa* (Forssk.) and *Atriplex halimus* (L.) under increasing salinity. Agric J 6:327–339

Boughalleb F, Denden M, Tiba BB (2009) Anatomical changes induced by increasing NaCl salinity in three fodder shrubs, Nitraria retusa, Atriplex halimus and Medicago arborea. Acta Physiol Plant 31:947–960

Boyer JS (1995) Measuring the water status of plants and soils. Academic, San Diego

Boyko H (1966) Basic ecological principles of plant growing by irrigation with highly saline or seawater. In: Boyko H (ed) Salinity and aridity. Dr. W. Junk Publishers, The Hague, pp 131–200

Briens M, Larher F (1982) Osmoregulation in halophytic higher plants: a comparative study of soluble carbohydrates, polyols, betaines and free proline. Plant Cell Environ 5:287–292

Bucci SJ, Scholz FG, Guillermo G, Meinzer FG, Hinojosa JA, Hoffmann WA, Agusto CF (2004) Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species. Tree Physiol 24:1119–1112

Canny MJ (1993) The transpiration stream in the leaf apoplast: water and solutes. Philos Trans R Soc Lond Ser B Biol Sci 341:87–100

Cao S, Du XH, Li LH, Liu YD, Zhang L, Pan X et al (2017) Overexpression of *Populus tomentosa* cytosolic ascorbate peroxidase enhances abiotic stress tolerance in tobacco plants. Russ J Plant Physiol 64:224–234

Carcamo HJ, Bustos MR, Fernandez FE, Bastias EI (2012) Mitigating effect of salicylic acid in the anatomy of the leaf of *Zea mays* L. lluteno ecotype from the Lluta Valley (Arica-Chile) under NaCl stress. IDESIA 30:55–63

Chalbi N, Martinez-Ballesta MC, Youssef NB, Carvajal M (2015) Intrinsic stability of Brassicaceae plasma membrane in relation to changes in proteins and lipids as a response to salinity. J Plant Physiol 175:148–156

Chaturvedi AK, Patel MK, Mishra A, Tiwari V, Jha B (2014) The SbMT-2 gene from a halophyte confers abiotic stress tolerance and modulates ROS scavenging in transgenic tobacco. PLoS One 9:e111379

Chaudhri II, Nagri N, Mallik IA (1964) Investigation on the role of *Suaeda fruticosa* in the reclamation of saline and alkaline soils of West Pakistan. Plant Soil 21:1–7

Chen M, Song J, Wang BS (2010) NaCl increases the activity of the plasma membrane H+-ATPase in C-3 halophyte *Suaeda salsa* callus. Acta Physiol Plant 32:27–36

Clair B, Fournier M, Oise Prevost MF, Beauchene J, Bardet S (2003) Biomechanics of buttressed trees: bending strains and stresses. Am J Bot 90:1349–1356

Clipson NJ (1987) Salt tolerancein the halophyte *Suaeda maritima* (L.) Dum.: growth, ion and water relations, and gas exchange in response to fluctuating salinity. J Exp Bot:38

Cosgrove WJ, Loucks DP (2015) Water managment: current and future challenges and research directions. Water Resour Res 51:4823–4839

Cucu B, Degreif D, Bertl A, Thiel G (2017) Vesicle fusion and fission in plants and yeast. Cell Calcium 67:40–45

Daoud S, Koyro H-W, Harrouni MC (2001) Salinity tolerance of beta vulgaris ssp. Maritima. I. Biomass production and osmotic adjustment (to appear in Lieth H (ed) Cash crop halophytes: potentials, pilot projects, basic and applied research on halophytes and saline irrigation.—“Ten years after the Al Ain meeting” T: VS Series, Kluwer academic publishers group (the Netherlands))

Das AJ, Kumar R (2016) Bioremediation of contaminated soil to combat toxicity on Withania somnifera through seed priming with biosurfactant producing plant growth promoting rhizobacteria. J Environ Manag 174:79–86

Davis SD, Mooney HA (1986) Water use patterns of four co-occurring chaparral shrubs. Oecologia 70:172–177

Day DS, Wiseman EP, Dickinson SB, Harris JR (2010) Contemporary concepts of root system architecture of urban trees. Arboricult Urban For 36:149–159

De Souza ER, Freire MBGS, Cunha KPV, Nascimento CWA (2012) Biomass, anatomical changes and osmotic potential in *Atriplex nummularia* Lindl. cultivated in sodic saline soil under water stress. Environ Exp Bot 82:20–27

De Villiers AJ (1993) Ecophysiological studies on several Namaqualand pioneer species, with special reference to the revegetation of saline mined soil. M. Sc. Thesis, University of Pretoria, Pretoria, Dekker, New York

Donovan LA, Ehleringer JR (1994) Water stress and use of summer precipitation in a Great Basin shrub community. Funct Ecol 8:289–297

Donovan LA, Linton MJ, Richards JH (2001) Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. Oecologia 129:328–333

Donovan LA, Richards JH, Linton MJ (2003) Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. Ecology 84:463–470

Duke NC (2011) Mangroves structure, form and process. In: Hopley D (ed) Encyclopedia of modern coral reefs. Springer, Dordrecht, pp 655–663

Dupuy L, Fourcaud T, Stokes A (2005) A numerical investigation into factors affecting the anchorage of roots in tension. Eur J Soil Sci 56:319–327

Epstein E (1998) How calcium enhances plant salt tolerance. Science 280:1906–1907

Essington ME (2005) Soil and water chemistry: an integrative approach. CRC Press, Boca Raton. EURATOM, 2000.2000/473/EURATOM-Commission Recommendation of 8 June 2000, Official Journal of the European Commission, no. 191, 27 June 2000

FAO (2009) Advances in the assessment and monitoring of salinization and status of biosaline agriculture. World Soil Reports No: 104, Rome, p 72

Faraday CD, Thomson WW (1986) Morphometric analysis of *Limonium* salt-glands in relation to ion efflux. J Exp Bot 37:471–481

Feng ZT, Sun QJ, Deng YQ, Sun SF, Zhang JG, Wang BS (2014) Study on pathway and characteristics of ion secretion of salt glands of *Limonium bicolor*. Acta Physiol Plant 36:2729–2741

Filella I, Penuelas J (2003) Partitioning of water and nitrogen in co-occurring Mediterranean woody shrub species of different evolutionary history. Oecologia 137:51–61

Flowers J, Colmer TD (2008) Salinity tolerance in halophytes. New Phytol 179:945–963

Flowers J, Colmer TD (2015) Plant salt tolerance: adaptations in halophytes. Ann Bot 115:327–331

Flowers J, Muscolo A (2015) Introduction to the special issue: halophytes in a changing world. AoB Plants 7:plv020

Flowers J, Trok P, Yeo A (1977) The mechanism of salt tolerance in halophytes. Ann Rev Plant Physiol 28:89–121

Flowers J, Galal K, Bromham L (2010) Evolution of halophytes: multiple origins of salt tolerance in land plants. Funct Plant Biol 37:604–612

Flowers TJ, Munns R, Colmer T (2015) Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. Ann Bot 115:419–431

Flowers J, Glenn P, Volkov V (2019) Could vesicular transport of Na^+ and Cl^- be a feature of salt tolerance in halophytes. Ann Bot 123:1–18

Franco JA, Bañón S, Vicente MJ, Miralles J, Martínez-Sánchez JJ (2011) Root development in horticultural plants grown under abiotic stress conditions—a review. J Hortic Sci Biotechnol 86:543–556

Gil R, Bautista I, Boscaiu M, Lidon A, Wankhade S, Sanchez H, Llinares J, Vicente O (2014) Responses of five Mediterranean halophytes to seasonal changes in environmental conditions. AoB Plants 6:plu049. https://doi.org/10.1093/aobpla/plu049

Glenn EP, O'Leary JW (1984) Relationship between salt accumulation and water content of dicotyledonous halophytes. Plant Cell Environ 7:253–261

Glenn E, Brown J, Blumwald E (1999) Salt tolerance and crop potential of halophytes. Crit Rev Plant Sci 18:227–255

Glick BR, Cheng Z, Czarny J, Duan J (2007) Promotion of plant growth by ACC deaminase-producing soil bacteria. Eur J Plant Pathol 119:329–339

Gorham J (1996) Mechanisms of salt tolerance of halophytes. In: Halophytes and biosaline agriculture. Marcel Dekker, New York

Gorham J, Hughes L, Wyn Jones RG (1980) Chemical composition of saltmarsh plants from YnysMôn (Anglesey): the concept of physiotypes. Plant Cell Environ 3:309–318

Grigore MN, Toma C (2007) Histo-anatomical strategies of Chenopodiaceae halophytes; adaptive, ecological and evolutionary implications. WSEAS Trans Biol Biomed 12:204–218

Hajibagher MA, Yeo AR, Flowers TJ (1985) Salt tolerance in *Suaeda maritima* (L) Dum. Fine structure and ion concentrations in the apical region of roots. New Phytol 99:331–343

Hameed BH, Krishni RR, Sata SA (2009) A novel agricultural waste adsorbent for the removal of cationic dye from aqueous solutions. J Hazard Mater 162:305–311

Hamidov A, Beltrao J, Neves A, Khaydarova V, Khamidov M (2007) *Apocynum lancifolium* and *Chenopodium album*—potential species to remediate saline soils. WSEAS Trans Environ Dev 3:123–128

Harrouni MC (1989) The effect of water stress on growth and development of barley and tef. Ph. D. Thesis, University College of North Wales, Bangor

Harrouni MC, Daoud S, El Alami A, Debbagh B, Chokr-Allah R, Bengaddour R (1999) Responses of some halophytes to seawater irrigation in Morocco. In: Hamdy A, Lieth H, Todorovic M, Moschenko M (eds) Halophyte uses in different climates II. pp 57–75

Harrouni MC, Daoud S, Koyro H-W (2001) Effect of seawater irrigation on biomass production and ion composition of 7 halophytic species in Morocco. In: Lieth H (ed) Cash crop halophytes: potentials, pilot projects, basic and applied research on halophytes and saline irrigation. TVS Series. Kluwer Academic Publishers, Dordrecht

Hasanuzzaman M, Nahar K, Alam M, Bhowmik PC, Hossain A, Rahman MM, Vara Prasad MN, Ozturk M, Fujita M (2014) Potential use of halophytes to remediate saline soils. BioMed Res Int 2014:1–12. Hindawi Publishing Corporation

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol Plant Mol Biol 51:463–499

Helalia AM, El-Amir S, Abou-Zeid ST, Zaghloul KF (1992) Bio-reclamation of saline-sodic soil by Amshot grass in Northern Egypt. Soil Tillage Res 2:109–115

Howard KW, Mullings E (1996) Hydrochemical analysis of ground-water flow and saline incursion in the Clarendon Basin, Jamaica. Ground Water 34:801–810

Hu Y, Schmidhalter U (2002) In: Hock H, Elstner N (eds) Limitation of salt stress to plant growth: plant toxicology, 4th edn. Marcel Dekker Inc., New York, pp 191–224

Ivan L, Oprică L (2013) Study of polyphenols and flavonoids contents of some halophytes species collected from dobrogea region. Bull Transilv Univ (Braşov) 6:121–128

Jacobsen AL, Ewers FW, Pratt RB, Paddock WA, Davis SD (2005) Do xylem fibers affect vessel cavitation resistance? Plant Physiol 139:546–556

James JJ, Tiller RL, Richards JH (2005) Multiple resources limit plant growth and function in a saline-alkaline desert community. J Ecol 93:113–126

Jha B, Sharma A, Mishra A (2011) Expression of SbGSTU (tau class glutathione S-transferase) gene isolated from *Salicornia brachiata* in tobacco for salt tolerance. Mol Biol Rep 38:4823–4832

Joseph D, Chakraborty K, Subin CS, Vijayan KK (2013) Halophytes of chenopodiaceae and aizoaceae from South-East coast of India as potential sources of essential nutrients and antioxidants. J Food Nutr Res 1:97–107

Joshi AJ, Iyengar ERR (1987) Effects of seawater salinity on free amino acids and mineral ions are *Suaeda nudiflora* Moq. Proc Indian Acad Sci 97:309–314

Junghans U, Polle A, Düchting P, Weiler E, Kuhlman B, Gruber F (2006) Adaptation to high salinity in poplar involves changes in xylem anatomy and auxin physiology. Plant Cell Environ 29:1519–1531

Kavitha K, George S, Venkataraman G, Parida A (2010) A salt-inducible chloroplastic monodehydroascorbate reductase from halophyte *Avicennia marina* confers salt stress tolerance on transgenic plants. Biochimie 92:1321–1329

Ke-Fu Z (1991) Desalinization of saline soils by *Suaeda salsa*. Plant Soil 135:303–305

Kelly DB, Goodin JR, Miller DR (1982) Biology of atriplex. In: Sen DN, Rajpurohit KS (eds) Tasks For vegetation science, vol 2. Contributions to the ecology of halophytes. Dr. W. Junk Publishers, The Hague

Khan MA, Qaiser M (2006) Halophytes of Pakistan: distribution, ecology, and economic importance. In: Khan MA, Barth H, Kust GC, Boer B (eds) Sabkha ecosystems, vol II. The south and central Asian countries. Springer, Dordrecht, pp 129–153

Khan MA, Ungar IA (2000) Alleviation of innate and salinity induced dormancy in *Atriplex griffithii*. Moq. Var. Stocksii boiss. Seed Sci Technol 28:29–37

Koyro H, Khan MA, Lieth H (2011) Halophytic crops: a resource for the future to reduce the water crisis? Emirates J Food Agric 23:1–16

Kumar V (2017) Chapter: 15: Phytoremediation as a potentially promising technology: prospects and future. In: Gautam A, Pathak C (eds) Metallic contamination and its toxicity, 1st edn. Daya Publishing House Division of Astral International Pvt. Ltd, New Delhi, pp 207–229

Leach RP, Wheeler KP, Flowers TJ, Yeo AR (1990) Molecular markers for ion compartmentation in cells of higher plants. II. Lipid composition of the tonoplast of the halophyte *Suaeda maritima* (L.) Dum. J Exp Bot 41:1089–1094

Leigh RA, Wyn Jones RG (1984) A hypothesis relating critical potassium concentrations for growth to the distribution and functions of this ion in the plant cell. New Phytol 97:1–1

Li K, Pang CH, Ding F, Sui N, Feng ZT, Wang BS (2012) Overexpression of *Suaeda salsa* stroma ascorbate peroxidase in Arabidopsis. S Afr J Bot 78:235–245

López-Portillo J, Ewers FW, Angeles G (2005) Sap salinity effects on xylem conductivity in two mangrove species. Plant Cell Environ 28:1285–1292

López-Portillo J, Ewers FW, Méndez-Alonzo R, Paredes López CL, Angeles G, Alarcón Jiménez AL, Lara-Domìnguez AL, Torres Barrera MC (2014) Dynamic control of osmolality and ionic composition of the xylem sap in two mangrove species. Am J Bot 101:1013–1022

Ma SC, Li FM, Xu BC, Huang ZB (2010) Effect of lowering the root/shoot ratio by pruning roots on water use efficiency and grain yield of winter wheat. Field Crops Res 115:158–164

Manousaki E, Kalogerakis N (2011) Halophytes—an emerging trend in phytoremediation. Int J Phytoremediation 13:959–969

Mansour MMF (1995) NaCl alteration of plasma membrane of *Allium cepa* epidermal cells. Alleviation by calcium. J Plant Physiol 145:726–730

Mansour MMF (2013) Plasma membrane permeability as an indicator of salt tolerance in plants. Biol Plant 57:1–10

Mansour MMF (2014) The plasma membrane transport systems and adaptation to salinity. J Plant Physiol 171:1787–1800

Mansour MMF, Ali EF (2017) Evaluation of proline functions in saline conditions. Phytochemistry 140:52–68

Mansour MMF, Salama KHA (2019) Cellular mechanisms of plant salt tolerance. In: Giri B, Varma A (eds) Microorganisms in saline environment: strategies and functions. Springer International Publishing AG, Cham

Mansour MMF, Salama KHA, Allam HYH (2015) Role of the plasma membrane in saline conditions: lipids and proteins. Bot Rev 81:416–451

Maricle BR, Koteyeva NK, Voznesenskaya EV, Thomasson JR, Edwards GE (2009) Diversity in leaf anatomy, and stomatal distribution and conductance, between salt marsh and freshwater species in the C_4genus *Spartina* (Poaceae). New Phytol 184:216–233

Mediavilla S, Escudero A (2003) Mature trees versus seedlings: differences in leaf traits and gas exchange patterns in three co-occurring Mediterranean oaks. Ann For Sci 60:455–460

Medina E, Lugo AE, Novelo A (1995) Contenido Mineral del Tejido Foliar de especiesde manglar de la Laguna de Sontecomapan (Veracruz, Mexico)ysurelacion con la salinidad. Biotropica 27:317–323

Meinzer FC, Moore PH (1988) Effect of apoplastic solutes on water potential in elongating sugarcane leaves. Plant Physiol 86:873–879

Mendez-Alonzo R, Moctezuma C (2015) Root biomechanics in *Rhizophora mangle*: anatomy, morphology and ecology of mangrove's flying buttresses. Ann Bot 115:833–840

Meng X, Zhou J, Sui N (2018) Mechanisms of salt tolerance in halophytes: current understanding and recent advances. Open Life Sci 13:149–154

Mickovski SB, Ennos AR (2003) Anchorage and asymmetry in the root system of *Pinus peuce*. Silva Fennica 37:161–173

Mitchell RJ, Zutter BR, Green TH, Perry MA, Gjerstad DH, Glover GR (1993) Spatial and temporal variation in competitive effects on soil moisture and pine response. Ecol Appl 3:167–174

Morsy AA, Salama KHA, Kamel A (2010) Changes in plasma membrane lipid and antioxidant enzyme activities of *Zygophyllum album* L. F. and *Zygophyllum coccineum* L. as affected by heavy metal pollution. Egypt J Exp Biol (Bot) 6:99–105

Munns R (1985) Na^+, K^+ and Cl^- in xylem sap flowing to shoots of NaCl-treated barley. J Exp Bot 36:1032–1042

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25:239–250

Munns R, Tester M (2008) Mechanism of salinity tolerance. Annu Rev Plant Biol 59:651–681

Nardini A, Salleo S, Jansen S (2011) More than just a vulnerable pipeline: xylem physiology in the light of ion-mediated regulation of plant water transport. J Exp Bot 62:4701–4718

Nawaz T, Hameed M, Ashraf M, Batool S, Naz N (2016) Modifications in root and stem anatomy for water conservation in some diverse blue panic (*Panicum antidotale* Retz.) ecotypes under drought stress. Arid Land Res Manag 27:286–297

Nicoll BC, Ray D (1996) Adaptive growth of tree root systems in response to wind action and site conditions. Tree Physiol 16:891–898

Ohira W, Honda K, Nagai M, Ratanasuwan A (2013) Mangrove stilt root morphology modeling for estimating hydraulic drag in tsunami inundation simulation. Trees 27:141–148

Ong JE, Gong WK, Wong CH (2004) Allometry and partitioning of the mangrove—Rhizophora apiculata. For Ecol Manag 188:395–408

Ortega L, Fry SC, Taleisnik E (2006) Why are *Chloris gayana* leaves shorter in salt-affected plants? Analyses in the elongation zone. J Exp Bot 57:3945–3952

Ourcival JM, Berger A (1995) Equilibrium between soil-water potential and predawn water potential of 2 pre-Saharan shrub species of Tunisia. J Arid Environ 30:175–183

Pajević S, Borišev M, Nikolić N, Krstić B, Pilipović A, Orlović S (2009) Phytoremediation capacity of poplar (*Populus* spp.) and willow (*Salix* spp.) clones in relation to photosynthesis. Arch Biol Sci 61:239–247

Parida AK, Das AB, Mohanty P (2004) Defense potentials to NaCl in a mangrove, *Bruguiera parviflora:* differential changes of isoforms of some antioxidative enzymes. J Plant Physiol 161:531–542

Parida AK, Veerabathini SK, Kumari A, Agarwal PK (2016) Physiological, anatomical and metabolic implications of salt tolerance in the halophyte *Salvadora persica* under hydroponic culture condition. Front Plant Sci 7:351. https://doi.org/10.3389/fpls.2016.00351

Park J, Okita W, Edwards GE (2009) Salt tolerant mechanisms in single-cell C4 species *Bienertia sinuspersici* and *Suaeda aralocaspica* (Chenopodiaceae). Plant Sci 176:616–626

Passioura JB (1991) An impasse in plant water relations. Bot Acta 104:405–441

Pedersen TJ, Palmgren MG (2017) Why do plants lack sodium pumps and would they benefit from having one? Funct Plant Biol 44:473–479

Peuke AD, Schraml C, Hartung W, Rennenberg H (2002) Identification of drought-sensitive beech ecotypes by physiological parameters. New Phytol 154:373–387

Pimentel D, Pimentel M (2008) Food, energy and society. CRC Press, Taylor and Francis, Boca Raton

Pla-Sentis (2005) Soil degradation and desertification in Mediterranean environments. In: Rubio JL & Calvo A (eds) 1996, Geoforiiia Edicioncs Logroiio

Popp M, Polania J (1989) Compatible solutes in different organs of mangrove trees. Ann Sci For 46:842–844

Prajapati K, Modi HA (2012) The importance of potassium in plant growth—a review. Indian J Plant Sci 1:177–186

Purakayastha TJ, Mandal A, Kumari S (2017) Phytoremediation of metal- and salt-affected soils. In: Arora S et al (eds) Bioremediation of salt affected soils: an Indian perspective. Springer International Publishing, Cham

Qadir M, Qureshi RH, Ahmad N (1996) Reclamation of a saline-sodic soil by gypsum and *Leptochloa fusca*. Geoderma 74:207–217

Qadir M, Oster JD, Schubert S, Noble AD, Sahrawat KL (2007) Phytoremediation of sodic and saline-sodic soils. Adv Agron 96:197–247

Rabhi M, Ferchichi S, Jouini J (2010) Phytodesalination of a salt-affected soil with the halophyte *Sesuvium portulacastrum* L. to arrange in advance the requirements for the successful growth of a glycophytic crop. Bioresour Technol 101:6822–6828

Ravindran KC, Venkatesa K, Balakrishnan V, Chellappan KP, Balasubramanian T (2007) Restoration of saline land by halophytes for Indian soils. Soil Biol Biochem 39:2661–2664

Reich PB, Hinckley TM (1989) Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily leaf diffusive conductance in two oak species. Funct Ecol 3:719–742

Repp GI, McAllister DR, Wiebe HH (1959) Salt resistance of protoplasm as a test for the salt tolerance of agricultural plants. Agron J 51:311–314

Rewald B, Raveh E, Gendler T, Ephrath JE, Rachmilevitch S (2012) Phenotypic plasticity and water flux rates of citrus root orders under salinity. J Environ Bot 1:1–11

Richards JH, Caldwell MM (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73:486–489

Richards CL, Pennings SC, Donovan LA (2005) Habitat range and phenotypic plasticity in salt marsh plants. Plant Ecol 176:263–273

Ritchie GA, Hinckley TM (1975) The pressure chamber as an instrument for ecological research. Adv Ecol Res 9:165–254

Rozema J (1991) Growth, water and ion relationships of halophytic monocotyledonae and dicotyledonae; a unified concept. Aquatic Botany 39:7–33

Rozentsvet OA, Nesterov VN, Bogdanova ES (2014) Membrane-forming lipids of wild halophytes growing under the conditions of Prieltonie of South Russia. Phytochemistry 105:37–42

Ruelland E, Kravets V, Derevyanchuk M (2015) Role of phospholipid signaling in plant environmental responses. Environ Exp Bot 114:129–143

Ruppel S, Franken P, Witzel K (2013) Properties of the halophyte microbiome and their implications for plant salt tolerance. Funct Plant Biol 40:940–951

Salt DE, Smith RD, Raskin L (1998) Phytoremediation. Ann Rev Plant Phys Plant Mol Biol 49:643–668

Sandalio LM, Dalurzo HC, Gómes M, Romero-Puertas MC, Del Rio LA (2001) Cadmium induced changes in the growth and oxidative metabolism of pea plants. J Exp Bot 52:2115–2126

Santiago M, Pagay V, Stroock AD (2013) Impact of electro viscosity on the hydraulic conductance of the bordered pit membrane: a theoretical investigation. Plant Physiol 163:999–1011

Santos J, Al-Azzawi M, Aronson J, Flowers TJ (2016) Database of salt-tolerant plants: helping put halophytes to work. Plant Cell Physiol 57:e10

Sellin A (1999) Does pre-dawn water potential reflect conditions of equilibrium in plant and soil water status? Acta Oecol 20:51–69

Serrato-Vlenti G, Ferro M, Ferraro D, Riveros F (1991) Anatomical changes in *Prosopis tamarugo* Phil. seedlings growing at different levels of NaCI salinity. Ann Bot 68:47–53

Shabala S (2011) Ecophysiology of halophytes: questions and challenges. Ecol Quest 14:101–102

Shabala L, Mackey A, Tian Y, Jacobsen SE, Zou D, Shabala S (2012) Oxidative stress protection and stomatal patterning as components of salinity tolerance mechanism in quinoa (*Chenopodium quinoa*). Physiol Plant 146:26–38

Shabala S, Hariadi Y, Jacobsen SE (2013) Genotypic difference in salinity tolerance in quinoa is determined by differential control of xylem Na^+ loading and stomata density. J Plant Physiol 170:906–914

Shindle LS, Bhosale LJ (1985) Studies on salt tolerance in *Aegiceras corniculatum* (L.) Blanco and *Sesuvium portulacastrum* (L). In: The mangroves: Proc. Nat. Symp. Biol, Util. Cons. Mangroves, Shivaji University, Kolhapur, pp 300–304

Silva P, Gerós H (2009) Regulation by salt of vacuolar H^+-ATPase and H^+-pyrophosphatase activities and Na^+/H^+ exchange. Plant Signal Behav 4:718–726

Slatyer RO (1967) Plant–water relationships. Academic, New York

Smith GR, Tanji KK, Jurinak JJ, Burau RG (1995) Chapter 7: Applications of a Pitzer equations-based model to hypersaline solutions. In: Loeppert RH, Schwab AP, Goldberg S (eds) Chemical equilibrium and reaction models. SSSA Spec. Pub. No. 42, Soil Sci. Soc. Am.

Srikanth S, Lum SKY, Chen Z (2015) Mangrove root: adaptations and ecological importance. Trees 30:451–465

Stark JR, Hanson PE, Goldstein RM, Fallon JD, Fong AL, Lee KE, Kroening SE, Andrews WJ (2000) Water quality in the upper Mississippi River Basin, Minnesota, Wisconsin, South Dakota, Iowa, and North Dakota, 1995–1998. United States Geological Survey, Circular 1211

Steiner M (1934) To the ecology of the salt march of the Nordostlichen united countries of Nordamerika. Jahrb Know Offered 81:94

Sui N, Han GL (2014) Salt-induced photoinhibition of PSII is alleviated in halophyte *Thellungiella halophila* by increases of unsaturated fatty acids in membrane lipids. Acta Physiol Plant 36:983–992

Sui N, Li M, Li K, Song J, Wang BS (2010) Increase in unsaturated fatty acids in membrane lipids of *Suaeda salsa* L. enhances protection of photosystem II under high salinity. Photosynthetica 48:623–629

Sui N, Tian SS, Wang WQ, Wang MJ, Fan H (2017) Overexpression of glycerol-3-phosphate acyltransferase from *Suaeda salsa* improves salt tolerance in Arabidopsis. Front Plant Sci 8:1337

Sun YL, Li F, Sui N, Sun XL, Zhao SJ, Meng QW (2010) The increase in unsaturation of fatty acids of phosphatidylglycerol in thylakoid membrane enhanced salt tolerance in tomato. Photosynthetica 48:400–408

Suska-Malawska M, Sulwiński M, Wilk M, Mętrak M (2019) Potential eolian dust contribution to accumulation of selected heavy metals and rare earth elements in the aboveground biomass of Tamarix spp. from saline soils in Kazakhstan. Environ Monit Assess 191:57

Tan WK, Lin Q, Lim TM, Kumar P, Loh CS (2013) Dynamic secretion changes in the salt glands of the mangrove tree species *Avicennia officinalis* in response to a changing saline environment. Plant Cell Environ 36:1410–1422

Tanji KK (2002) Salinity in the soil environment. In: Lauchli A, Luttge U (eds) Salinity environment-plant-molecules. Kluwer Academic, Dordrecht, pp 21–51

Temel S, Surmen M (2018) Mineral content changes of some halophytes species evaluates as alternative forage crops for ruminants' nutrition. Fresenius Environ Bull 27:7340–7347

Thomson WW, Faraday CD, Oross JW (1988) Salt glands. In: Baker DA, Hall JL (eds) Solute transport in plant cells and tissues. Longman Scientific and Technical, Harlow, pp 498–537

Tipirdamaz R, Gagneul D, Duhazé C, Aïnouche A, Monnier C, Özkum D, Larher F (2006) Clustering of halophytes from an inland salt marsh in Turkey according to their ability to accumulate sodium and nitrogenous osmolytes. Environ Exp Bot 57:139–153

Tomlinson PB (1986) The botany of mangroves. Cambridge University Press, Cambridge

Ushakova SA, Kovaleva NP, Gribovskaya IV, Dolgushev VA, Tikhomirova NA (2005) Effect of NaCl concentration on productivity and mineral composition of *Salicornia europaea* as a potential crop for utilization NaCl in LSS. Adv Space Res 36:1349–1353

Ustin SL, Jacquemoud S, Palacios-Orueta A, Whiting ML (2009) Remote sensing based assessment of biophysical indicators for land degradation and desertification. In: Röder A, Hill J (eds) Tecent advances in remote sensing and geoinformation processing for land degradation assessment. CRC Press, London, pp 15–44

Vamerali T, Saccomani M, Bona S, Mosca G, Guarise M, Ganis A (2003) A comparison of root characteristics in relation to nutrient and water stress in two maize hybrids. Plant Soil 255:157–167

Van Doorn WG, Hiemstra T, Fanourakis D (2011) Hydrogel regulation of xylem water flow: an alternative hypothesis. Plant Physiol 157:1642–1649

Vargas R, Pankova EI, Balyuk SA, Krasilnikov PV, Khasankhanova GM (2018) Handbook for saline soil management. Published by the Food and Agriculture Organization of the United Nation and Lomonosov Moscow State University

Vasquez EA, Glenn EP, Guntenspergen GR, Brown JJ, Nelson SG (2006) Salt tolerance and osmotic adjustment of *Spartina alterniflora* (Poaceae) and the invasive M haplotype of *Phragmites australis* (Poaceae) along a salinity gradient. Am J Bot 93:1784–1790

Waisel Y (1972) Biology of halophytes. Academic, New York

Walter H (1961) Salinity problems in the acid zones. The adaptations of plants to saline soils. Arid Zone Res 14:65–68

Wang SM, Zhang JL, Flowers TJ (2007) Low-affinity Na+ uptake in the halophyte *Suaeda maritima*. Plant Physiol 145:559–571

Wang YC, Qu GZ, Li HY, Wu YJ, Wang C, Liu GF et al (2010) Enhanced salt tolerance of transgenic poplar plants expressing a manganese superoxide dismutase from *Tamarix androssowii*. Mol Biol Rep 37:1119–1124

Weber DJ (2009) Adaptive mechanisms of halophytes in desert regions. In: Ashraf M, Öztürk MA, Athar HR (eds) Salinity and water stress: improving crop efficiency. Springer, New York, pp 179–185

Wu H (2018) Plant salt tolerance and Na^+ sensing and transport. Crop J 6:215–225

Wu J, Seliskar DM, Gallagher JL (2005) The response of plasma membrane lipid composition in callus of the halophyte *Spartina patens* (Poaceae) to salinity stress. Am J Bot 92:852–858

Xu HM, Tam NFY, Zan QJ, Bai M, Shin PKS, Vrijmoed LLP (2014) Effects of salinity on anatomical features and physiology of a semi-mangrove plant *Myoporum bontioides*. Mar Pollut Bull 85:738–746

Yancey PH, Clark ME, Hand SC, Bowlus RD, Somero GC (1982) Living with water stress: evolution of osmolyte systems. Science 217:1214

Yang MF, Song J, Wang BS (2010) Organ-specific responses of vacuolar H^+-ATPase in the shoots and roots of C-3 halophyte *Suaeda salsa* to NaCl. J Integr Plant Biol 52:308–314

Yense NP (2000) Salt tolerance plants and their uses. Halophytes DataBase, Arizona

Youssef AM (2009) Salt tolerance mechanisms in some halophytes from Saudi Arabia and Egypt. Res J Agric Biol Sci 5:191–206

Yuan F, Leng B, Wang B (2016) Progress in studying salt secretion from the salt glands in recretohalophytes: how do plants secrete salt? Front Plant Sci 7:977

Zahran MA, Abdel Wahid AA (1982) Halophytes and human welfare. In: Sen DN, Rajpurohit KS (eds) Tasks for vegetation science, vol 2. Contributions to the ecology of halophytes. Junk Publishers, The Hague, pp 235–257

Zhang T, Song J, Fan JL, Feng G (2015) Effects of saline water logging and dryness/moist alternations on seed germination of halophyte and xerophyte. Plant Species Biol 30:231–236

Zwieniecki MA, Melcher PJ, Holbrook NM (2001) Hydrogel control of xylem hydraulic resistance in plants. Science 291:1059–1062

Chapter 8
Ecophysiology and Responses of Plants Under Drought

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Contents

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Abstract Drought stress (DS) is the most prevalent abiotic stresses limiting crop productivity across the world. Plants have evolved various mechanisms to tolerate drought effects. Drought resistance in plants, viz. escape, avoidance, tolerance and recovery, is anchored in genetics and physiology. Some plants have evolved smaller leaves and reduced stomata to reduce transpiration, some develop erect plant leaves for greater interception of solar radiation while others can invest on root elongation to tap water from deeper layers of soil. These responses to drought are expressed through regulations of proteins critical to water transport, assimilate mobilization and gene expression. Accumulation of compatible solutes and phyto-protectants like osmolytes, and antioxidants, also plays a major role in drought tolerance. Various drought-related physiological traits such as osmotic adjustment, root architecture, stomata physiology, plant-water relations and levels of phytohormones like abscisic acid (ABA) have been used as maker to evaluate drought resistance in plants. Plant response to drought is complex and involving several genes, gene regulators, transcription factors and plant hormones. Genetic improvement through QTL and gene discovery in crops like rice and wheat for osmotic adjustment, root architecture, biomass and grain yield have been used to increased resistance of these crops through marker-assisted breeding and genetic engineering. However, the dynamic nature of drought and its interaction of other abiotic stresses particularly heat constantly endanger plant to become more vulnerable. Hence, developing crops with enhanced tolerance to combined drought and associated stresses will ensure broad resistance to DS. Therefore, understanding physiological and molecular basis of drought resistance in crops is critical in breeding for better drought-tolerant crops. Present review will summarize current research on physiological responses of plants under DS.

Keywords Ecophysiology · Drought response · Drought tolerance · Transgenic plant · QTL

Abbreviations

ABA	Abscisic acid
DS	Drought stress
OA	Osmotic adjustment
QTL	Quantitative trait loci
ROS	Reactive oxygen species
RWC	Relative water content

8.1 Introduction

There is a complex interaction between *plants* and their environments including sunlight, air, soil and its water status. Physiological activities of the plant are maintained as long as there is balance between the evapotranspiration demand and ability of plant to trap water from soil. However, when there is a shift in the balance towards evapotranspiration, water supply through the root is no longer sufficient, and plant become water stressed. Therefore, response of plants to its environment is affected by evapotranspiration which depends on available water in plant tissues.

Drought is the most prevalent abiotic stress effecting crop productivity in various ecologies of the world. Water is vital for plant growth, development and productivity. Temporary or permanent water deficit results in DS which limits physiological development of the plant. *Drought causes multifaceted effects in* plants including changes in the morphophysiological, biochemical and genetic changes (Salehi-Lisar and Bakhshayeshan-Agdam 2016). DS results in the decline of CO_2 assimilation rates due to reduced stomatal conductance ultimately in declined overall growth and water-use efficiency (WUE) in plants and crops such as rice (Farooq et al. 2009). Bota et al. (2004), Chaves and Oliveira (2004) and Farooq et al. (2009) reported an impairment of Rubisco activity and RuBP content which limit photosynthesis activities particularly at severe DS in many crop plants.

In addition, reactive oxygen species resulting from drought has fatal consequences in plants. They carry unpaired electron which becomes hyperreactive capable of breaking up macromolecules including lipids, DNA and proteins in the cell. However, after a series of stress, reactive oxygen is removed by a variety of antioxidant enzymes (Farooq et al. 2009) and antioxidants metabolites (Jaleel et al. 2009). Drought-induced changes are mostly to alter metabolic functions in plants such as reduced photosynthesis pigments synthesis which eventually affect plant biomass and grain yield (Jaleel et al. 2009; Farooq et al. 2009; Anjum et al. 2011a, b). Abscisic acid (ABA) regulates many physiological processes including stomatal opening, gene expression and protein storage leading to enhanced tolerance to abiotic stress. *ABA*-signalling modulates these physiological changes by preventing water loss for adaptation to DS.

Responses of plants to water stress differ significantly depending on intensity and duration of stress and growth stage of the plant (Chaves et al. 2003; Jaleel et al. 2008). Drought resistance is improved through various mechanisms in plants depending on the species. For instance, rice and maize developed extensive deep root growth, upregulation of photosynthetic and antioxidant enzymes (Ji et al. 2012; Khanna-chopra and Selote 2007). Many drought-tolerant plants have higher water uptake, increased rate of xylem sap flow and low shoot water potential through enhanced root, shoot and leaf architecture. The response of plants to dehydration stress is classified in two major mechanisms: dehydration avoidance and dehydration tolerance. Dehydration tolerance is further divided into acclimatisation of plants (ability to adjust to changes in its environment through which plants survive, grow and reproduce under DS) and tolerance. Survival as a result of dehydration is the capacity of plants to maintain higher plant water content under soil water deficit condition. Most plant survive drought by high cellular hydration; high RWC; stable water potential; higher accumulation of osmolytes, like proline and saccharides; and regulation of turgor pressure. In contrast, dehydration tolerance leads to survival under DS at low plant water content through resilience in plant metabolism (Blum and Tuberosa 2018). Survival dormancy which includes balanced cellular homeostasis, formation of intracellular prism, accumulation of compatible solutes, late embryogenesis abundant (LEA) proteins and antioxidants in drought-tolerant plants (Farrant et al. 2012; Giarola et al. 2017). Early report from Blum et al. (1999) gave significant proof that osmoregulation in wheat accounts for differential growth and yield under severe DS. Similarly, Xu et al. (2014) reported a significant reduction in the ratio of green leaf length to total leaf length of the top three leaves in selected rice genotypes under severe DS as a measure of degree of drought tolerance.

In recent studies, transcriptome analysis has revealed that several genes are differentially expressed (down- and upregulations of genes) under DS. Extensive studies by Janiak et al. (2015) and Tardieu (2016) revealed that mechanisms controlling plant under DS are multifaceted due to the complex interaction between response genetic components, viz. genes, microRNAs (miRNAs), transcription factors, proteins, ions, metabolites, cofactors and hormones. Advances in genomics and high-resolution genotyping with precise phenotype information from multi-environment testing have facilitated identification of genetic segment improving yield under DS. Quantitative trait loci (QTLs) and candidate genes have been reported in many crops including rice (Zhou et al. 2010), chickpea (Jaganathan et al. 2015; Kale et al. 2015), wheat (Maccaferri et al. 2016) and maize (Millet et al. 2016) which have enhanced physiological (water-use efficiency (q), osmotic adjustment, harvest index, stomatal conductance, leaf water potential and net leaf CO_2 exchange rate) and molecular responses increase in LEA protein, accumulation of sucrose sugar, ABA content of the leaf, genetic recombination and gene expression of crops plant to DS.

8.2 Drought Responses

Drought stress is a multidimensional discomfort to plant health leading to uttered functions at morphophysiological, biochemical and genetic levels in plants. Biotechnology and genetic engineering strategies have been employed in crops for enhanced tolerance to drought. These strategies work through the expression of genes conferring stress tolerance through enzymes involved in signalling and regulatory pathways (Seki et al. 2003; Shinozaki et al. 2003). Various genes used for the synthesis of structural and functional metabolites (Wang et al. 2003) help plant responses to DS and its resulting environmental effects (Table 8.1).

Table 8.1 Genetic analysis of traits associated with response of plant to drought stress

Gene/QTLs	Crop	Site/traits	Gene effect	Mechanism	Reference
OsPIP2;4	Rice and maize	Root	Promote water transport and root conductivity	Tolerance	Sakurai et al. (2005)
DRO1	Rice	Root	Promote root growth angle for greater water uptake	Avoidance	Uga et al. (2013)
HAV1	Rice	Leaf	Higher RWC and increased biomass production	Tolerance	Fu et al. (2007)
Aquaporins: NtAQP1, NtPIP;1	Tobacco	Root	Increased leaf osmotic pressure through osmolyte transport	Avoidance	Majid et al. (2008)
$qDTY_{1.2}$ and $qDTY_{2.2}$	Rice	Panicle	Enhanced increased grain yield under drought stress	Tolerance	Sandhu et al. (2014)
$qDTY_{12.1}$	Rice	Flower	Increased grain yield under drought stress	Avoidance	Bernier et al. (2009)
Dhn1, Dhn2, Dhn4	Barley	Root	Enhanced drought resistant, stimulates ABA in the root	Avoidance	Close et al. (1989)
OsGLO3, OsOXO3, OsCATC	Rice	Chloroplast	Increase photosynthetic efficiency through GOC bypass for chloroplastic CO_2 concentration	Tolerance	Shen et al. (2019)

8.2.1 Drought Avoidance

Drought avoidance is the ability of plants to maintain relatively higher tissue water during soil water deficit periods. Avoidance mechanism differ among crops, season and/or drought scenario. Plants have developed specialized features that enable them to overcome water loss which include stomata characteristics, cuticular resistance, leaf area and leaf orientation. Stomata are the pores of exchange for water vapour, carbon dioxide and oxygen between plant and its immediate environment during photosynthesis. In rice, drought-resistant genotypes often maintain their leaf stomata open during moderate stress to sustain the photosynthetic rate by maximizing capture solar radiation. However, at severe stress, plant leaves are rolled to reduced stomatal conductance and escape of captured CO_2 through the stomata. Therefore, the adaptation of a plant to drought can be increased by decreased number of stomata and sunken stomata in the epidermal cells which decrease loss due to transpiration and increase cuticular resistance.

Numerous studies on drought avoidance mechanism have been reported in literature that described various adaptations of plants to DS. Holbrook and Putz (1996) and Dichio et al. (2003) reported that lower osmotic pressure in plants would enable plant leaves to withstand greater transpirational stress, thereby enhancing plants' ability to extract water from dry and deeper soils. In addition, the lower aboveground plant growth under drought has been reported as an adaptive mechanism.

The energy balance for restricted above-ground plant growth and shoot elongation and increased root growth to trap water from deeper soil layers is mediated through protective hormones like ABA (Chaves et al. 2003). Xu and Zhou (2008) reported that stomatal density and size in rice were affected differently under mild and severe stress. Stomata density was increased in mild stress but reduced under severe stress. Osakabe et al. (2014) indicated that stomatal behaviour, which often linked with soil moisture content, largely depends on hormonal signals such as ABA that exist in root-shoot network. In addition, Wilkinson and Davies (2010) also reported that ABA is the major hormone manufactured in the roots and mobilized to the shoots particularly the leaves leading to reduced shoot growth and stomata closure. Uga et al. (2013) revealed that DEEPER ROOTING 1 (DRO1) gene coding for QTL that regulates root growth angle was negatively controlled by auxin. In which case, high transcript accumulation of DRO1 in shallow-rooted rice genotypes resulted in drought avoidance ultimately leading to high yield under DS. Therefore, drought avoidance mechanisms through stomata modification and root architecture and elongation are key adapted mechanism by plants to tolerate drought. Even some desert plants exist as seeds (dormancy state) in the soil until a wet year or other favourable weather to stimulate regrowth.

8.2.2 Drought Tolerance

Drought tolerance is the ability of plants to continue normal physiological activities in very dry conditions for prolonged periods of time. DS cause various morphological and functional interruption in sexual organs, leading to sterility or premature abortion of the seed (Saini and Westgate 1999). Drought tolerance mechanisms are mainly controlled by genetic factors. Certain report has stated that majority of crop plants that showed tolerance are able to combine high yield potential under optimum conditions with relatively good yield under DS (Venuprasad et al. 2007; Dixit and Kumar 2014).

Water-soluble proteins in plants, usually induced during stress, enhance drought tolerance through hydration of various cellular components (Osakabe et al. 2014). DS responsive genes/proteins have been identified by several groups. These include membrane-stabilizing proteins and LEA proteins which improve water holding capacity of the plant and increase drought tolerance. Membrane-stabilizing proteins and LEA proteins act as molecular chaperones under DS in ATP-dependent manner to stabilize cellular proteins and prevent them from denaturation under DS. Usually, plant cells maintain a high K^+/Na^+ ratio in the cytosol with relatively high K^+ levels (100–200 mM) and low Na^+ levels (1–10 mM) (Higinbotham 1973). An imbalance in Na^+ concentration in the cells will result in toxic effects on enzyme activities leading to disruption in metabolism, and consequently plant becomes more vulnerable to DS (Hasegawa et al. 2000). Drought tolerance is achieved by alteration in the metabolic pathways of the plant or enhanced osmotic adjustment to maintain cellular turgor. Recently, much progress in drought tolerance has been reported through analysis of QTL associated with root and yield under DS. Initiation of lateral root and root hair growth under drought was reported in drought-tolerant rice lines possessing drought-tolerant QTL (Dixit et al. 2015). These traits are expressed only under DS and have great potential to increase drought tolerance and grain yield under DS. Identification of QTL associated with carbon isotope discrimination as an indicator of water-use efficiency enhanced drought tolerance in rice (Dingkuhn et al. 1991; Govindaraj et al. 2009). Ye et al. (2018) reported genetic and genomics analysing for QTLs associated with root system in improving drought tolerance in rice. In addition, QTL associated with the accumulation of stem photosynthetic reserve prior to grain filling leading to grain filling and increase in yield under DS, was mapped in wheat (Salem et al. 2007). Moreover, QTLs associated with water-soluble carbohydrate (Bennett et al. 2012) and chlorophyll content (Kumar et al. 2012) have shown to provide over 30% of genetic variation in wheat under drought. Stay-green associated QTLs ensure delay in leaf senescence with high grain yield under reproductive stage DS by reducing the size of canopies at anthesis and enhanced water uptake during the post-anthesis DS (George-Jaeggli et al. 2017).

In summary, many factors contribute to tolerance adaptation of crop under drought. Stem reserve accumulation which ensures a continuous grain filling during drought, enhanced water-use efficiency, stay-green trait which delays senescence and lateral root growth and root hair formation for greater access to soil moisture are important traits for drought tolerance.

8.2.3 Drought Acclimation

Acclimation to DS is a major protective mechanism in plants. The basis for plant acclimation was first reported by Sakai and Larcher (1987) when they defined stress as a build-up of environmental demand on plant causing an initial disturbance in its functions followed by a normalized activity and a resulting resistant if the stress is survived. Probably, the most effective acclimation mechanisms of plant to DS are those developed as a result of combined environmental factors that affect the plant's physiological process. For instance, treatment of vesicular-arbuscular mycorrhiza (VAM) in combination with repeated drought cycles (acclimation) on pepper (*Capsicum annuum* L.) enhanced drought resistance, as indicated by the high leaf water potential, high turgor pressure, high relative water content and non-wilted plants (Davies et al. 1992).

Beneficial bacterial interactions with plants have also shown enhanced drought resistance when drought sets in. Inoculation of wheat with bacteria *A. brasilense* Sp245 under DS resulted in high grain yield and better grain quality through improved water relations and improved cell wall elasticity indicating that there is combined higher water status plus increased elastic adjustment for enhanced drought tolerance in wheat (Creus et al. 2004). The effects of *A. brasilense* help in producing phytohormones such as auxins (Dimkpa et al. 2009). Phytohormones (indoleacetic acid: IAA, ethylene, gibberellins, cytokinins and ABA) produced by plants are not only essential for their growth and physiological functions (Barea and Brown 1974; Teale et al. 2006; Egamberdieva 2013) but also critical in helping plants survive abiotic stresses particularly drought (Skirycz and Inzé 2010; Fahad et al. 2015).

Salicylic acid pretreatment significantly alleviates drought-induced stress effects through protecting D1 protein and PSII of wheat leaves to restore photosynthetic function (Janda et al. 2014). Exposure to short period of moderate DS resulted in enhanced drought tolerance in wheat through improving antioxidant potential (Selote and Khanna-Chopra 2004). Drought-tolerant wheat genotypes have light antioxidant enzyme activities compared to the susceptible ones (Khanna-Chopra and Selote 2007). It has also been reported that high antioxidant enzyme activities and antioxidant content lead to delayed leaf senescence in wheat (Semwal and Khanna-Chopra 2018; Semwal et al. 2014). Acclimation is therefore important in stabilizing plant physiological functions under DS.

8.3 Plant-Water Relations in Response to Drought Stress

Plant-water relations are the life wire traits of plants under drought and can be used in estimating the severity of DS based on differential response of genotypes to the stress. Several water relations factors have been reported, and there is a wide genetic variability for water status and photosynthetic parameters under DS compared to optimum condition (Kiani et al. 2007). A temperature-based crop water stress index (CWSI) was developed by Idso et al. (1981). The CWSI is defined as (Idso et al. 1981; Jackson et al. 1981):

$$\text{CWSI} = \frac{T_{\text{l}} - T_{\text{wet}}}{T_{\text{dry}} - T_{\text{wet}}}$$

where T_{l} is the leaf temperature; T_{wet} = lower canopy temperature in well-watered condition; and T_{dry} = upper canopy temperature in DS condition. This was mainly given to estimate when hydration or irrigation will be provided to the plant and in most cases the practical application is difficult. A more precise estimation of the water status in plant has been given. Audebert et al. (2013) used that method, coupled to infrared camera measurement of canopy temperature to successfully identify rice lines with good maintenance of transpiration capacity.

8.3.1 Water Potential

Water potential is the relative tendency of water to move from one part of the plant to another based on the osmotic difference of the two regions. Leaf water potential (Ψ_{w}) associated with drought resistance can be used to predict drought tolerance in segregating genetic populations (Jongdee et al. 2002). Leaf Ψ_{w} at wilting or turgor loss point is a determinant of the tolerance of leaves to DS and contributes to drought tolerance in plants. Leaf Ψ_w is considered as an indicator of the whole-plant water status especially under drought condition. Kiani (2015) reported that rice cultivars maintaining critical Ψw under high transpiration and soil water deficits in afternoons give high yields in drought-prone environments. Jongdee et al. (2002) reported consistent genotypic variation in rice for the maintenance of high Ψw across water deficit experiments. Drought-tolerant wheat genotypes maintain high Ψ_w under DS compared to the susceptible genotypes (Khanna-Chopra and Selote 2007; Semwal and Khanna-Chopra 2018). The genetic effect for water potential is additive and closely associated with gene controlling yield (Liu et al. 2005). However, Ψw usually gives low broad-sense heritability especially in upland which makes its inheritance poor. Genetic improvement for high water potential in simple biparental crop improvement for drought tolerance is not likely to give a faster progress in enhancing heritability for water potential. Lande and Thompson (1990) and Mackill et al. (1999) suggested marker-assisted selection (MAS) as a favourable technique for improving Ψw traits as it is being controlled by few QTLs. Recent findings however have shown that Ψw is a polygenic trait controlled by several QTLs and difficult for direct selection due to the measurement problems in large genetic populations and its low heritability (Teulat et al. 2001; Kiani et al. 2008; Bernier et al. 2009). A combination of MAS with successive pyramiding through repeated backcrossing of candidates with favourable allele will give a faster progress in improving Ψw in field crop. Such progresses have been reported for rice (Price et al. 2002), maize (Mir et al. 2012) and other cereal and legumes (Witcombe et al. 2007). Several loci and genes have been characterized to develop the concept and models of complex water relation traits associated with drought tolerance traits (Uga et al. 2013; Tricker et al. 2018). Through transgenic approach, rice plants delayed wilting more than 15 days by maintaining high plant water status through *HVA1 LEA* transgene isolated from barley (Babu et al. 2004). These approaches pave the way to the mapping and cloning of genetic segment and genes that control drought tolerance through turgor management and hormonal regulation of plant water potential with precision.

8.3.2 Relative Water Content

Relative water content (RWC) indicates the proportion of water in the shoot as per the total biomass. Generally, RWC decreased with increasing water stress in all crop genotypes and shows high correlation with yield and related traits under drought. Therefore, genotypes which maintained high RWC ($\geq$0.65) under stress conditions are believed to be tolerant and produce higher yield. Bennet et al. (1987) and Schonfeld et al. (1988) revealed that improved behaviour of drought-tolerant soybean, maize and wheat in water-limited environments is attributed to osmoregulation at the onsets of drought. Lawlor and Cornic (2002) showed that the rate of foliar photosynthesis decreases as the RWC and leaf water potential decrease. Kiani et al. (2007) revealed high significant positive correlations between RWC, turgor potential (Ψ_t) and photosynthesis (P_n). Significant positive correlation between RWC, Ψ_w and stomatal conductance (g_s) indicates stomata response to water status in the shoots and in turn higher photosynthetic rate under DS. Genetic gain was reported for RWC in relation to grain yield under DS. During conditions of continued DS, leaf rolling gives an indication of leaf water status in plants which is a desirable trait. Genotypes and breeding lines with higher leaf rolling are known as drought susceptible as leaf rolling reduction in the extraction of soil water. Biochemical and physiological analysis of wheat genotypes showed higher RWC and larger accumulation of free proline which enhanced antioxidant defence and lower drought susceptibility index in tolerant genotypes under drought (Bayoumi et al. 2008; Semwal and Khanna-Chopra 2018). Bayoumi et al. (2008) further revealed that RWC and proline content are constitutive traits. Constitutive characters are expected to show low GxE interaction and hence favourable characters for selection under drought as its capable of given precise genotypic difference under drought in different environments. The *HVA1* gene, identified in barley, was tested in transgenic rice under prolonged DS cycles to understand the mechanism of dehydration tolerance (Table 8.1). The transgenic rice plants overexpressing *HVA1* gene maintained higher leaf RWC and exhibited less reduction in biomass under DS compared to non-transgenic plants (Blum 2005; Fu et al. 2007).

8.3.3 Osmotic Adjustment

The accumulation of compatible solutes and ions in the cell sap under DS helps to maintain turgor potential (Morgan and Tan 1996) and osmotic potential (Kerepesi and Galiba 2000) to sustain plant growth. This cellular mechanism is known as osmotic adjustment (OA), which helps plants in overcoming negative effects of DS. Plants with active OA are less affected in situation of poor water extraction ability or low shoot water status because OA maintains turgor and delays leaf rolling (Turner 1986). Although variation in inorganic ions, especially K^+, Na^+ and Cl^- and NO_3^- ions, creates the osmotic potential for crop, K^+ and Na^+ are the main inorganic ions that create the most fluctuations in osmotic balance in leaves and roots followed by Na^+ and Cl^-, while the NO_3^- ion usually showed less contribution. Bajji et al. (2001) studied the regulation and involvement of OA in the maintenance of turgor in growing and expanded leaves of two cultivars of durum wheat adapted to aridity. Sugars played a major role in OA in wheat leaves followed by proline. Compatible organic solutes including amino acids, sugars, glycerol etc. serve to balance the osmotic potential of intracellular and extracellular ions in resistance to DS caused by soil water deficit (Chen and Jiang 2010). Silva et al. (2010) reported that among the ions, soluble sugars play a major role in OA and soluble sugar concentration increased with the severity of DS. OA has been shown to contribute to grain yield under DS (Blum 1989; Chen and Jiang 2010; Silva et al. 2010). OA has been reported to positively correlate with yield in many crops, legumes etc. (Blum 2017; Khanna-Chopra et al. 2019).

Above reports suggest that there is an overlap in the genetic segments controlling OA and grain yield (Tuberosa et al. 2002; Yin et al. 2004). Co-located QTLs have been reported for yield, root traits, biomass and osmotic potential on chromosome 1 in rice (Liu et al. 2005). QTLs for grain yield under DS in rice co-located with QTLs for osmotic potential on chromosomes 1,3,5 and 9 explained 75% phenotypic variation for yield and 50% phenotypic variation for osmotic potential (Liu et al. 2005). The overlapping of QTLs for different traits indicates substantial linkage or pleiotropism a useful tool for selection for crop improvement. Two chromosomal regions 7H and 6H on chromosomes 1 and 3, respectively, were involved in several OA-related trait variations in barley, and region 7H is conserved for cereals and could be considered as region controlling OA (Teulat et al. 1998).

8.3.4 Water-Use Efficiency (WUE)

Water-use efficiency (WUE) is the ratio of crop productivity in terms of biomass and grain yield to water used or transpired (Evans and Sadler 2008). It is a genetic character that depends on the rate of photosynthesis and transpiration and is often considered as an essential determinant of crop yield under DS (Passioura 2006). WUE is an important component of adaptation to DS in crop plants including wheat (Fotovat et al. 2007), rice (Belder et al. 2004) and maize (Paredes et al. 2014). Breeding crop cultivars with high WUE have been highlighted as an important and economic approach to raise crop yield and improve food production in drought-prone environments (Lal et al. 2012; Haefele et al. 2016). Carbon isotope discrimination (CID) measurement in grain or leaf has been developed for estimating WUE at the leaf level (Hall et al. 1994). Studies have showed that the extent of carbon discrimination is a good indicator of WUE in crop plants (Hall et al. 1994; Condon et al. 2002). CID has shown a negative correlation with WUE in crop plants (Abdelbagi and Hall 1993; Hall et al. 1994) including wheat (Condon et al. 2002) and rice (Dingkuhn et al. 1991). Hence, low CID has been successfully used as a selection tool for high WUE and grain yield improvement in crop plant under DS (Condon et al. 2002).

Several studies related to WUE including crop physiological and morphological traits under DS have been reported (Borrell and Hammer 2000; Richards et al. 2002). Many of these studies reported a substantial benefit of high WUE in reducing water use for growth maintenance and optimum crop yields under DS (Zhang et al. 2012; Richards et al. 2002). Crops with high WUE tend to conserve water, thus avoiding drought and improving crop resistance to DS (Rivero et al. 2007). Crop cultivars with good WUE had better tolerance and recorded increased productivity under DS (Bacelar et al. 2009). Under water deficit condition plants control water relations by reducing transpirational water loss leading to maintenance of photosynthesis and increased WUE (Shimazaki et al. 2007). Higher WUE under DS was associated with reduced transpiration and increased yield in rice (Yang et al. 2003). However, selection for improved WUE in breeding for DS conditions does not necessarily translate to improved drought resistance or increased yield in all situations (Masle et al. 2005). Plant traits that reduce crop water use and transpiration, such as reduced leaf area and biomass, and consequently affect crop production are the main driver of higher WUE (Blum 2009). Hence, higher drought tolerance and improved yield have been linked with reduced WUE in some studies (Moutinho-Pereira et al. 2007; Bacelar et al. 2009). A major avenue for improved productivity under DS therefore is to breed for 'effective use of water' such that water use is controlled during the early growth stage in order to avoid lack of water during reproduction stage. This can be achieved through a maximum capture of soil water for transpiration and consequently biomass production, reduced soil evaporation and non-stomatal transpiration (Blum 2009). Effective use of water through the improvement of plant water status enhances the sustainability of assimilate partitioning and grain yield under DS (Kirkegaard et al. 2007).

Several genes including the expression of *Arabidopsis HARDY* (HRD) gene, overexpression of *NAC9* gene in rice (Redillas et al. 2012) and *HVA1* gene in wheat (Bahieldin et al. 2005) have been found to be involved in increased WUE in crop plants. In addition, a few Qtls directly associated with WUE have been identified in crop plants. For example, Xu et al. (2009) identified 7 Qtls for WUE located in five chromosomal regions in rice, while Zhang and Xu (2002) identified 10 Qtls affecting per plant WUE and 6 Qtls controlling leaves and stem WUE in wheat. Furthermore, a number of crops with improved WUE and drought tolerance have been developed (Bahieldin et al. 2005; Oh et al. 2005) through conventional breeding and maker-assisted selection. However, the introduction of a single QTL or gene related to a higher WUE in crops has resulted in shortfalls in some other agronomic performance (Wang et al. 2003). Hence, an in-depth understanding of gene regulation of WUE and crop physiology is needed to develop crop cultivars with high WUE and drought tolerance without a detrimental effect on other agronomic performance. There is a need to identify and integrate traits related to improved tolerance and high WUE in a manner that will not involve yield penalties.

8.4 Response of Root Traits Under Drought Stress

Root response is of prime importance to crop productivity under DS. This is because the root size, architecture and distribution determine the ability of plants to access and take up the water for proper physiological functioning of shoots (Henry 2012; Sperry et al. 2002). Plant root systems are important for adaptation and maintenance of crop growth and yield under DS. Maintenance of root growth under DS helps plants to keep up enough water supply for shoot growth and increased productivity. Several plant root traits are known to be associated with drought tolerance at the organism, organ and tissue level (Fig. 8.1; Maseda and Fernandez 2006; Wasson et al. 2012). Among root traits, root system size in relation to the shoot size (allometry) is of fundamental importance for the acquisition of water under DS (Addington et al. 2006; Maseda and Fernandez 2006). Plants can respond to DS by diverting a

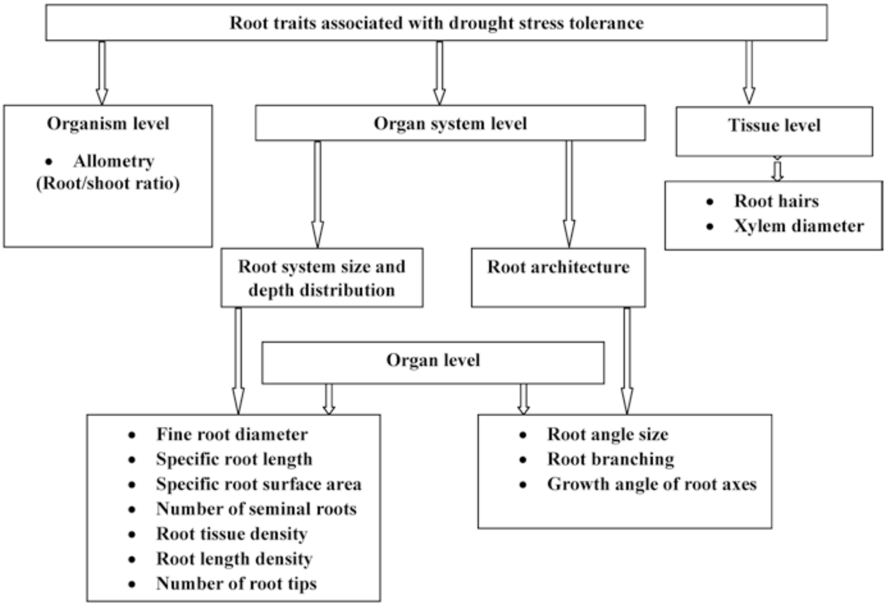

Fig. 8.1 Summary of plant root traits associated with drought stress tolerance. Higher root-to-shoot ratio under stress results in improved hydraulic status, plant capacity to acquire water from deeper depth to support existing shoot and subsequently crop productivity. Plant root can also alleviate the effect of drought through increased specific root, root hair density and distribution at deeper depth. Architectural root properties such as narrow root angle and more intensive root branching are root traits adapted by plants to improve hydraulic lift and enhance greater utilization of water in deeper depth in the soil profile under drought stress condition

lot of assimilate to root growth, thus stimulating root growth while lessening shoot growth with subsequent extraction of more water from deeper soil layers (Diaz-Espejo et al. 2012; Rich and Watt 2013). Increased root versus shoot growth can compensate for water shortage and results in the maintenance of stomatal conductance under DS like the levels under adequate water supply, thereby maintaining crop productivity close to irrigated levels under DS (Addington et al. 2006; Maseda and Fernandez 2006). Studies have indicated that higher root to shoot ratio is one of the major reasons for better adaptation to DS in drought-tolerant maize (Zhao et al. 2018; Grzesiak et al. 1999), wheat (Dhanda et al. 2004) and rice (Azhiri-Sigari et al. 2000; Asch et al. 2005). For example, Ji et al. (2012) and Lemoine et al. (2013) observed that roots of drought-tolerant rice genotypes grew thicker, larger and deeper under DS. Diaz-Espejo et al. (2012) and Sperry et al. (2002) also reported that enhanced root-to-leaf area ratio and initiation of growth of new root tips under DS improved hydraulic status, plant capacity to acquire water to support existing shoot and subsequently crop productivity.

Root growth according to soil water distribution is another vital feature of root response to DS (Wasson et al. 2012). Plant root can moderate the effect of DS by increasing extraction and uptake of water and reducing carbon investment required for water acquisition through increased specific root and root length, small fine root diameters, increased root hair density and distribution at deeper depth (Maseda and Fernandez 2006; Rewald et al. 2011). The ability of plant root to continue elongation in order to absorb water from deeper layers of soil helps plants to avoid water deficit near the soil surface and significantly increases plant efficiency under DS (Ho et al. 2005; Schenk and Jackson 2005; Hund et al. 2009). Deep rooting traits have been associated with improved water uptake and DS adaptation in rice (Kato et al. 2006; Gowda et al. 2011), wheat (Lilley and Kirkegaard 2011; Manschadi et al. 2008) and maize (Ribaut et al. 2009; Zhao et al. 2018). Crop varieties with thicker coarse roots, less root near the surface, increased root density in medium and deep layers and greater lateral (fine) root that enhances overall deeper root system have been found with the ability to access more water from the soil to sustain shoot growth and development under DS (Henry 2012; Wasson et al. 2012; Lynch 2013). Few but long lateral roots have been associated with deeper rooting, greater water uptake and higher grain yield under DS in maize (Zhan et al. 2015). Studies have shown that roots can accumulate high levels osmolytes for OA during DS (Ribaut et al. 2009). OA in roots maintains turgidity as water potential decreases in the growing cells and plays a vital role in the maintenance of root elongation under DS (Ribaut et al. 2009; Zhao et al. 2018). Roots, growing in deep depths, also become thinner due to restriction of the lateral expansion rate of the cells (Doussan et al. 2006), thereby enabling the root to further reduce their use of water under DS (Wasson et al. 2012).

In addition to root system size, its distribution, architectural root properties such as narrow root angle, greater hierarchical structure and more intensive root branching are the traits adapted by plants to improve hydraulic lift and enhance greater utilization of water in deeper depth in the soil during DS (Doussan et al. 2006; Wasson et al. 2012). Growth angle of root axes has been strongly associated with temporal and spatial water acquisition efficiency (Poorter and Nagel 2000; Fitter 2002) and is a useful trait for tolerance to DS (Manschadi et al. 2008). In rice, for instance, the growth angle of nodal roots influences the vertical distribution of root and rooting depth, with cultivars exhibiting a narrow basal root angle having a deep root system, which enhances water uptake and improves the productivity of upland rice (Kato et al. 2006). Likewise, Manschadi et al. (2006) demonstrated that the angular spread of seminar roots affects drought adaptation in wheat. It was observed that wheat genotypes with a narrow angle of seminar roots were deeply rooted and had access to soil water from deeper depth compared to genotypes with wide angle of seminar roots.

Seminal roots' number also influences plant adaptation to DS because seminal roots grow in deep soil layers and can increase water uptake from deep layers of soil (Manschadi et al. 2006, 2008). It has been reported that a high number of seminal root axes result in more intensive root branching, which improves the ability of roots to access and take up water (Manschadi et al. 2008). Furthermore, the diameter of xylem in seminal roots also helps in saving deep soil water for use during DS, resulting in improved productivity (Manschadi et al. 2006). Although the genetic control of root traits is still poorly understood due to the effect of environmental factors and complexity of root traits measurement under field condition, the genome location and size of

Table 8.2 Quantitative trait loci (QTL) associated with root traits under drought stress condition in major crop plants

Crop	Gene	Traits	Chromosome information	References
Rice	*Price_2002C_1758s*	Increased root length	Chromosome 1	Price et al. (2002)
	MacMillian_2006_1533w		Chromosome 1	MacMillan et al. (2006)
	Zhang_2000_53c	Increased root number	Chromosome 1	Zheng et al. (2000)
	Zhang_2003_517w		Chromosome 1	Zheng et al. (2003)
	Qtl12.1	Deep root length	Chromosome 1	Bernier et al. (2009)
	Qtl12.1	Greater specific root length	Chromosome 1	
Wheat	*qTaL-2B1-2B*	Maximum root length	Chromosome 2B	
	qPRL-2B1-2B	Primary root length	Chromosome 2B	
	qLRL-1A	Lateral root length	Chromosome 1A	
	qRN-3D	Increased root tip number	Chromosome 3D	
	qTRL-2B	Increased total root length	Chromosome 2B	
	QRN.9gw-3A	Increased seminal root number	Chromosome 4A	Christopher et al. (2013)
	QRA.qgw-2A	Increased seminal root angle	Chromosome 2A	
	QDRR-1, QDRR-1	Deep root growth	Chromosome 1B	Hamada et al. (2012)
	QRN	Increased seminal root number	Chromosome 5A	
Maize	*Root-ABA1qtl*	Increased root number	Chromosome 2	Giuliani et al. (2005)
		Increased root diameter		
		Increased root branching		
		Crown root angle		
		Increase root-shoot dry weight ratio		

qualitative trait loci (QTL) controlling root traits have been successfully estimated with the use of molecular markers. Research has been carried out to map root QTL for many root growth-associated traits under DS in several crops (Table 8.2; Ochoa et al. 2006) including rice (Price et al. 2002), wheat (Ren et al. 2012; Hamada et al. 2012) and maize (Giuliani et al. 2005). In addition, effort has been made on genetic engineering and inclusion of root trait genes in crop plants for DS adaptation (Table 8.3).

Table 8.3 Genetic engineering for root traits in crop plants for improving drought tolerance

Crop	Genes	Effect	References
Wheat	*TAZFP34*	Increased root to shoot ratio by maintaining root elongation and reduced shoot growth compared to non-transgenic plants	Chang et al. (2016)
	TaNAC69	Upregulation of genes responsible for adaptation to DS through increased root length and greater root biomass compared to non-transgenic plants	Xue et al. (2011)
Rice	*DRO1*	Associated with deep rooting, drought tolerance and increased grain yield compared to non-transgenic plants	Uga et al. (2013)
	The *WUSCHEL*-related homeobox gene *WOX11*	Regulates crown root initiation, development and elongation for enhanced drought tolerance compared to non-transgenic plants	Zhao et al. (2015)
	OsAPY	Root hair elongation and development for improved water uptake compared non-transgenic plants	Yuo et al. (2009)
	OSNAC10	Induces thicker root with enlarged stele, cortex and epidermis for improved drought tolerance and increased grain yield compared to non-transgenic plants	Jeong et al. (2010)
Maize	Aquaporin genes *PIPI* and *RWC-3*	Higher water uptake compared with non-transgenic plants	Giuliani et al. (2005)

Root is the major organ through which plants perceive, respond and maintain growth and yield under DS. Adequate root development is vital for plant survival under DS when moisture is only available in deeper soil layer. Different types of roots have essential features which determine plant water absorption ability as an adaptation strategy under DS (Waisel and Eshel 2002). Several studies have demonstrated that traits like root length, number of lateral roots, root density, specific root length, fine root diameter, root angle, specific root surface area, number of seminal roots, crown root number and number of root tips are important for improving plant water acquisition and productivity under DS. It has been demonstrated from previous studies that water uptake and productivity of crops could be enhanced through genetic improvement, with a good number of QTL and genes already identified for root traits involved in adaptation to DS in crops such as rice wheat and maize. Hence, root traits play a vital role in plant survival and productivity under DS.

8.5 Photosynthesis Under Drought Stress

Photosynthesis is one of the most important processes that influences crop productivity and is directly affected by DS (Farooq et al. 2009). Crop yield under DS depends mainly on the effects of water stress on photosynthesis (Bahavar et al. 2009). The effect of DS on photosynthesis has been extensively studied for many

Table 8.4 Effect of drought stress on photosynthesis in crops

Photosynthetic factor	Effect	Crop	References
CO_2 assimilation	Decreased CO_2 assimilation rate and hence photosynthesis	Wheat	Lu and Zhang (1999) Yordanov et al. (2001) Molnár et al. (2002) Azhand et al. (2015) Perdomo et al. (2017)
	Imposed significant limitation on photosynthetic capacity	Rice and maize	Perdomo et al. (2017)
Internal CO_2 concentration	Decreased Decreased	Wheat Rice and maize	Molnár et al. (2002) Perdomo et al. (2017)
Water use efficiency	Decreased	Wheat	Molnár et al. (2002)
Transpiration	Decreased transpiration and photosynthesis	Wheat	Molnár et al. (2002)
	Decreased transpiration and photosynthesis	Rice	Ji et al. (2012) Yang et al. (2014)
Electron transport rate	Decreased	Wheat	Haupt-Herting and Fock (2000)
Rubisco activity	Decreased Decreased	Wheat Rice	Martin and Ruiz-Torres (1992) Zhou et al. (2007)
Photosynthetic apparatus	Photoinhibition	Rice	Zhou et al. (2007)
	Photoinhibition	Maize	Liu et al. (2012)
ATP synthesis	Inhibition of ATP synthesis, decreased chloroplast ATP content and activity	Rice	Farooq et al. (2009)

plant species (Tables 8.4 and 8.5; Yordanov et al. 2001). These studies demonstrated that DS results in a substantial reduction in number of leaves and leaf area development that leads to decreased light interception and consequently photosynthetic efficiency (Anjum et al. 2011a, b). Furthermore, DS causes a significant damage to photosynthetic pigments and apparatus, thereby reducing carbon assimilation and chlorophyll content (Saeidi and Abdoli 2015). Because photosynthesis takes place predominantly in the green leaves and depends on the chlorophyll-bearing leaf area of plants (Athar and Ashraf 2005), drought-induced reduction in chlorophyll-bearing leaf surface and chlorophyll content, therefore, results in reduction in net photosynthesis (Bijanzadeh and Emam 2010; Din et al. 2011). For example, DS significantly decreased chlorophyll a and chlorophyll b contents, chlorophyll a/b ratio and consequently photosynthetic efficiency in wheat (Sharifi and Mohammadkhani 2015).

Table 8.5 Summary of genetically modified crop plants for improved photosynthesis under drought stress

Genes	Crop	Mechanism of action	Effect on net photosynthesis	References
Bifunctional trehalose-6 phosphate as a fusion gene of a fusion gene of *otsA* and *ots*	Rice	Higher amounts of trehalose prevent photo-oxidative damage of PS II Limits reductions in quantum yield of PS II	Increased net photosynthesis compared to non-transformed plants	Garg et al. (2002)
pMnSoD	Rice	Increased expression of superoxide dismutase which results in better reactive oxygen species in plant chloroplast	Increased net photosynthesis Rapid recovery of photosynthesis compared to non-transformed plants	Wang et al. (2005)
Nicotiana protein kinase (*NPK1*)	Maize	Protects dehydration damage of photosynthetic machinery under drought stress	Maintained higher photosynthesis	Shou et al. (2004)
Transgenic rice producing PEP carboxylase	Rice	Alleviates the inhibition of photosynthesis caused by drought stress	Maintained high photosynthesis than non-transformed plants under DS	Ding et al. (2007) Bao-Yuan et al. (2011)

Similarly, DS reduced the photosynthetic rate owing to the decreased photochemical efficiency of chlorophyll fluorescence in rice (Puteh et al. 2013). Reduction in plant water potential and stomatal conductance, impaired activities of photosynthetic enzymes and ATP synthesis are other key factors that limit the rate of photosynthesis under DS (Yamance et al. 2003; Farooq et al. 2009). A number of studies (Table 8.5) have shown that DS substantially decreased net photosynthesis in rice (Farooq et al. 2009), wheat (Sharifi and Mohammadkhani 2015), maize (Anjum et al. 2011a, b; Nielsen et al. 2009) and other plant species (Gomes et al. 2010; Medrano et al. 2002). These studies generally indicated that drought-induced reduction in photosynthesis is associated with stomatal and non-stomatal limitations (Fig. 8.2).

8.5.1 Effect of Drought Stresses on Stomatal Factors Responsible for the Regulation of Photosynthesis

8.5.1.1 Stomatal Closure in Response to Drought Stress

Plants' ability to close stomata in order to minimize transpirational water loss in response to DS is the primary factor responsible for decreased photosynthesis under DS (Ashraf and Harris 2013; Clauw et al. 2015). Drought-induced stomata closure

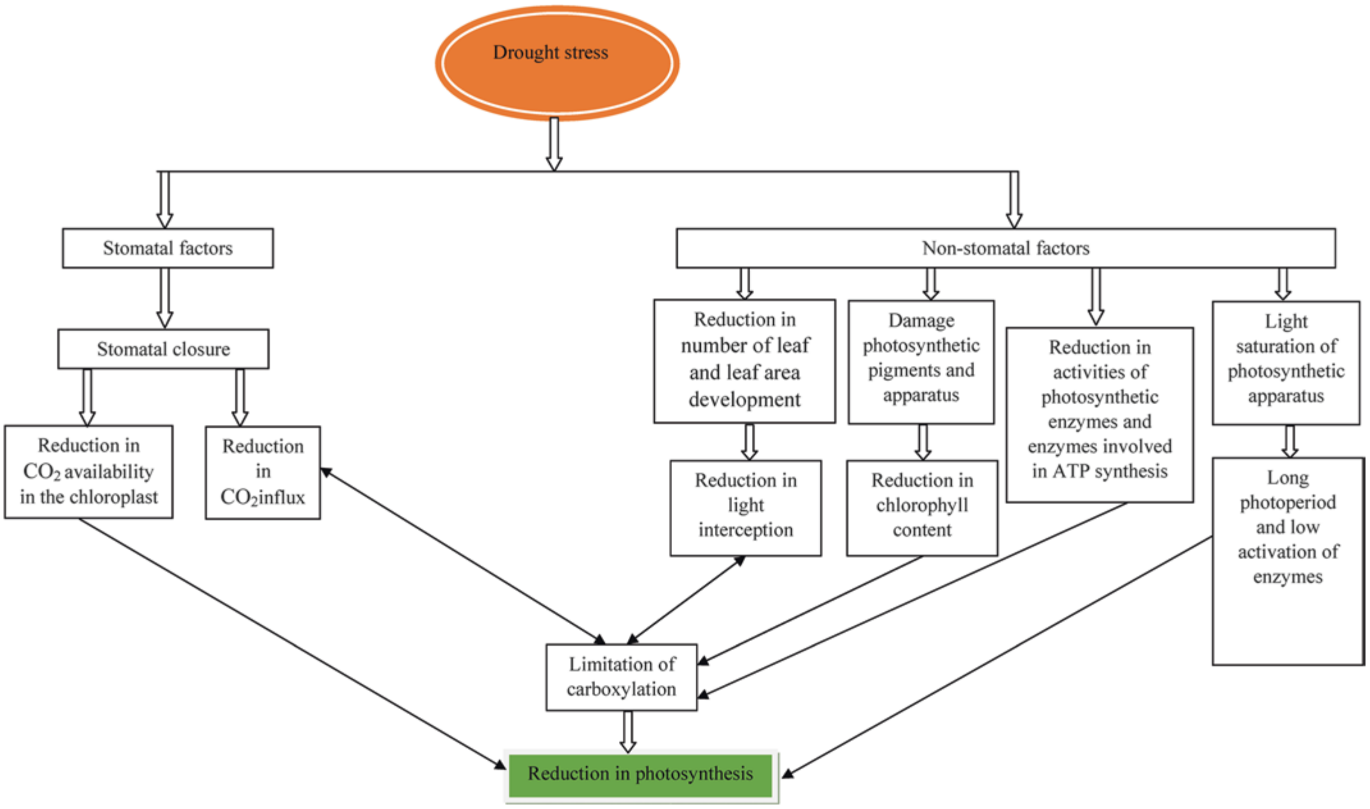

Fig. 8.2 Mechanism of drought-induced reduction in photosynthesis. Stomatal closure under stress results in reduction in CO_2 availability in the chloroplast and CO_2 influx which results in the reduction in carboxylation and hence photosynthesis. Drought also limits photosynthesis due to a decline in the activities of Rubisco, phosphoenolpyruvate carboxylase, NADP-malic enzyme, fructose-1, 6-bisphosphatase and pyruvate orthophosphate dikinase (PPDK). Drought limits photosynthetic surface area due to a reduced number of leaf expansion and leaf number, damage of photosynthetic pigments and apparatus and light saturation of photosynthetic apparatus

reduces CO_2 availability in the mesophyll, CO_2/O_2 ratio and increase photorespiration, thereby reducing photosynthesis and causing photodamage of photosystem II (Medrano et al. 2002; Clauw et al. 2015). Decrease in photosynthesis due to reduced stomatal conductance has been reported in many crops including maize, wheat and rice (Saglam et al. 2014; Ji et al. 2012; Yang et al. 2014; Ashraf and Harris 2013; Azhand et al. 2015). However, there is a good control on stomatal function and greater CO_2 conservation capacity in drought-tolerant crops to allow carbon fixation under DS, therefore improving water-use efficiency, enabling the plant to photosynthesize under stomatal limiting condition and enhancing rapid stomata opening when the stress is relieved (Table 8.3; Sausen and Rosa 2010; Freitas et al. 2011). High photosynthetic capacity under DS conditions has been generally associated with a high stomatal conductance and efficiency of photosynthetic machinery in drought-tolerant plant species (Table 8.4; Gilbert et al. 2011; Dos santos et al. 2017). Bao-Yuan et al. (2011) reported a slow decline in the rate of photosynthesis in transgenic drought-tolerant rice compared to the rapid decline in non-transformed plants under DS, while Shou et al. (2004) observed that drought-tolerant maize maintained efficient photosynthesis due to the protection of the photosynthetic machinery from dehydration under DS. Similarly, drought-tolerant wheat genotypes showed an efficient photosynthetic system due to the maintenance of reasonable level of stomata conductance compared to the susceptible genotypes under DS (Sharifi and Mohammadkhani 2015).

8.5.1.2 Effect of Drought Stress on CO_2 Assimilation, Internal CO_2 Concentration and Photosynthetic Potential

The rate of photosynthesis in plants has been reported to decrease proportional to the decrease in the leaf RWC and Ψ_w under DS (Lawlor 1995). At low RWC, reduction in CO_2 assimilation and internal CO_2 concentration in plants is the primary indication of stomatal limitation in restricting photosynthesis under DS (Flexas and Medrano 2002). A number of studies (Table 8.4; Cornic 2000; Tang et al. 2002) have reported a reduction in CO_2 assimilation, CO_2 concentration in leaf intercellular spaces and plant photosynthetic potential as a result of drought-induced stomatal limitations. These studies suggested that CO_2 availability in the chloroplast is regulated by plant stomatal conductance. Lawlor and Cornic (2002) demonstrated the use of increased ambient CO_2 to overcome stomatal limitation so as to increase CO_2 concentration in the leaf intercellular spaces and chloroplast, in order to restore plant photosynthetic potential similar to that of within 80–100% RWC. However, under reduced RWC, photosynthetic potential decreases and cannot be restored by increased ambient CO_2. Decreased stomatal conductance under DS has also been shown to limit CO_2 concentration in the mesophyll cells at the Rubisco site of different plant species (Chaves et al. 2003; Ghannoum 2009; Lopes et al. 2011).

8.5.2 Effect of Drought Stress on Non-stomatal Factors Responsible for the Regulation of Photosynthesis

Although stomata limitation is the major factor attributed for the reduction in plant photosynthesis under DS (Clauw et al. 2015), many studies have indicated that non-stomata factors are also responsible for the significant reduction in plant photosynthetic capacity under DS (Fig. 8.2; Farooq et al. 2009; Signarbieux and Feller 2011). The major non-stomatal limitations of photosynthesis include inhibition of photochemical and metabolic process, impaired activities of photosynthetic enzymes and altered ATP synthesis (Farooq et al. 2009).

8.5.2.1 Effect of Drought Stress on Photochemical Events

DS usually reduces plant requirement of light energy (Kato et al. 2003), thus allowing excess light to saturate the photosynthetic apparatus which results in photoinhibition and consequently reduces plant's photosynthesis rate (Athar and Ashraf 2005). Several studies have reported that saturation of photosynthetic apparatus with excess light under DS results in the production of toxic byproducts ROS in the chloroplast, which results in oxidative damage of photosynthetic apparatus thereby reducing photosynthesis rate (Table 8.4; Asada 1999; Chaves et al. 2003; Murata et al. 2007). Excess light decreased the photosynthetic activity and altered the structure of photosystem I and II in rice, wheat and maize (Werner et al. 2001; Zhou et al. 2007; Liu et al. 2012).

8.5.2.2 Effect of Drought Stress on Metabolic Factors

Drought stress limits photosynthetic metabolism through inference with major photosynthetic enzymes such as ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco), regeneration of RuBP and ATP synthesis (Lawlor and Cornic 2002). Drought-induced reduction in plant photosynthetic capacity has been reported as a consequence of impaired activities of Rubisco, pyruvate phosphate dikinase and phosphoenol pyruvate carboxylase enzymes (Reddy et al. 2004). DS reduces RuBP content which results in decreased CO_2 assimilation and plant photosynthesis (Flexas and Medrano 2002; Reddy et al. 2004). Decreased RuBP content and its regeneration under DS resulted in a substantial reduction in photosynthesis in plants (Reddy et al. 2004; Zhou et al. 2007). Rubisco content and Rubisco activity declined under DS, leading to a decline in net photosynthesis rate in rice, wheat and maize (Guan et al. 2015; Flexas and Medrano 2002; Medrano et al. 2002).

Impaired ATP synthesis is considered one of the main factors that limit photosynthesis under DS (Lawlor and Cornic 2002). ATP content in chloroplast declines due to the retarded activity and inhibition of enzymes involved in ATP synthesis under DS (Farooq et al. 2009). DS reduces chloroplast ATP content and activity and hence the level of ATP available for photosynthesis (Dubey 1997; Tezara et al. 1999). Studies have reported inhibition of photophosphorylation, ATP synthesis and consequently plant photosynthesis even under mild DS (Meyer and de Kouchkovsky 1992; Tezara et al. 1999).

8.6 ABA Physiology and Signalling Under Drought Stress

Abscisic acid (ABA) is an essential plant hormone, which regulates water status, stomatal movement and various physiological processes in response to DS in plants (Finkelstein et al. 2002). ABA is synthesized in roots and leaves, and its production in plant root is usually regarded as an early response to DS (Schachtman and Goodger 2008). The importance and mechanism of ABA in the regulation of plant tolerance to DS are well documented (Fig. 8.3; Taiz and Zeiger 2006; Jia and Zhang 2008), and many studies have reported the mechanism of ABA action at the physiological and molecular levels (Chinnusamy et al. 2008; Ferrandino and Lovisolo 2014; Mehrotra et al. 2014). ABA mediates plant adaptation to DS through alteration of guard cell ion transport which promotes stomatal resistance, improves ROS defence and enhances the expression of key enzymes (Kim et al. 2010; Liu et al. 2013). The study of Xu et al. (2012) in rice showed that ABA is necessary for signalling at the initial stage of DS. Furthermore, as DS progresses, ABA responds by initiating a root-to-shoot signal that induces stomata closure and thereby reduces stomatal conductance and transpirational water loss accompanied by and changes in plant photosynthesis (Taiz and Zeiger 2006).

Several studies have found that DS is associated with ABA accumulation in various plant species, but the extent of ABA accumulation varies with species differing in drought tolerance (Jiang and Hartung 2008; Wang et al. 2008; Kim et al. 2010). The content of ABA increased significantly in drought-tolerant maize seedlings under DS than drought-susceptible ones (Zhang et al. 2012). The involvement of ABA in drought adaptation is also reported in rice (Liang et al. 2014) and wheat (Vysotskaya et al. 2003, 2004). Accumulation of ABA in plant root is indispensable for enhancing plant growth because it modulates root architecture to adapt to DS (Sharp and LeNoble 2002). Under DS, ABA increases ion and water influx in the root, thereby regulating leaf turgidity and decreasing transpiration (Dodd et al. 2008). Drought-induced ABA accumulation also increases ratio of root-to-shoot growth, thereby increasing water use efficiency (Saab et al. 1990). Many studies indicated that drought-induced increase in ABA concentration in plant root helps to maintain root growth and increases root hydraulic conductivity and, hence, plant water uptake, thus eradicating the development of water deficit in the shoot (Plauborg et al. 2010; Liu et al. 2015). For example, under DS, ABA accumulation maintained maize root elongation and enhanced its adaptation towards resource utilization by restricting the production of ethylene (Liang et al. 1997; Spollen et al. 2000). Similarly, Vysotskaya et al. (2004) observed a high concentration of ABA in wheat root and subsequent increase in root hydraulic conductance to meet the

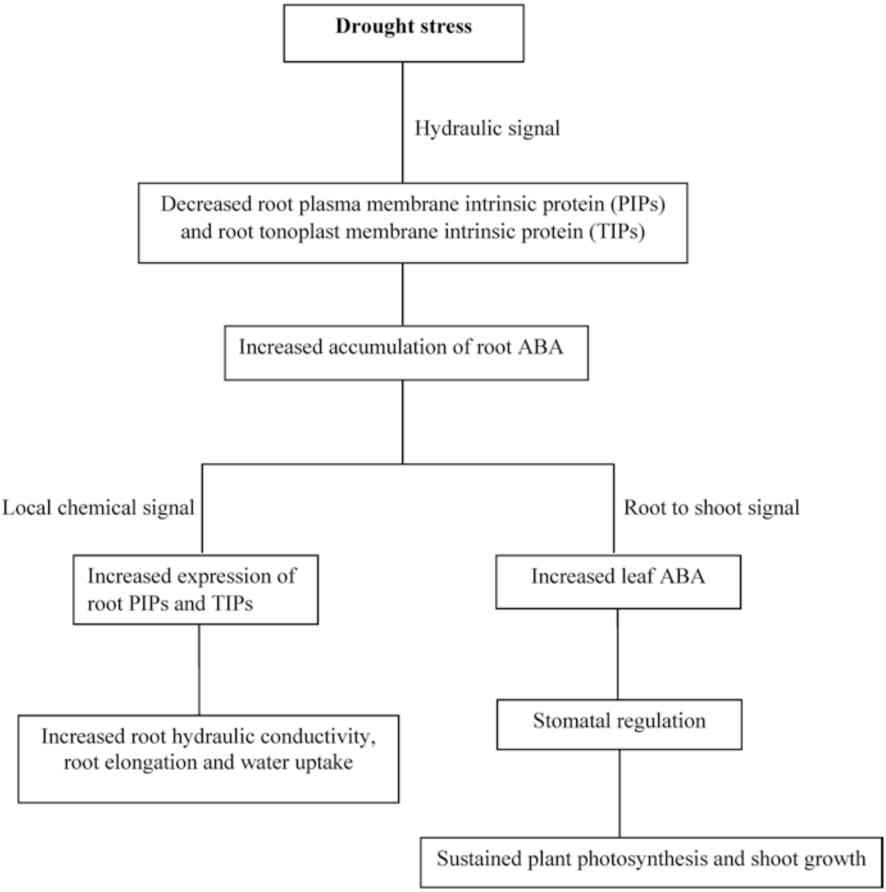

Fig. 8.3 Mechanism of ABA-dependent responses in plant under drought stress. Under drought stress, root PIP and TIP expression decreases as ABA accumulates; as stress progresses, root PIP and TIP expression increases resulting in increased root hydraulic conductivity, elongation, and hence water uptake; root ABA accumulation induces increase in shoot ABA concentration, resulting in stomatal closure, maintenance of photosynthesis, and ultimately improved performance under drought stress

increased transpiration demand under DS. Increase in root ABA concentration and subsequence enhancement of hydraulic conductivity have been attributed to the improvement of aquaporin functioning and osmotic regulation which protects cells from damage and led to sustained growth under DS (Tardieu et al. 2010; Travaglia et al. 2010). Activation of ABA signalling in the root under DS enhanced better soil exploration and water utilization, thus improving the plant's ability to cope with DS (Duan et al. 2013). ABA can also act in the maintenance of root meristem and stem cell by promoting the suppression of stem cell differentiation (Zhang et al. 2010). In addition, ABA originating from the root is transported to the shoot where it controls stomata conductance and causes stomata closure and reduced leaf expansion, thus reducing leaf water loss and enhancing survival under DS (Sun and Li 2014).

The role of ABA in stomata closure and reduced stomata conductance is vital for fast growth resumption, recovery of plant water content and ultimately increased yield under DS (Zhang et al. 2012). Increased ABA concentration in leaves associated with stomata closure and reduced stomata conductance under DS has been confirmed in various plant species (Davies and Zhang 1991; Munns and Sharp 1993) including rice (Ding et al. 2016), wheat (Saradadevi et al. 2014) and maize (Li et al. 2008; Wang et al. 2008). In wheat drought-induced increase in ABA concentration during the late grain filling stage accelerated grain filling (Yang et al. 2004). Similarly in rice, there was a high stomata conductivity and reduced transpirational water loss as a result of increased ABA accumulation under DS (Ding et al. 2016).

In addition to its role in controlling stomatal aperture, which is required to limit transpirational water loss under water deficit conditions, ABA initiates the expression of numerous genes such as enzymes for osmo-protectant synthesis which are critical for stress tolerance in plants (Fujita et al. 2011). ABA regulates plants response to drought tolerance by inducing stress-responsive genes and gene prod-

Table 8.6 ABA-signalling genes identified in crops and their response/effect on drought tolerance

Crop	Gene	Function	References
Rice	Senescence-associated and ABA-dependent genes *OSNAP* and *OsNAC5*	Improve yield under drought at flowering stage	Sperotto et al. (2009); Chen et al. (2014); Liang et al. (2014)
	OsPP2C06/OsAB12, OsPP2C09 and *OsPP2C68*	Improve the source sink mobilization during grain filling	Sperotto et al. (2009)
	DSM2	Enhance drought resistance mediated by an increase in xanthophylls and non-photochemical quenching, with increased spikelet fertility and seed setting rate	Du et al. (2010)
	OsSLI1	Improve drought tolerance and panicle development	Huang et al. (2014)
Maize	ABA aldehyde oxidase (AAO)	ABA biosynthesizing genes upregulated in response of drought stress	Zhu (2002)
	9-cis-epoxycarotenoid dioxygenase (NCED)	Improve drought tolerance	Zhu et al. (2008)
	LOS5/ABA3	Improve drought tolerance	Zhu et al. (2008)
	ZmOST1	Enhance drought responses	Vilela et al. (2015)
	ZmPP2C	Enhance drought responses	Liu et al. (2009)
Wheat	*HVA1*	Improve biomass yield under DS	Sivamani et al. (2000)
	TaSnRK2.8	Modulation of water relations and plant growth under drought	Zhang et al. (2012)
	TaWRKY2 and *TaWRKY19*	Enhance differential stress tolerance in transgenic Arabidopsis plants	Niu et al. (2012)

ucts that act as osmo-protectants (Rabbani et al. 2003). Studies have indicated that many of the genes controlled by DS are regulated by ABA. Rabbani et al. (2003) reported that about 43 stress-inductive genes were induced by ABA in rice. Although several studies attempted to enhance drought tolerance by modifying plant ABA biosynthetic pathway have failed, however, the knowledge of ABA as an important regulator of plant response to DS has been annexed for developing drought-tolerant crop species (Bao et al. 2016). ABA-signalling genes have been successfully identified to enhance drought tolerance and improve biomass and crop yield under DS (Table 8.6; Sivamani et al. 2000; Aswath et al. 2005). Transgenic crops overexpressing the major ABA synthesis gene NCED (9-cis-epoxycarotenoid dioxygenase) and ABA receptor PYR (pyrabactin resistance) have been shown to confer drought tolerance (Zhang et al. 2009; Gonzalez-Guzman et al. 2014). Similarly, overexpression of *TaSnRK2.3* and *TaSnRK2.8* gene in *Arabidopsis* increased tolerance to DS as a result of increased expression of ABA stress-responsive genes (Zhang et al. 2010).

ABA is the key regulator of plant tolerance to DS. Under DS, the concentration of ABA increases in plants through ABA biosynthesis. The increased ABA initiates signal transduction that leads to plants' cellular response to DS. ABA is substantially increased under DS improving water balance through enhanced root elongation, hydraulic conductivity, cuticular resistance and stomatal closure, thus enabling plant to cope with DS. Due to advancement of molecular genetics, the understanding of ABA-signalling mechanisms under DS has provided avenues for improving crop performance. ABA-signalling genes and genes involved in ABA synthesis have been identified. Studies on the effect of ABA over accumulation using transgenics on crop yield are presently limited.

8.7 Conclusion

Drought stress is a multidimensional factor that has a complex effect on plants' physiology and growth. However, plants are able to cope with drought stress through the development of several morphological, physiological, biochemical and molecular mechanisms. These mechanisms can be through escape, avoidance or tolerance depending on the species, prevailing environmental conditions and severity of the stress. Through escape mechanism, plants are able to complete their life cycle before the onset of drought stress with consequence of early maturity and in some cases reduced yield. In avoidance mechanism, plants either take up more water from the soil or conserve available moisture by regulating stomata aperture. In tolerance mechanism, plants develop some adaptations to cope with water deficit conditions including deep root system and high water use efficiency. The regulation of these adaptations involves the expression of several drought-tolerant genes through drought signalling pathways such as ABA, ethylene and hormone signals. It has been demonstrated from previous studies that drought tolerance could be enhanced through genetic improvement, with a good number of qtls and genes already identified to confer drought tolerance in crop plants, although efforts has been made to transfer these genes from one plant to another to produce transgenic plants with enhanced drought tolerance. However, due to the complexity of drought stress and its interaction with many other environmental factors, further studies are needed to identify, transfer and integrate multiple genes in a manner that will not result in yield penalties as well as to test already developed transgenic lines under multiple field conditions.

References

Abdelbagi MA, Hall AE (1993) Inheritance of carbon isotope discrimination and water-use efficiency in cowpea. Crop Sci 33:498–503

Addington RN, Donovan LA, Mitchell RJ, Vose JM, Pecot SD, Jack SB, Hacke UG, Sperry JS, Oren R (2006) Adjustments in hydraulic architecture of *Pinus palustris* maintain similar stomatal conductance in xeric and mesic habitats. Plant Cell Environ 29:535–545

Anjum SA, Xie XY, Wang LC, Saleem MF, Man C, Lei W (2011a) Morphological, physiological and biochemical responses of plants to Drought Stress. Afr J Agric Res 6(9):2026–2032

Anjum SA, Wang LC, Farooq M, Hussain M, Xue LL, Zou CM (2011b) Brassinolide application improves the drought tolerance in maize through modulation of enzymatic antioxidants and leaf gas exchange. J Agron Crop Sci 197:177–185

Asada K (1999) The water-water cycle in chloroplasts: scavenging of active oxygens and dissipation of excess photons. Annu Rev Plant Physiol Plant Mol Biol 50:601–639

Asch F, Dingkuhn M, Sow A, Audebert A (2005) Drought-induced changes in rooting patterns and assimilate partitioning between root and shoot in upland rice. Field Crop Res 93:223–236

Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: an overview. Photosynthetica 51:163–190

Aswath CR, Kim SH, MO SY, Kim DH (2005) Transgenic plants of creeping bent grass harboring the stress-inducible gene, 9-cis-epoxycarotenoid dioxygenase, are highly tolerant to drought and NaCl stress. Plant Growth Regul 47:129–139

Athar HR, Ashraf M (2005) Photosynthesis under DS. In: Pessarakli M, Marcel, Dekker (eds) Handbook of photosynthesis, 2nd edn. Taylor and Francis, Inc., New York, pp 793–809

Audebert A, Grenier C, Ospina Y, Selvaraj M, Jaramillo S, Rodriguez F, Dardou A, Abdourasmane K, Sow M, Futakuchi K, Venuprasad R, Ndjiondjop MN (2013) Canopy temperature as field phenotyping trait for rainfed-lowland rice breeding program for drought tolerance. In: La science rizicole pour la sécurité alimentaire à travers le renforcement de l'agriculture familiale et l'agro-industrie en Afrique: 3ème Congrès du riz en Afrique 2013, 21–24 octobre 2013, Yaoundé, Cameroun. Programme et résumés. Centre du riz pour l'Afrique, IRAD, FAO. Cotonou: ADRAO [Centre du Riz pour l'Afrique], Résumé, p. 32. Africa Rice Congress. 3, Yaoundé, Cameroun, 21 October 2013/24 October 2013

Azhand M, Saeidi M, Abdoli M (2015) Evaluation of the relationship between gas exchange variables with grain yield in barley genotypes under terminal drought stress. Int J Biosci 6:366–374

Azhiri-Sigari TA, Yamauchi A, Kamoshita A, Wade LJ (2000) Genotypic variation in response of rainfed lowland rice to drought would help to elucidate how rooting depth and deep root and rewatering II. Root Growth Plant Prod Sci 3:180–188

Babu RC, Zhang J, Blum A, Ho THD, Wu R, Nguyen HT (2004) HVA1, a LEA gene from barley confers dehydration tolerance in transgenic rice (*Oryza sativa* L.) via cell membrane protection. Plant Sci 166(4):855–862

Bacelar EA, Moutinho-Pereira JM, Goncalves BC, Lopes JI, Correia CM (2009) Physiological responses of different olive genotypes to drought conditions. Acta Physiol Plant 31(3):611–621

Bahavar N, Ebadi A, Tobeh A, Jamati-e-Somarin SH (2009) Effects of nitrogen application on growth of irrigated chickpea (*Cicer arietinum* L.) under drought stress in hydroponics conditions. Res J Environ Sci 3(4):448–455

Bahieldin A, Hesham HT, Eissa HF, Saleh OM, Ramadan AM, Ahmed IA, Dyer WE, El-Itriby HA, Madkour MA (2005) Field evaluation of transgenic wheat plants stably expressing the *HVA1* gene for drought tolerance. Physiol Plant 123:421–427

Bajji M, Lutts S, Kinet JM (2001) Water deficit effects on solute contribution to osmotic adjustment as a function of leaf ageing in three durum wheat (*Triticum durum* Desf.) cultivars performing differently in arid conditions. Plant Sci 160(4):669–681

Bao G, Zhuo C, Qian C, Xiao T, Guo Z, Lu S (2016) Co-expression of NCED and ALO improves vitamin C level and tolerance to drought and chilling in transgenic tobacco and stylo plants. Plant Biotechnol J14:206–214

Bao-Yuan Z, Zai-Song D, Ming Z (2011) Alleviation of drought stress inhibition on photosynthesis by overexpression of PEPC in rice. Acta Agron Sin 37:112–118

Barea JM, Brown ME (1974) Effects on plant growth by Azotobacter paspali related to synthesis of plant growth regulating substances. J Appl Bacteriol 37:583–593

Bayoumi TY, Eid MH, Metwali EM (2008) Application of physiological and biochemical indices as a screening technique for drought tolerance in wheat genotypes. Afr J Biotechnol 7(14):76–87

Belder P, Bouman BAM, Cabangon R, Guoan L, Quilang EJP, Li Y, Spiertz JHJ, Tuong TP (2004) Effect of water-saving irrigation on rice yield and water use in typical lowland conditions in Asia. Agric Water Manag 65:193–210

Bennet J, Sinclair T, Muchow R, Costello S (1987) Dependence of stomata conductance on leaf water potential, turgor and relative water content in field grown soybean and maize. Crop Sci 27:984–990

Bennett D, Izanloo A, Reynolds M, Kuchel H, Langridge P, Schnurbusch T (2012) Genetic dissection of grain yield and physical grain quality in bread wheat (*Triticum aestivum* L.) under water-limited environments. Theor Appl Genet 125:255–271

Bernier J, Serraj R, Kumar A, Venuprasad R, Impa S, Gowda RPV, Oane R, Spaner D, Atlin G (2009) The large-effect drought-resistance QTL qtl12.1 increases water uptake in upland rice. Field Crop Res 110:139–146

Bijanzadeh E, Emam Y (2010) Effect of defoliation and drought stress on yield components and chlorophyll content of wheat. Pak J Biol Sci 13:699–705

Blum A (1989) Osmotic adjustment and growth of barley genotypes under drought stress. Crop Sci 29(1):230–233

Blum A (2005) Drought resistance, water-use efficiency, and yield potential—are they compatible, dissonant, or mutually exclusive? Aust J Agric Res 56:1159–1168

Blum A (2009) Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under DS. Field Crop Res 112:119–123

Blum A (2017) Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. Plant Cell Environ 40:4–10

Blum A, Tuberosa R (2018) Dehydration survival of crop plants and its measurement. J Exp Bot 69:975–981

Blum A, Zhang J, Nguyen HT (1999) Consistent differences among wheat cultivars in osmotic adjustment and their relationship to plant production. Field Crops Res 64:287–291

Borrell AK, Hammer GL (2000) Nitrogen dynamics and the physiological basis of stay-green in sorghum. Crop Sci 40:1295–1307

Bota J, Hipólito Medrano H, Flexas J (2004) Blackwell Publishing, Ltd. Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress? New Phytol 162:671–681

Chang H, Chen D, Kam J, Richardson T, Drenth J, Guo X (2016) Abiotic stress upregulated TaZFP34 represses the expression of type-B response regulator and SHY2 genes and enhances root to shoot ratio in wheat. Plant Sci 252:88–102

Chaves MM, Oliveira MM (2004) Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. J Exp Bot 55:2365–2384

Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought—from genes to the whole plant. Funct Plant Biol 30:239–264

Chen H, Jiang JG (2010) Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. Environ Rev 18:309–319

Chen X, Wang Y, Lv B, Li J, Luo L, Lu S, Zhang X, Ma H, Ming F (2014) The NAC family transcription factor *OsNAP* confers abiotic stress response through the ABA pathway. Plant Cell Physiol 55:604–619

Chinnusamy V, Gong Z, Zhu JK (2008) Abscisic acid-mediated epigenetic processes in plant development and stress responses. J Integr Plant Biol 50:1187–1195

Christopher J, Christopher M, Jennings R, Jones S, Fletcher S, Borrell A, Manschadi A, Jordan D, Mace E, Hammer G (2013) QTL for root angle and number in a population developed from bread wheats (*Triticum aestivum*) with contrasting adaptation to water-limited environments. Theor Appl Genet 126:1563–1574

Clauw P, Coppens F, De Beuf K (2015) Leaf responses to mild drought stress in natural variants of Arabidopsis. Plant Physiol 167:800–816

Close TJ, Kortt AA, Chandler PM (1989) A cDNA-based comparison of dehydration-induced proteins (dehydrins) in barley and corn. Plant Mol Biol 13(1):95–108

Condon AG, Richards RA, Rebertzke GJ, Farquhar GD (2002) Improving intrinsic water-use efficiency and crop yield. Crop Sci 42:122–131

Cornic G (2000) Drought stress inhibits photosynthesis by decreasing stomatal aperture—not by affecting ATP synthesis. Trends Plant Sci 5:187–188

Creus CM, Sueldo RJ, Barassi CA (2004) Water relations and yield in Azospirillum-inoculated wheat exposed to drought in the field. Can J Bot 82(2):273–281

Davies FT Jr, Potter JR, Linderman RG (1992) Mycorrhiza and repeated drought exposure affect drought resistance and extraradical hyphae development of pepper plants independent of plant size and nutrient content. J Plant Physiol 139(3):289–294

Davies WJ, Zhang J (1991) Root signals and the regulation of growth and development of plants in drying soil. Annu Rev Plant Physiol Plant Mol Biol 42:55–76

Dhanda SS, Sethi GS, Behl RK (2004) Indices of drought tolerance in wheat genotypes at early stages of plant growth. J Agron Crop Sci 190:6–12

Diaz-Espejo A, Buckley TN, Sperry JS, Cuevas MV, de Cires A, Elsayed-Farag S, Martin-Palomo MJ, Muriel JL, Perez-Martin A, Rodriguez-Dominguez CM, Rubio-Casal AE, Torres-Ruiz JM, Fernández JE (2012) Steps toward an improvement in process-based models of water use by fruit trees: a case study in olive. Agric Water Manag 114:37–49

Dichio BC, Xiloyannis K, Angelopoulos V, Nuzzo S, Bufo A, Celano G (2003) Drought-induced variations of water relations parameters in Olea europaea. Plant Soil 257:381–389

Dimkpa C, Weinand T, Asch F (2009) Plant–rhizobacteria interactions alleviate abiotic stress conditions. Plant Cell Environ 32(12):1682–1694

Din J, Khan SU, Ali I, Gurmani AR (2011) Physiological and agronomic response of canola varieties to drought stress. J Anim Plant Sci 21:78–82

Ding ZS, Zhao M, Jing YX, Li LB, Kuang TY (2007) Effect of over expression of maize ppc gene on photosynthesis in transgenic rice plants. Acta Agron Sin 33:717–722

Ding L, Li Y, Wang Y, Gao L, Wang M, Chaumont F, Shen Q, Guo S (2016) Root ABA accumulation enhances rice seedling drought tolerance under ammonium supply: interaction with aquaporins. Front Plant Sci 7:1206

Dingkuhn M, Farquhar GD, De Datta SK, O'toole JC, Datta S (1991) Discrimination of 13C among upland rices having different water use efficiencies. Aust J Agric Res 42(7):1123–1131

Dixit SA, Kumar A (2014) Rice breeding for high grain yield under drought: a strategic solution to a complex problem. Int J Agron 2014:15

Dixit S, Biswal AK, Min A, Henry A, Oane RH, Raorane ML, Longkumer T, Pabuayon IM, Mutte SK, Vardarajan AR, Miro B, Govindan G, Albano-Enriquez B, Pueffeld M, Sreenivasulu N, Slamet-Loedin I, Sundarvelpandian K, Tsai YC, Raghuvanshi S, Hsing YC, Kumar A, Kohli A

(2015) Action of multiple intra-QTL genes concerted around a co-localized transcription factor underpins a large effect QTL. Sci Rep 5:15183

Dodd IC, Egea G, Davies WJ (2008) Abscisic acid signaling when soil moisture is heterogeneous: decreased photoperiod sap flow from drying roots limits abscisic acid export to the shoots. Plant Cell Environ 31:1263–1274

Dos santos CM, Endres L, Ferreira LM, Silva JV, Rolim EV, Filho HCW (2017) Photosynthetic capacity and water use efficiency in *Ricinus communis* (L.) under drought stress in semi-humid and semi-arid areas. Ann Braz Acad Sci 89(4):3015–3029

Doussan C, Pierret A, Garrigues E, Pagès L (2006) Water uptake by plant roots: ii—modelling of water transfer in the soil root-system with explicit account of flow within the root system—comparison with experiments. Plant Soil 283:99–117

Du H, Wang N, Cui F, Li X, Xiao J, Xiong L (2010) Characterization of the beta-carotene hydroxylase gene *DSM2* conferring drought and oxidative stress resistance by increasing xanthophylls and abscisic acid synthesis in rice. Plant Physiol 154:1304–1318

Duan L, Dietrich D, Ng CH, Chan PMY, Bhalerao R, Bennett MJ (2013) Endodermal ABA signaling promotes lateral root quiescence during salt stress in Arabidopsis seedlings. Plant Cell 25:324–341

Dubey RS (1997) Photosynthesis in plants under stressful conditions. In: Pessarakli M (ed) Handbook of photosynthesis, vol 1997. Marcel and Decker, New York, pp 859–875

Egamberdieva D (2013) The role of phytohormone producing bacteria in alleviating salt stress in crop plants. In: Biotechnological techniques of stress tolerance in plants. Studium, Houston, pp 21–39

Evans RG, Sadler EJ (2008) Methods and technologies to improve efficiency of water use. Water Res 44:W00E04

Fahad S, Hussain S, Bano A, Saud S, Hassan S, Shan D, Tabassum MA (2015) Potential role of phytohormones and plant growth-promoting rhizobacteria in abiotic stresses: consequences for changing environment. Environ Sci Pollut Res 22(7):4907–4921

Farooq M, Wahid A, Lee DJ (2009) Exogenously applied polyamines increase drought tolerance of rice by improving leaf water status, photosynthesis and membrane properties. Acta Physiol Plant 31(5):937–945

Farrant JM, Cooper K, Nell H (2012) Desiccation tolerance. In: Shabala S (ed) Plant desiccation tolerance. CABI Publishing, Wallingford, pp 238–265

Ferrandino A, Lovisolo C (2014) Abiotic stress effects on grapevine (*Vitis vinifera* L.): focus on abscisic acid-mediated consequences on secondary metabolism and berry quality. Environ Exp Bot 103:138–147

Finkelstein RR, Gampala SS, Rock CD (2002) Abscisic acid signalling in seeds and seedlings. Plant Cell 14:15–45

Fitter AH (2002) Characteristics and functions of root systems. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. Marcel Dekker, New York, pp 249–259

Flexas J, Medrano H (2002) Drought-inhibition of photosynthesis in C3 plants: stomatal and non-stomatal limitations revisited. Ann Bot 89:183–189

Fotovat R, Valizadeh M, Toorchi M (2007) Association between water-use efficiency components and total chlorophyll content (SPAD) in wheat (*Triticum aestivum* L.) under well-watered and drought stress conditions. J Food Agric Environ 5(3 & 4):225–227

Freitas C, Silva A, Bezerra FML, Lacerda CF, Pereira Filho JV, Sousa GG (2011) Produção de matériaseca e trocasgasosasemcultivares de mamoneira sob níveis de irrigação. R Bras Eng Agríc Ambiental 15:1168–1174

Fu D, Huang B, Xiao Y, Muthukrishnan S, Liang GH (2007) Overexpression of barley hva1 gene in creeping bentgrass for improving drought tolerance. Plant Cell Rep 26(4):467–477

Fujita Y, Fujita M, Shinozaki K, Yamaguchi-Shinozaki K (2011) ABA-mediated transcriptional regulation in response to osmotic stress in plants. J Plant Res 124:509–525

Garg AK, Kim JK, Owens TG, Ranwala AP, Choi YD, Kochian LV, Wu RJ (2002) Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses. Proc Natl Acad Sci 99(25):15898–15903

George-Jaeggli B, Mortlock MY, Borrell AK (2017) Bigger is not always better: reducing leaf area helps stay-green sorghum use soil water more slowly. Environ Exp Bot 138:119–129

Ghannoum O (2009) C4 photosynthesis and water stress. Ann Bot 103:635–644

Giarola V, Hou Q, Bartels D (2017) Angiosperm plant desiccation tolerance: hints from transcriptomics and genome sequencing. Trends Plant Sci 22:705–717

Gilbert ME, Zwieniecki MA, Holbrook NM (2011) Independent variation in photosynthetic capacity and stomatal conductance leads to differences in intrinsic water use efficiency in 11 soybean genotypes before and during mild drought. J Exp Bot 62:2875–2887

Giuliani S, Sanguineti MC, Tuberosa R, Bellotti M, Salvi S, Landi P (2005) Root-ABA1, a major constitutive QTL, affects maize root architecture and leaf ABA concentration at different water regimes. J Exp Bot 56:3061–3070

Gomes FP, Oliva MA, Mielke MS, Almeida AAF, Aquino LA (2010) Osmotic adjustment, proline accumulation and cell membrane stability in leaves of Cocos nucifera submitted to drought stress. Sci Hortic 126:379–384

Gonzalez-Guzman M, Rodriguez L, Lorenzo-Orts L, Pons C, Sarrion-Perdigones A, Fernandez MA (2014) Tomato PYR/PYL/RCAR abscisic acid receptors show high expression in root, differential sensitivity to the abscisic acid agonist quinabactin and the capability to enhance plant drought resistance. J Exp Bot 65:4451–4464

Govindaraj P, Vinod KK, Arumugachamy S, Maheswaran M (2009) Analysing genetic control of cooked grain traits and gelatinization temperature in a double haploid population of rice by quantitative trait loci mapping. Euphytica 66:165–176

Gowda VRP, Henry A, Yamauchi A, Shashidhar HE, erraj R (2011) Root biology and genetic improvement for drought avoidance in rice. Field Crop Res 122:1–13

Grzesiak S, Hura T, Grzesiak MT, Piefikowski S (1999) The impact of limited soil moisture and waterlogging stress conditions on morphological and anatomical root traits in maize (*Zea mays* L.) hybrids of different drought tolerance. Acta Physiol Plant 21:305–315

Guan XK, Song L, Wang TC, Turner NC, Li FM (2015) Effect of drought on the gas exchange, chlorophyll fluorescence and yield of six different-era spring wheat cultivars. J Agron Crop Sci 201:241–320

Haefele SM, Kato Y, Singh S (2016) Climate ready rice: augmenting drought tolerance with best management practices. Field Crop Res 190:60–69

Hall AE, Richards RA, Condon AG, Wright GC, Farquhar GD (1994) Carbon isotope discrimination and plant breeding. Plant Breed Rev 12:81–113

Hamada A, Nitta M, Nasuda S, Kato K, Fujita M, Matsunaka H, Okumoto Y (2012) Novel QTLs for growth angle of seminal roots in wheat (*Triticum aestivum* L.). Plant Soil 354:395–405

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Biol 51(1):463–499

Haupt-Herting S, Fock HP (2000) Exchange of oxygen and its role in energy dissipation during drought stress in tomato plants. Physiol Plant 110:489–495

Henry A (2012) IRRI's drought stress research in rice with emphasis on roots: accomplishments over the last 50 years. Plant Root 7:5–19

Higinbotham N (1973) Electropotentials of plant cells. Annu Rev Plant Physiol 24(1):25–46

Ho MD, Rosas JC, Brown KM, Lynch JP (2005) Root architectural tradeoffs for water and phosphorus acquisition. Funct Plant Biol 32:737–748

Holbrook NM, Putz FE (1996) From epiphyte to tree: differences in leaf structure and leaf water relation associated with the transition in growth form in eight species of hemiepiphytes. Plant Cell Environ 19:631–642

Huang X, Duan M, Liao J, Yuan X, Chen H, Feng J (2014) OsSLI1, a homeodomain-containing transcription activator, involves abscisic acid-related stress response in rice (*Oryza sativa* L.). Sci World J 2014:809–853

Hund A, Ruta N, Liedgens M (2009) Rooting depth and water use efficiency of tropical maize inbred lines, differing in drought tolerance. Plant Soil 318:311–325

Idso SB, Jackson RD, Pinter PJ Jr, Reginato RJ, Hatfield JL (1981) Normalizing the stress-degree-day parameter for environmental variability. Agric Meteorol 24:45–55

Jackson RD, Idso SB, Reginato RJ, Pinter PJ Jr (1981) Canopy temperature as a crop water stress indicator. Water Resour Res 17(4):1133–1138

Jaganathan D, Thudi M, Kale S, Azam S, Roorkiwal M, Gaur PM, Varshney RK (2015) Genotyping-by-sequencing based intra-specific genetic map refines a “QTL-hotspot” region for drought tolerance in chickpea. Mol Gen Genomics 290(2):559–571

Jaleel CA, Gopi R, Sankar B, Gomathinayagam M, Panneerselvam R (2008) Differential responses in water use efficiency in two varieties of Catharanthus roseus under drought stress. C R Biol 331:42–47

Jaleel CA, Paramasivm M, Wahid A, Farooq M, Al-Juburi HJ, Ramamurthy S, Panneerselvam R (2009) Drought stress in plants: a review on morphological characteristics and pigments composition. Int J Agric Biol 11(1):100–105

Janda T, Gondor OK, Yordanova R, Szalai G, Pál M (2014) Salicylic acid and photosynthesis: signalling and effects. Acta Physiol Plant 36(10):2537–2546

Janiak A, Kwaśniewski M, Szarejko I (2015) Gene expression regulation in roots under drought. J Exp Bot 67(4):1003–1014

Jeong JS, Kim YS, Baek KH, Jung H, Ha SH, Do Choi Y, Kim M, Reuzeau C, Kim JK (2010) Root-specific expression of OsNAC10 improves drought tolerance and grain yield in rice under field drought conditions. Plant Physiol 153:185–197

Ji KX, Wang YY, Sun WN, Lou QJ, Mei HW, Shen SH, Chen H (2012) Drought-responsive mechanisms in rice genotypes with contrasting drought tolerance during reproductive stage. J Plant Physiol 169:336–344

Jia W, Zhang J (2008) Stomatal movements and long distance signaling in plants. Plant Signal Behav 3:772–777

Jiang F, Hartung W (2008) Long-distance signalling of abscisic acid (ABA): the factors regulating the intensity of the ABA signal. J Exp Bot 59:37–43

Jongdee B, Fukai S, Cooper M (2002) Leaf water potential and osmotic adjustment as physiological traits to improve drought tolerance in rice. Field Crop Res 76(2–3):153–163

Kale SM, Jaganathan D, Ruperao P, Chen C, Punna R, Kudapa H, Garg V (2015) Prioritization of candidate genes in “QTL-hotspot” region for drought tolerance in chickpea (*Cicer arietinum* L.). Sci Rep 5:15296

Kato MC, Hikosaka K, Hirotsu N, Makin A, Hirose T (2003) The excess light energy that is neither utilized in photosynthesis nor dissipated by photoprotective mechanisms determines the rate of photoinactivation in photosystem II. Plant Cell Physiol 44:318–325

Kato Y, Abe J, Kamoshita A, Yamagishi J (2006) Genotypic variation in root growth angle in rice (*Oryza sativa* L.) and its association with deep root development in upland fields with different water regimes. Plant Soil 287:117–129

Kerepesi I, Galiba G (2000) Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings. Crop Sci 40(2):482–487

Khanna-Chopra R, Selote DS (2007) Acclimation to drought stress generates oxidative stress tolerance in drought-resistant than-susceptible wheat cultivar under field conditions. Environ Exp Bot 60(2):276–283

Khanna-Chopra R, Semwal VK, Lakra N, Pareek A (2019) 5 Proline-a key player in conferring tolerance to salinity and drought stress. In: Hasanuzzaman M, Fujita M, Oku H, Islam T (eds) Plant tolerance to environmental stress: role of exogenous phytoprotectants. CRC Press (Taylor and Francis), Boca Raton, pp 59–80

Kiani G (2015) Validation of SSR markers linked to restoring fertility (Rf) genes and genotyping of rice lines at Rf loci. J Agric Sci Technol 17:1931–1938

Kiani SP, Grieu P, Maury P, Hewezi T, Gentzbittel L, Sarrafi A (2007) Genetic variability for physiological traits under drought conditions and differential expression of water stress-associated genes in sunflower (*Helianthus annuus* L.). Theor Appl Genet 114(2):193–207

Kiani SP, Maury P, Sarrafi A, Grieu P (2008) QTL analysis of chlorophyll fluorescence parameters in sunflower (*Helianthus annuus* L.) under well-watered and water-stressed conditions. Plant Sci 175(4):565–573

Kim TH, Böhmer M, Hu H, Nishimura N, Schroeder JI (2010) Guard cell signal transduction network: advances in understanding abscisic acid, CO_2, and Ca^{2+} Signaling. Annu Rev Plant Biol 61:561–591

Kirkegaard JA, Lilley JM, How GN, Graham JM (2007) Impact of subsoil water use on wheat yield. Aust J Agric Res 58:303–315

Kumar S, Sehgal SK, Kumar U, Prasad PVV, Joshi AK, Gill BS (2012) Genomic characterization of drought tolerance-related traits in spring wheat. Euphytica 186:265–276

Lal R, Delgado JA, Gulliford J, Nielsen D, Rice CW, Van Pelt RS (2012) Adapting agriculture to drought and extreme events. J Soil Water Conserv 67:162–167

Lande R, Thompson R (1990) Efficiency of marker-assisted selection in the improvement of quantitative traits. Genetics 124(3):743–756

Lawlor DW (1995) The effects of water deficit on photosynthesis. In: Smirnoff N (ed) Environment and plant metabolism, vol 995. BIOS Scientific Publishers, Oxford, pp 129–160

Lawlor DW, Cornic G (2002) Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell Environ 25:275–295

Lemoine R, Camera SL, Atanassova R, Dédaldéchamp F, Allario T, Pourtau N, Bonnemain JL, Laloi M, Coutos-Thévenot P, Maurousset L, Faucher M, Girousse C, Lemonnier P, Parrilla J, Durand M (2013) Source-to-sink transport of sugar and regulation by environmental factors. Front Plant Sci 4:272

Li WX, Oono Y, Zhu J, He XJ, Wu JM, Iida K (2008) The *Arabidopsis* NFYA5 transcription factor is regulated transcriptionally and post transcriptionally to promote drought resistance. Plant Cell 20:2238–2251

Liang BM, Sharp RE, Baskin TI (1997) Regulation of growth anisotropy in well-watered and water-stressed maize roots (I. Spatial distribution of longitudinal, radial, and tangential expansion rates). Plant Physiol 115:101–111

Liang C, Wang Y, Zhu Y, Tang J, Hu B, Liu L (2014) OsNAP connects abscisic acid and leaf senescence by fine-tuning abscisic acid biosynthesis and directly targeting senescence-associated genes in rice. Proc Natl Acad Sci U S A 111:10013–10018

Lilley JM, Kirkegaard JA (2011) Benefits of increased soil exploration by wheat roots. Field Crop Res 122:118–130

Liu H, Zou G, Liu G, Hu S, Li M, Yu X, Luo L (2005) Correlation analysis and QTL identification for canopy temperature, leaf water potential and spikelet fertility in rice under contrasting moisture regimes. Chin Sci Bull 50(4):317–326

Liu Q, Zhang Y-C, Wang C-Y, Luo Y-C, Huang Q-J, Chen S-Y, Zhou H, Liang-Hu Q, Chen Y-Q (2009) Expression analysis of phytohormone-regulated microRNAs in rice, implying their regulation roles in plant hormone signaling. FEBS Lett 583(4):723–728

Liu J, Guo YY, Bai YW, Camberato JJ (2012) Effects of drought stress on the photosynthesis in maize. Russ J Plant Physiol 65(6):849–856

Liu X, Zhang H, Zhao Y, Feng Z, Li Q, Yang HQ (2013) Auxin controls seed dormancy through stimulation of abscisic acid signaling by inducing ARF-mediated ABI3 activation in *Arabidopsis*. Proc Natl Acad Sci U S A 110:15485–15490

Liu C, Rubæk GH, Liu F, Andersen MN (2015) Effect of partial root zone drying and deficit irrigation on nitrogen and phosphorus uptake in potato. Agric Water Manag 159:66–76

Lopes MS, Araus JL, van Heerden PDR, Foyer CH (2011) Enhancing drought tolerance in C4 crops. J Exp Bot 62:3135–3153

Lu C, Zhang J (1999) Effects of water stress on photosystem II photochemistry and its thermostability in wheat plants. J Exp Bot 50(336):1199–1206

Lynch JP (2013) Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. Ann Bot 112:347–357

Maccaferri M, El-Feki W, Nazemi G, Salvi S, Canè MA, Colalongo MC, Tuberosa R (2016) Prioritizing quantitative trait loci for root system architecture in tetraploid wheat. J Exp Bot 67(4):1161–1178

Mackill DJ, Nguyen HT, Zhang J (1999) Use of molecular markers in plant improvement programs for rainfed lowland rice. Field Crop Res 64(1–2):177–185

MacMillan K, Emrich K, Piepho HP, Mullins CE, Price AH (2006) Assessing the importance of genotype x environment interaction for root traits in rice using a mapping population ii: conventional QTL analysis. Theor Appl Genet 113:953–964

Majid M, Akbar M, Tomoaki H, Katsuhara M (2008) Drought stress alters water relations and expression of *PIP*-type aquaporin genes in *Nicotiana tabacum* plants. Plant Cell Physiol 49(5):801–813

Manschadi AM, Christopher J, DeVoil P, Hammer GL (2006) The role of root architectural traits in adaptation of wheat to water-limited environments. Funct Plant Biol 33:823–837

Manschadi AM, Hammer GL, Christopher JT, DeVoil P (2008) Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.). Plant Soil 303:115–129

Martin B, Ruiz-Torres NA (1992) Effects of water-deficit stress on photosynthesis, its components and component limitations, and on water use efficiency in wheat (*Triticum aestivum* L.). Plant Physiol 100:733–739

Maseda PH, Fernandez RJ (2006) Stay wet or else: three ways in which plants can adjust hydraulically to their environment. J Exp Bot 57:3963–3977

Masle J, Gilmore SR, Farquhar GD (2005) The ERECTA gene regulates plant transpiration efficiency in Arabidopsis. Nature 436:866–870

Medrano H, Escalona JM, Bota J, Gulías J, Flexas J (2002) Regulation of photosynthesis of C3 plants in response to progressive drought: the stomatal conductance as a reference parameter. Ann Bot 89:895–905

Mehrotra R, Bhalothia P, Bansal P, Basantani MK, Bharti V, Mehrotra S (2014) Abscisic acid and abiotic stress tolerance-different tiers of regulation. J Plant Physiol 171:486–496

Meyer S, de Kouchkovsky Y (1992) ATPase state and activity in thylakoids from normal and water-stressed lupin. FEBS Lett 303:233–236

Millet E, Welcker C, Kruijer W, Negro S, Nicolas S, Praud S, Draye X (2016) Genome-wide analysis of yield in Europe: allelic effects as functions of drought and heat scenarios. Plant Physiol 172(2):749–764

Mir RR, Zaman-Allah M, Sreenivasulu N, Trethowan R, Varshney RK (2012) Integrated genomics, physiology and breeding approaches for improving drought tolerance in crops. Theor Appl Genet 125(4):625–645

Molnár I, Gáspár L, Stéhli L, Dulai S, Sárvári E, Király I, Galiba G, Molnár-Láng M (2002) The effects of drought stress on the photosynthetic processes of wheat and of Aegilops biuncialis genotypes originating from various habitats. Acta Biol Szegediensis 46(3–4):115–116

Morgan JM, Tan MK (1996) Chromosomal location of a wheat osmoregulation gene using RFLP analysis. Funct Plant Biol 23(6):803–806

Moutinho-Pereira JM, Magalhães N, Gonçalves B, Bacelar E, Brito M, Correia C (2007) Gas exchange and water relations of three Vitis vinifera L. cultivars growing under Mediterranean climate. Photosynthetica 45(2):202–207

Munns R, Sharp RE (1993) Involvement of abscisic acid in controlling plant growth in soil of low water potential. Aust J Plant Physiol 20:425–437

Murata N, Takahashi S, Nishiyama Y, Allakhverdiev SI (2007) Photoinhibition of photosystem II under environmental stress. Biochim Biophys Acta 1767:414–421

Nielsen DC, Vigil MF, Benjamin JG (2009) The variable response of dryland corn yield to soil water content at planting. Agric Water Manag 96:330–336

Niu CF, Wei W, Zhou QY, Tian AG, Hao YJ, Zhang WK, Ma B, Lin Q, Zhang ZB, Zhang JS, Chen SY (2012) Wheat WRKY genes TaWRKY2 and TaWRKY19 regulate abiotic stress tolerance in transgenic Arabidopsis plants. Plant Cell Environ 35:1156–1170

Ochoa IE, Blair MW, Lynch JP (2006) QTL analysis of adventitious root formation in common bean under contrasting phosphorus availability. Crop Sci 46:1609–1621

Oh SJ, Song SI, Kim YS, Jang HJ, Kim SY, Kim M, Kim YK, Kim NYK, Nahm BH, Kim JK (2005) Arabidopsis CBF3/DREB1A and ABF3 in transgenic rice increased tolerance to abiotic stress without stunting growth. Plant Physiol 138:341–351

Osakabe Y, Yamaguchi-Shinozaki K, Shinozaki K, Tran LSP (2014) ABA control of plant macroelement membrane transport systems in response to water deficit and high salinity. New Phytol 202(1):35–49

Paredes P, de Melo-Abreu JP, Alves I, Pereira LS (2014) Assessing the performance of the FAO AquaCrop model to estimate maize yields and water use under full and deficit irrigation with focus on model parameterization. Agric Water Manag 144:81–97

Passioura JB (2006) Increasing crop productivity when water is scarce—from breeding to field management. Agric Water Manag 80:176–196

Perdomo JA, Capo-Bauca S, Carmo-Silva E, Galmes J (2017) Rubisco and Rubisco Activate play an important role in the biochemical limitations of photosynthesis in rice, wheat and maize front. Plant Sci 8:840

Plauborg F, Abrahamsen P, Gjettermann B, Mollerup M, Iversen BV, Liu F, Andersen MN, Hansen S (2010) Modelling of root ABA synthesis, stomatal conductance, transpiration and potato production under water saving irrigation regimes. Agric Water Manag 98:425–439

Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Aust J Plant Physiol 27:595–607

Price AH, Cairns JE, Horton P, Jones HG, Griffiths H (2002) Linking drought-resistance mechanisms to drought avoidance in upland rice using a QTL approach: progress and new opportunities to integrate stomatal and mesophyll responses. J Exp Bot 53(371):989–1004

Puteh AB, Saragih AA, Ismail MR, Mondal MA (2013) Chlorophyll fluorescence parameters of cultivated (*Oryza sativa* L. ssp. indica) and weedy rice (*Oryza sativa* L. var. nivara) genotypes under water stress. Aust J Crop Sci 7(9):1277–1283

Rabbani MA, Maruyama K, Abe H, Khan MA, Katsura K, Ito Y, Yoshiwara K, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2003) Monitoring expression profile of rice (*Oryza sativa* L.) genes under cold drought and high-salinity stress, and ABA application using both cDNA microarray and RNA gel blot analyses. Plant Physiol 133:1755–1767

Reddy AR, Chaitanya KV, Vivekanandan M (2004) Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J Plant Physiol 161:1189–1202

Redillas MC, Jeong JS, Kim YS, Jung H, Bang SW, Choi YD, Ha SH, Reuzeau C, Kim JK (2012) The overexpression of OsNAC9 alters the root architecture of rice plants enhancing drought resistance and grain yield under field conditions. Plant Biotechnol J 10:792–805

Ren Y, He X, Liu D, Li J, Zhao X, Li B, Tong Y, Zhang A, Li Z (2012) Major quantitative trait loci for seminal root morphology of wheat seedlings. Mol Breed 30:139–148

Rewald B, Ephrath JE, Rachmilevitch S (2011) A root is a root is a root? Water uptake rates of citrus root orders. Plant Cell Environ 34:33–42

Ribaut JM, Betran J, Monneveux P, Setter T (2009) Drought tolerance in maize. In: Handbook of maize: its biology. Springer, New York, pp 311–344

Rich SM, Watt M (2013) Soil conditions and cereal root system architecture: review and considerations for linking Darwin and Weaver. J Exp Bot 64:1193–1208

Richards RA, Rebetzke GJ, Condon AG, van Herwaarden AF (2002) Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. Crop Sci 42:111–121

Rivero RM, Kojima M, Gepstein A, Sakakibara H, Mittler R, Gepstein S, Blumwald E (2007) Delayed leaf senescence induces extreme drought tolerance in a flowering plant. Proc Nat Acad Sci USA 104:19631–19636

Saab IN, Sharp RE, Pritchard J, Voetberg GS (1990) Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. Plant Physiol 93:1329–1334

Saeidi M, Abdoli M (2015) Effect of drought stress during grain filling on yield and its components, gas exchange variables, and some physiological traits of wheat cultivars. J Agric Sci Technol 17:885–898

Saglam A, Kadioglu A, Demiralay M, Terzi R (2014) Leaf rolling reduces photosynthetic loss in maize under severe drought. Acta Bot Croat 73(2):315–332

Saini HS, Westgate ME (1999) Reproductive development in grain crops during drought. Adv Agron 68:59–96

Sakai A, Larcher W (1987) Frost survival of plants. Ecological studies 62. Springer, Berlin

Sakurai J, Ishikawa F, Yamaguchi T, Uemura M, Maeshima M (2005) Identification of 33 rice aquaporin genes and analysis of their expression and function. Plant Cell Physiol 46(9):1568–1577

Salehi-Lisar SY, Bakhshayeshan-Agdam H (2016) Drought stress in plants: causes, consequences, and tolerance. In: Hossain M, Wani S, Bhattacharjee S, Burritt D, Tran LS (eds) Drought stress tolerance in plants, vol 1. Springer, Cham, p 243

Salem KFM, Roder MS, Borner A (2007) Identification and mapping quantitative trait loci for stem reserve mobilisation in wheat (*Triticum aestivum* L.). Cereal Res Commun 35:1367–1374

Sandhu N, Singh A, Dixit S, Cruz MTS, Maturan PC, Jain RK, Kumar A (2014) Identification and mapping of stable QTL with main and epistasis effect on rice grain yield under uplanddrought stress. BMC Genet 15(1):63

Saradadevi R, Bramley H, Siddique KHM, Edwards E, Palta JA (2014) Contrasting stomatal regulation and leaf ABA concentrations in wheat genotypes when split root systems were exposed to terminal drought. Field Crops Res 162:77–86

Sausen TL, Rosa LMG (2010) Growth and carbon assimilation limitations in Ricinus communis (*Euphorbiaceae*) under soil water stress conditions. Acta Bot Bras 24:648–654

Schachtman DP, Goodger JQD (2008) Chemical root to shoot signaling under drought. Trends Plant Sci 13:281–287

Schenk HJ, Jackson RB (2005) Mapping the global distribution of deep roots in relation to climate and soil characteristics. Geoderma 126:129–140

Schonfeld M, Johnson R, Carver B, Mornhinweg D (1988) Water relations in winter wheat as drought resistant indicators. Crop Sci 28:526–531

Seki M, Kamei A, Yamaguchi-Shinozaki K, Shinozaki K (2003) Molecular responses to drought, salinity and frost: common and different paths for plant protection. Curr Opin Biotechnol 14(2):194–199

Selote DS, Khanna-Chopra R (2004) Drought-induced spikelet sterility is associated with an inefficient antioxidant defence in rice panicles. Physiol Plant 121(3):462–471

Semwal VK, Khanna-Chopra R (2018) Reproductive sink enhanced drought induced senescence in wheat fertile line is associated with loss of antioxidant competence compared to its CMS line. Physiol Mol Biol Plants 24(4):591–604

Semwal VK, Singh B, Khanna-Chopra R (2014) Delayed expression of SAGs correlates with longevity in CMS wheat plants compared to its fertile plants. Physiol Mol Biol Plants 20(2):191–199

Sharifi K, Mohammadkhani N (2015) Effects of drought stress on photosynthesis factors in wheat genotypes during anthesis. Cereal Res Commun AkadémiaiKiadó, Budapest 44(2):229–239

Sharp RE, LeNoble ME (2002) ABA, ethylene and the control of shoot and root growth under water stress. J Exp Bot 53:33–37

Shen BR, Wang LM, Lin XL, Yao Z, Xu HW, Zhu CH, He ZH (2019) Engineering a new chloroplastic photorespiratory bypass to increase photosynthetic efficiency and productivity in rice. Mol Plant 12(2):199–214

Shimazaki K, Doi M, Assmann SM, Kinoshita T (2007) Light regulation of stomatal movement. Annu Rev Plant Biol 58:219–247

Shinozaki K, Yamaguchi-Shinozaki K, Seki M (2003) Regulatory network of gene expression in the drought and cold stress responses. Curr Opin Biotechnol 6:410–417

Shou H, Bordallo P, Wang K (2004) Expression of the nicotiana protein kinase (NPK1) enhanced drought tolerance in transgenic maize. J Exp Bot 55(399):1013–1019

Signarbieux C, Feller U (2011) Non-stomatal limitations of photosynthesis in grassland species under artificial drought in the field. Environ Exp Bot 71:192–197

Silva EN, Ferreira-Silva SL, Viégas RA, Silveira JA (2010) The role of organic and inorganic solutes in the osmotic adjustment of drought-stressed Jatropha curcas plants. Environ Exp Bot 69(3):279–285

Sivamani E, Bahieldin A, Wraith JM, Al-Niemi T, Dyer WE, Ho TD (2000) Improved biomass productivity and water use efficiency under water deficit conditions in transgenic wheat constitutively expressing the barley HVA1 gene. Plant Sci 155:1–9

Skirycz A, Inzé D (2010) More from less: plant growth under limited water. Curr Opin Biotechnol 21(2):197–203

Sperotto RA, Ricachenevsky FK, Duarte G, Boff T, Lopes K, Sperb ER, Grusak MA, Fett JP (2009) Identification of up-regulated genes in flag leaves during rice grain filling and characterization of *OsNAC5*, a new ABA-dependent transcription factor. Planta 230(5):985–1002

Sperry JS, Stiller V, Hacke UG (2002) Soil water uptake and water transport through root systems. In: Waisel Y, Eshel A, Kafkafi U (eds) The hidden half, 3rd edn. Marcel Dekker, Inc, New York, pp 663–681

Spollen WG, LeNoble ME, Samuels TD, Bernstein N, Sharp RE (2000) Abscisic acid accumulation maintains maize primary root elongation at low water potentials by restricting ethylene production. Plant Physiol 122:967–976

Sun J, Li C (2014) Cross talk of signaling pathways between ABA and other phytohormones. In: Zhang D-P (ed) Abscisic acid: metabolism, transport and signaling. Springer, Berlin, pp 243–253

Taiz L, Zeiger E (2006) Chapter 23: abscisic acid: a seed maturation and stress signal. In: Plant physiology, 4th edn. Sinauer Associates, Sunderland, p 89

Tang AC, Kawamitsa Y, Kanechi M, Boyer JS (2002) Photosynthesis at low water potentials in leaf discs AQ1 lacking epidermis. Ann Bot 89:861–870

Tardieu F (2016) Too many partners in root–shoot signals. Does hydraulics qualify as the only signal that feeds back over time for reliable stomatal control? New Phytol 212(4):802–804

Tardieu F, Parent B, Simonneau T (2010) Control of leaf growth by abscisic acid: hydraulic or non-hydraulic processes? Plant Cell Environ 33:636–647

Teale WD, Paponov IA, Palme K (2006) Auxin in action: signalling, transport and the control of plant growth and development. Nat Rev Mol Cell Biol 7:847–859

Teulat B, This D, Khairallah M, Borries C, Ragot C, Sourdille P, Charrier A (1998) Several QTLs involved in osmotic-adjustment trait variation in barley (*Hordeum vulgare* L.). Theor Appl Genet 96(5):688–698

Teulat B, Borries C, This D (2001) New QTLs identified for plant water status, water-soluble carbohydrate and osmotic adjustment in a barley population grown in a growth-chamber under two water regimes. Theor Appl Genet 103(1):161–170

Tezara W, Mitchell VJ, Driscoll SP, Lawlor DW (1999) Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. Nature 401:914–917

Travaglia C, Reinoso H, Cohen AC, Luna C, Castillo C, Bottini R (2010) Exogenous ABA increases yield in field-grown wheat with a moderate water restriction. J Plant Growth Regul 29:366–374

Tricker PJ, ElHabti A, Schmidt J, Fleury D (2018) The physiological and genetic basis of combined drought and heat tolerance in wheat. J Exp Bot 69(13):3195–3210

Tuberosa R, Sanguineti MC, Landi P, Giuliani MM, Salvi S, Conti S (2002) Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two water regimes. Plant Mol Biol 48(5–6):697–712

Turner NC (1986) Adaptation to water deficits: a changing perspective. Funct Plant Biol 13(1):175–190

Uga Y, Sugimoto K, Ogawa S, Rane J, Ishitani M, Hara N, Kitomi Y, Inukai Y, Ono K, Kanno N, Inoue H, Takehisa H, Motoyama R, Nagamura Y, Wu J, Matsumoto T, Takai T, Okuno K, Yano M (2013) Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nat Genet 45(9):1097–1102

Venuprasad R, Lafitte HR, Atlin GN (2007) Response to direct selection for grain yield under drought stress in rice. Crop Sci 47:285–293

Vilela B, Nájar E, Lumbreras V, Leung J, Pagès M (2015) Casein kinase 2 negatively regulates abscisic acid-activated SnRK2s in the core abscisic acid-signaling module. Mol Plant 8:709–721

Vysotskaya LB, Kudoyarova GR, Veselov S, Jones HG (2003) Unusual stomatal behaviour on partial root excision in wheat seedlings. Plant Cell Environ 27:69–77

Vysotskaya LB, Arkhipova TN, Timergalina LN, Dedov AV, Veselov SY, Kudoyarova GR (2004) Effect of partial root excision on transpiration, root hydraulic conductance and leaf growth in wheat seedlings. Plant Physiol Biochem 42:251–255

Waisel Y, Eshel A (2002) Functional diversity of various constituents of a single root system. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half, vol 2002, 3rd edn. Marcel Dekker, New York, pp 157–174

Wang W, Vinocur B, Altman A (2003) Plant response to drought, salinity and extreme temperatures: toward genetic engineering for stress tolerance. Planta 218:1–14

Wang Y, Ying J, Kuzma M, Chalifoux M, Sample A, McArthur C, Uchacz T, Sarvas C, Wan J, Tennis DT, McCourt P, Huang Y (2005) Molecular tailoring of farnesylation for plant drought tolerance and yield protection. Plant J 43:413–424

Wang C, Yang A, Yin H, Zhang J (2008) Influence of water stress on endogenous hormone contents and cell damage of maize seedlings. J Integr Plant Biol 50:427–434

Wasson AP, Richards RA, Chatrath R, Misra SC, Sai Prasad SV, Rebetzke GJ, Kirkegaard JA, Christopher J, Watt M (2012) Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. J Exp Bot 63(9):3485–3498

Werner C, Ryel RJ, Correira O, Beyschlag W (2001) Effects of photoinhibition on whole-plant carbon gain assessed with a photosynthesis model. Plant Cell Environ 24:27–40

Wilkinson S, Davies WJ (2010) Drought, ozone, ABA and ethylene: new insights from cell to plant to community. Plant Cell Environ 33(4):510–525

Witcombe JR, Hollington PA, Howarth CJ, Reader S, Steele KA (2007) Breeding for abiotic stresses for sustainable agriculture. Philos Trans R Soc B 363(1492):703–716

Xu Z, Zhou G (2008) Responses of leaf stomatal density to water status and its relationship with photosynthesis in a grass. J Exp Bot 59(12):3317–3325

Xu Y, This D, Pausch R, Vonhof W, Coburn J, Comstock J, McCouch S (2009) Leaf-level water use efficiency determined by carbon discrimination in rice seedlings: genetic variation associated with population structure and QTL mapping. Theor Appl Genet 118:1065–1081

Xu ZY, Lee KH, Dong T, Jeong JC, Jin JB, Kanno Y (2012) A vacuolar beta-glucosidase homolog that possesses glucose-conjugated abscisic acid hydrolyzing activity plays an important role in osmotic stress responses in *Arabidopsis*. Plant Cell 24:2184–2199

Xu Z, Shimizu H, Ito S, Yagasaki Y, Zou C, Zhou G, Zheng Y (2014) Effects of elevated CO_2, warming and precipitation change on plant growth, photosynthesis and peroxidation in dominant species from North China grassland. Planta 239(2):421–435

Xue GP, Way HM, Richardson T, Drenth J, Joyce PA, Mcintyre CL (2011) Over-expression of TaNAC69 leads to enhanced transcript levels of stress up-regulated genes and dehydration tolerance in bread wheat. Mol Plant 4:697–712

Yamance K, Hayakawa K, Kawasaki M (2003) Bundle sheath chloroplasts of rice are more sensitive to drought stress than mesophyll chloroplasts. J Plant Physiol 160:1319–1327

Yang J, Zhang J, Wang Z, Liu L, Zhu Q (2003) Post-anthesis water deficits enhance grain filling in two-line hybrid rice. Crop Sci 43:2099–2108

Yang J, Zhang J, Wang Z, Xu G, Zhu Q (2004) Activities of key enzymes in sucrose-to-starch conversion in wheat grains subjected to water deficit during grain filling. Plant Physiol 135:1621–1629

Yang PM, Huang QC, Qin GY, Zhao SP, Zhou JG (2014) Different drought-stress responses in photosynthesis and reactive oxygen metabolism between autotetraploid and diploid rice. Photosynthetica 52(2):193–202

Ye H, Roorkiwal M, Valliyodan B, Zhou L, Chen P, Varshney RK, Nguyen HT (2018) Genetic diversity of root system architecture in response to drought stress in grain legumes. J Exp Bot 69(13):3267–3277

Yin X, Struik PC, Kropff MJ (2004) Role of crop physiology in predicting gene-to-phenotype relationships. Trends Plant Sci 9(9):426–432

Yordanov I, Tsonev T, Velikova V, Georgieva K, Ivanov P, Tsenov N, Petrova T (2001) Changes in CO_2 assimilation, transpiration and stomatal resistance of different wheat cultivars experiencing drought under field conditions. J Plant Physiol 27(3–4):20–33

Yuo T, Toyota M, Ichii M, Taketa S (2009) Molecular cloning of a root hairless gene rth1 in rice. Breed Sci 59(1):13–20

Zhan A, Schneider H, Lynch J (2015) Reduced lateral root branching density improves drought tolerance in maize. Plant Physiol 168:1603–1615. https://doi.org/10.1104/pp.15.00187

Zhang ZB, Xu P (2002) Review on QTL study of wheat traits. Dev Res Technol World 1:52–58

Zhang Y, Tan J, Guo Z, Lu S, He S, Shu W (2009) Increased abscisic acid levels in transgenic tobacco over-expressing 9cis-epoxycarotenoid dioxygenase influence water and NO production and antioxidant defences. Plant Cell Environ 32:509–519

Zhang H, Mao X, Wang C, Jing R (2010) Over-expression of a common wheat gene TaSnRK2.8 enhances tolerance to drought, salt and low temperature in *Arabidopsis*. PLoS One 5(12):16041

Zhang L, Gao M, Hu J, Zhang X, Wang K, Ashraf M (2012) Modulation role of abscisic acid (ABA) on growth, water relations and Glycine betaine metabolism in two maize (*Zea mays* L.) cultivars under drought stress. Int J Mol Sci 13:3189–3202

Zheng H-g, Chandra Babu R Md, Pathan MS, Ali L, Huang N, Courtois B, Nguyen HT (2000) Quantitative trait loci for root-penetration ability and root thickness in rice: comparison of genetic backgrounds. Genome 43(1):53–61

Zheng BS, Yang L, Zhang WP, Mao CZ, Wu YR, Yi KK, Liu FY, Wu P (2003) Mapping QTLs and candidate genes for rice root traits under different water-supply conditions and comparative analysis across three populations. Theor Appl Genet 107(8):1505–1515

Zhao Y, Cheng SF, Song YL, Huang YL, Zhou SL, Liu XY (2015) The interaction between rice ERF3 and WOX11 promotes crown root development by regulating gene expression involved in cytokinin signaling. Plant Cell 27(9):2469–2483

Zhao J, Xue Q, Kirk EJ, Hoe X, Hao B, Thomas HM, Xu W, Steven RE, Susan AO, David KB (2018) Shoot and root traits in drought tolerant maize (*Zea mays* L.) hybrids. J Integr Agric 17:60345–60347

Zhou YH, Jianhua ML, Zhang YD (2007) Inhibition of photosynthesis and energy dissipation induced by water and high light stresses in rice. J Exp Bot 58(5):1207–1217

Zhou L, Zeng Y, Zheng W, Tang B, Yang S, Zhang H et al (2010) Fine mapping a QTL qCTB7 for cold tolerance at the booting stage on rice chromosome 7 using a near-isogenic line. Theor Appl Genet 121(5):895–905

Zhu J-K (2002) S D S S T P. Annu Rev Plant Biol 53(1):247–273

Zhu J, Jeong JC, Zhu Y, Sokolchik I, Miyazaki S, Zhu JK (2008) Involvement of *Arabidopsis* HOS15 in histone deacetylation and cold tolerance. Proc Natl Acad Sci U S A 105:4945

Chapter 9
Strategies for Drought Tolerance in Xerophytes

Hanan Ahmed Hashem and Alsafa Hassan Mohamed

Contents

Abstracts Almost 35% of the Earth's land surface is covered by desert ecosystems. Areas that suffer from water scarcity are expected to increase owing to global climate changes. Water deficiency has become a worldwide threat due to its lethal effect on plant growth, development, and reproduction which foreshadows a food problem and enormous economic losses. Xerophytes, drought-tolerant plants, are able to grow and live under these harsh conditions. Although xerophytic plants are not closely related taxa, they all have similar forms, structures and shape to survive in such a xeric habitat. Xerophytes and their different mechanisms of adaptation to arid region have become of an international focus nowadays. This chapter discusses frontier knowledge about morphological, anatomical, and physiological adaptations and strategies of survival enabling xerophytes to develop and complete their life cycles in arid and semiarid regions. In addition, a special interest is given to the transcriptomic analysis of xerophytes to reveal the molecular basis for their drought tolerance.

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Finally, we provide an overview on the importance of xerophytes as a treasure of genetic resources for genetic enhancement of stress resistance of important forage and crop species in areas of arid climate.

Keywords Anatomical adaptation · Carbohydrates · Morphological adaptation · Osmotic adjustment · Photosynthesis

9.1 Introduction

Deserts represent one of the harshest ecosystems on earth, combining drought and extreme temperatures. In order to endure these environmental conditions and to get the supreme benefit of the nutrients and other supply within, these plants progress certain morphological, anatomical, physiological, and reproductive strategies. The strategies that exist by the plants under their habitat conditions is known as adaptation. Drought adaptation in plants takes place through four main strategies: drought avoidance, tolerance, escape, and recovery (Fang and Xiong 2015). During (1979) stated that drought tolerance is the ability of the plant to endure and remain active despite a lack of water in the environment. Proctor (2000) gives a more physiological definition which considers plants that can tolerate drought to be capable of maintaining a relatively normal metabolism at lower cell volumes and water presence while tolerating increased ionic concentrations in the cytoplasm and external environment. This takes place through osmotic adjustment, improved antioxidative capacity, and physical desiccation tolerance of the organ (Yoshimura et al. 2008) through regulations of thousands of genes and series of metabolic pathways to diminish or reform the resulting stress damage (Passioura 1997).

Drought avoidance is the ability of plants to stop the occurrence of desiccation itself or to go into a dormant stage during periods of scarce water; it is often found in dormant-able plants, in which metabolic activity imperceptibly slows down; simultaneously, this plant stage will pertain its ability to gain carbon and develop. Drought avoidance is the capacity of a plant to maintain high plant water potential during water shortage through adaptive traits such as minimization of water loss (water savers) and optimization of water uptake (water spenders) (Basu et al. 2016). This is achieved by attuning specific morphological constructs or growth rate to reduce radiation absorption, transpiration, transpiration area, etc., to deter the deleterious effects caused by drought stress (Luo 2010; Basu et al. 2016).

Drought escape is the natural or artificial adjustment of plants' life cycle, growth period or planting time of plants to align the growing season to be different from a fixed local seasonal or climatic drought (Manavalan et al. 2009). Farmers usually plant crops with shorter life cycles, thus avoiding the seasonal drought stress in agricultural production as they complete their life cycle before the drought.

Drought recovery is a plant's capability to continue growing and gain yield (for crops) following exposure to extreme drought stress that causes a complete loss of turgor pressure and leaf dehydration (Luo 2010).

Drought resistance of plants is quite complex; plants often converge different mechanisms to confer drought resistance at different developmental stages.

Considering resistance to water deficit, plants can be classified into three types: xerophytes (chiefly in arid areas, tolerate to 5% RH (relative humidity) without injury), mesophytes (usually in semiarid and sub-humid areas, tolerate to 50% RH without injury), and hydrophytes (mainly existing in environments with enough moisture or water and tolerate to 90% RH without injury (Warming et al. 1909; Larcher 1983). Studying adaptation strategies in xerophytes, as a model system for drought/strong light stress tolerance, had received a lot of researchers' attention. Recently, in par with the exponential development of modern biology theories and technology (such as molecular genomics, genetics, proteomics, and metabolomics), researches had uncovered many of xerophytic strategies to cope with drought stress. Basic knowledge as well as the recent findings regarding xerophytic plants' special features that enable them to survive in almost lifeless environments will be presented in this chapter.

9.2 Types of Xeric Habitats on the Earth

9.2.1 Physically Dry Habitats

Limited water retaining capacity of the soil and dry climate, e.g., rock surface, desert, wasteland, etc.

9.2.2 Physiologically Dry Habitats

Excess amount of water is present, but it is not easily absorbed by the plants. These habitats might be with high salty water or high acidity or the water either very hot or cold.

9.2.3 Physically and Physiologically Dry Habitats

Mist of water, plant can't absorb water directly from the atmosphere, e.g., mountain slopes

9.3 Xerophytes: Definition, Types, and Classification

9.3.1 Definition of Xerophytes

A xerophyte is derived from the Greek words xero, which means dry, and phyte, which means plant; it is a plant capable of living in an environment with limited water, e.g., deserts and succulent plants, where little rainwater is the usual phenomena. However, limited xerophytes may be found in moist habitats, e.g., tropical forests (Michael and Clive 2001).

9.3.2 Types of Xerophytic Plants

9.3.2.1 Xerophytic Plants Are Classified Into Several Categories

According to Their Morphology and Life Cycle Pattern

Ephemeral annuals: They are annuals and complete their life cycle within a very short period. Dubbed drought evaders, they may be dormant during water-deficit conditions. Examples of Papilionaceae are some inconspicuous compositae and members of families Zygophyllaceae and Boraginaceae. Succulent plants grow in habitats with less or no water. They store water when it is accessible. They have succulent and fleshy organs such as succulent with fleshy stem, e.g., *Euphorbia* and *Opuntia*, and succulent fleshy leaves also known as malacophyllous; these have no leaves or reduced to spines, e.g., *Aloe, Agave,* and *Bryophyllum*. In addition to non-succulent xerophytes, these plants are perennial and tolerate extensive shortage of water in the soil. These are known as true xerophytes or euxerophytes. They have several anatomical, morphological, and physiological features that allow them survival under dry conditions, e.g., *Calotropis, Ephedra,* and *Nerium* (Zeng et al. 2010).

According to Their Drought Resisting Power

Drought-escaping plants (Ephemeral) are short-lived xerophytic plants. They live in the form of seeds and fruits during dry phases. They have rigid and hardy seed coats and pericarps. The seeds germinate into new plants, becoming mature and finishing their life cycles within a few weeks under favorable conditions. So, the drought evaders or drought escapers remain safe at extreme conditions. Moreover, the drought-enduring plants generally do not possess any xerophytic adaptations. They are small in size and have the ability to tolerate scarcity conditions. Under unfavorable conditions, majority of them will wilt and die, and the tolerated and living one can undergo to the next generation and, finally, the drought-resistant plants that own special features in order to resist extreme conditions of temperature and drought.

Xerophytes grow on a variety of habitats and are classified based on their habitats into nine categories: oxylophytes (acid soils), lithophytes (on rocks), halophytes (on saline soils), chersophytes (wasteland), psammophytes (sand and gravels), eremophytes (deserts and steppes), psychrophytes (cold soils), psilophytes (savannah), and sclerophytes (forest and bushland) (Nikita 2019).

9.4 Adaptation Strategies of Xerophytes

Xerophytic plants develop special structural and physiological features when growing under undesirable environments targeted mostly as follows:

(a) Absorb as much water as possible from the surroundings
(b) Restore water in their organs for a very long time
(c) To minimize transpiration rate
(d) To prevent water consumption

The most significant adaptations of xerophytic plants can be summarized as the following:

1. Morphological (external) adaptations
2. Anatomical (internal) adaptations
3. Physiological adaptations

9.4.1 Morphological (External) Adaptations

Although the xerophytic plants are not closely related groups, they all exhibit same form, shapes, and structure to be able to survive in xeric habitat. There are two types of structure modifications in xerophytic plants: xeromorphic characters that are genetically fixed and inherited regardless of the growing conditions, whether in deserts or humid regions, and xeroplastic characters; those are encouraged by drought and are perpetually related to water-deficit conditions. They are not inherited. These characteristics may disappear from plants given that all conditions are desirable (Fig. 9.1a–c).

Numerous modifications occur externally owing to reduce of surface area and making water vapor-rich environment through reflective feature and cuticle in the xeric plants.

The external morphological adaptations are as follows.

Fig. 9.1 Morphological adaptation of xerophytic plants

9.4.1.1 Xerophytic Roots

Root systems of xerophytes are well developed with extensive branches as compared with the shoot system. When water is limited to the surface layer, a superficial root system will develop as in desert plants. Concerning with perennial xerophytes, roots grow deeply in order to invade the layers where water is accessible. To enable the roots to grip an adequate amount of water, root hairs are developed extensively beside the growing tips of the rootlets.

9.4.1.2 Xerophytic Stem

Xerophytic stem is either aerial or underground, usually hard and woody, and covered with wax or condensed hairs as in *Equisetum* and *Calotropis*, respectively. The wax is considered as the first line of protection for the aerial parts that protect xerophytes against biotic and abiotic factors. Xerophytic stems may be modified into:

Spiny stem (thorns) helps in reducing the transpiration surface. Moreover, the spines usually protect the plant against grazing animals, e.g., *Zilla spinosa*.

Succulent stem, the main stem, becomes globular and fleshy for storage of water and food, e.g., *Opuntia.*

In leafy stem, xerophytes are adjusted into leaf-like green, flattened, and fleshy structures. They are either phylloclades with several internodes, e.g. *Ruscus* and *Muehlenbeckia*, or cladodes with a single flattened green internode (needle-like), e.g., *Asparagus*. Phylloclades or cladodes are photosynthetic, and they are developed on plants which do not usually have green foliage leaves and replaced with brown scales.

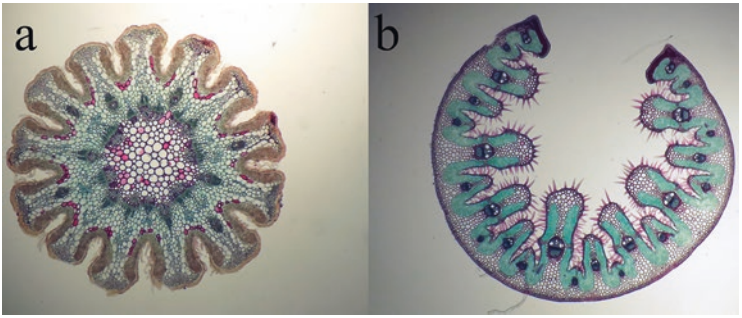

Fig. 9.2 Anatomical adaptation (**a**) xerophytic stem (**b**) xerophytic leaf

9.4.1.3 Xerophytic Leaves

Xerophytic leaves are greatly caducous (drop early) and scaly as in *Casuarina*, *Ruscus*, and *Asparagus*. Most xerophytes have reduced leaves covered with thick cuticle and dense coating of silica or wax and might be reduced to spines as in *Ulex*. While evergreen xerophytes have needle-shaped leaves, e.g., *Pinus*, and fleshy or storage leaves (succulents). Plants with succulent leaves mostly have reduced stems, e.g., *Aloe and Mesembryanthemum* and several members of family Chenopodiaceae. Sometimes the leaves of xerophytic plants may be covered with white curly hairs which protect the stomatal guard cells that are known as trichophyllous, e.g., *Nerium* and *Calotropis procera*, another type of xerophytic leaves is rolling leaves; so, stomata are shut away from the outside for decreasing water loss, e.g., sun-dune grass.

9.4.2 Anatomical (Internal) Adaptations

All anatomical modifications are developed for water reduction in the xeric plants (Fig. 9.2a–b).

9.4.2.1 Cuticle

Heavy wax deposition on the surface of the epidermis. The smooth surface of the cuticle reflects the light rays (has the highest ultraviolet light (UV) reflectivity) and bar access from the depths of the plant tissues, therefore preventing substantial water loss (Mulroy 1979); the cuticle's low water permeability is considered as one of the most vital factors in ensuring the survival of the plant (Mauseth 2006).

9.4.2.2 Epidermis

It is single layered or may have multiple epidermis with small and compact cells.

In stems the epidermis is radially elongated with deposition of wax, tannin, resin, and cellulose to reflect light which minimizes water evaporation from the surface of plant while in certain leaves of grasses has specialized epidermis to enable them to roll. These specialized cells of epidermis are known as bulliform cells with thin walled and enlarged usually evident in the depressions become more swollen than those seen in the ridges. During dry periods, these specific motor cells ease the leaves rolling by becoming flaccid while in moist conditions regain their usual turgidity which causes leaf unrolling.

9.4.2.3 Hairs

The hairs shield the stomata and prevent exaggerated loss of water. The stem and leaf surfaces of xeric plant develop ridges and furrows or pits; the latter consider the sites of stomata. Hairs present in these pits to guard the stomata from direct wind impact.

9.4.2.4 Stomata

In xerophytes, reduction of water loss is an important challenge. The sunken type is the common and found in the furrows or pits. In the rolling leaves, stomata are found on the upper surface and protected from the direct wind decreasing the transpiration rate in xerophytic grasses (Jordaan and Kruger 1998). In dorsiventral leaves, stomata are usually present on the lower surface.

9.4.2.5 Hypodermis

One or several layers of thick-walled compacted cells and sometimes be filled with tannin and mucilage.

9.4.2.6 Ground Tissue

The mechanical tissues are well-developed and represented by sclerenchyma in the stem and the metamorphosed stem as the photosynthetic organ represented by chlorenchyma of cortex as the leaves are either withered or fall in the early season. Ground tissues in succulent stems and leaves are filled with thin-walled parenchymatous cells storing an extreme amount of mucilage, water, and latex which make these organs swollen and fleshy; mesophyll of the leaves is compact with no intercellular spaces. Palisade tissue develops in several layers. Spongy parenchyma develops broadly to store water especially in succulent leaves.

9.4.2.7 Conducting Tissues

Phloem and xylem are fully developed in the xerophytic body (numerous vascular bundles) in order to have easy access to water. Xerophytes have a vascular system composed of phloem and xylem tissues. Xylem tissues help in transpiration, since the woody pipelines pull the water upward to the stomata and help the water move through the plant and act as a cooling mechanism in hot temperatures. The phloem tissues haul minerals and water to every part of the plant via their sieve-like system. If not for the phloem, areas of the plant would be deprived from water and proper minerals crucial for the plant's survival (Talia 2013).

9.4.3 Physiological Mechanisms for Adaptation

In drought avoidance/tolerance, complex molecular networks are involved. At the initial stage of water deficit, plants usually are still capable of absorbing water from underground with efficiency through the root system, slightly close stomata to diminish water loss from transpiration, and adjust metabolism to mirror the available carbon resource (Hu and Xiong 2014). As stress conditions raised, some osmolytes, e.g., prolines, spermines, soluble sugars, and betaine, accumulate in the plant cells to keep the cell turgor pressure stable (Seki et al. 2007). Numerous oxidation-protective enzymes, e.g., superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR), exhibit variations in activities; this is quite frequent in drought-stressed plants (Goswami et al. 2013). More general responses of plants to water-deficit stress include altered expressions of numerous genes, especially those related to stress signal transduction pathways and the transcription and regulation of thousands of functional proteins, collectively contributing to the molecular control of drought resistance. There are evidences that all plants, sensitive as well as tolerant, use similar, conserved mechanisms in response to environmental stress factors causing cellular dehydration, e.g., drought, salt, or high temperature stress (Hussain et al. 2018; Vinocur and Altman 2005). Physiological mechanisms for adaptation in xerophytes are summarized in (Fig. 9.3).

9.4.3.1 Photosynthesis

Photosynthesis is one of the most temperature-sensitive processes in plants (Yamori et al. 2014). High temperature in the arid regions has direct and indirect limiting effects on photosynthesis. The indirect effects include the effect on stomatal conductance, photorespiration, restricted CO_2 diffusion, as well as alteration in gas diffusion coefficient and Rubisco (ribulose bisphosphate carboxylase/oxygenase) specificity, whereas high temperature values directly affected the activity of several Calvin cycle enzymes, injured the thylakoids membrane, and damaged photosystem II (PSII) (Wise et al. 2004; Feller 2006; Kurek et al. 2007). In addition, several

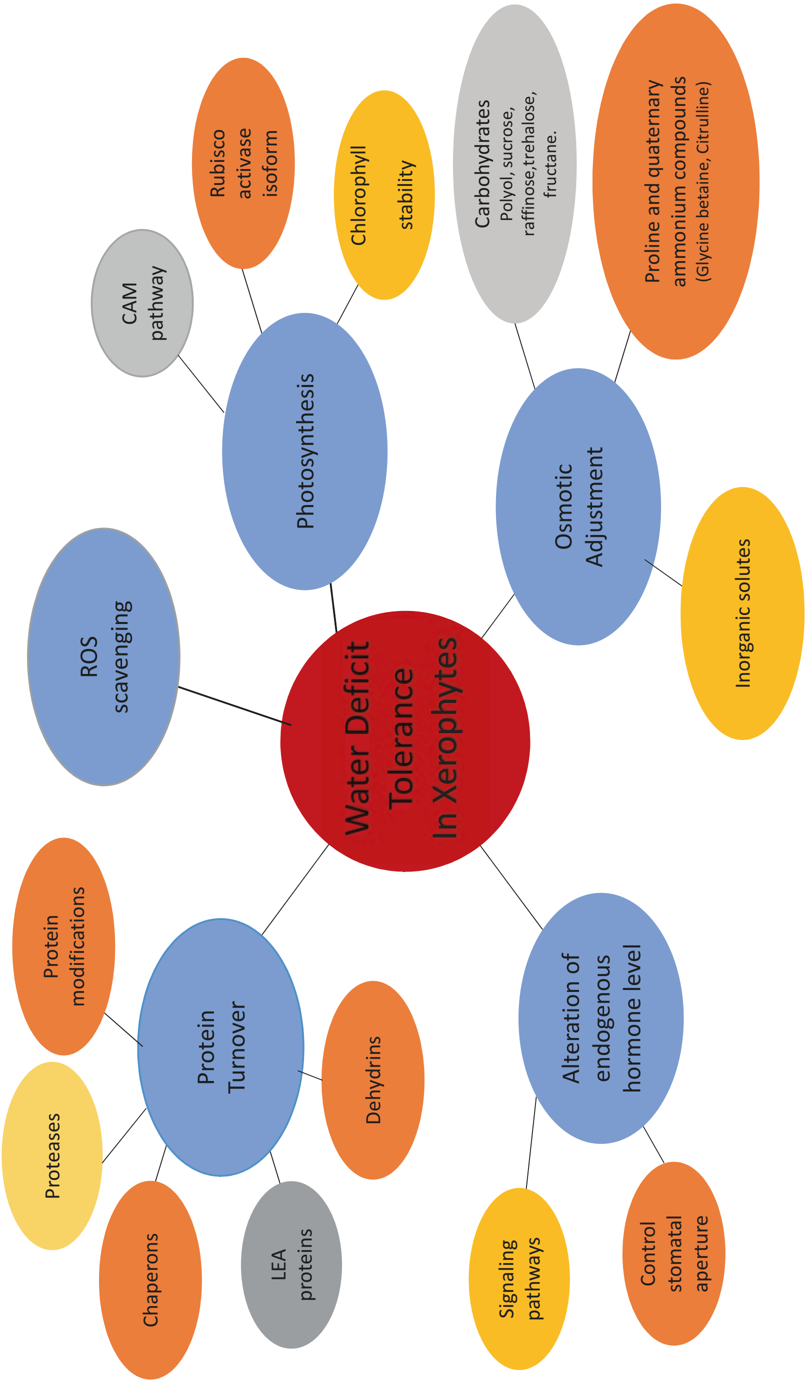

Fig. 9.3 Simplified schematic diagram summarizing physiological mechanisms for adaptation in xerophytes

studies proved that Rubisco activase (RCA) expression and endogenous levels are modulated by high temperature and hence constrain photosynthetic efficiency of plants at heat stress (Sánchez de Jiménez et al. 1995; Law and Crafts-Brandner 2001). Rubisco activase (RCA) is a nuclear-encoded, cytosol-synthesized chloroplast protein that modulates the activity of Rubisco by enhancing the ATP-dependent removal of inhibitory sugar phosphates from Rubisco active sites (Salvucci and Ogren 1996). This action of RCA is crucial for photosynthesis because it frees the active site of Rubisco for impulsive carbamylation by CO_2 (Salvucci and Ogren 1996; Spreitzer and Salvucci 2002).

Generally, plants have developed three photosynthetic mechanisms including C_3, C_4, and crassulacean acid metabolism (CAM) to assimilate atmospheric CO_2 (Fig. 9.4). Plants using C_4 and CAM photosynthetic pathways can adapt better to drought-prone climate (Ashraf and Harris 2013). C_3 plants open their stomata in daytime for CO_2 intake and fixation and close their stomata at night. This mechanism is obsolete when C_3 plants confront water limitation because it does not retain moisture under drought stress conditions. C_4 plants have developed a metabolic pump to concentrate CO_2 in the bundle sheath cells and perform CO_2 fixation in mesophyll cells and bundle sheath cells separately (Chaves et al. 2003). This specific mechanism allows higher water-use efficiency than that of C_3 plants and facilitates survival for C_4 plants in arid areas (Chaves et al. 2003). On the one hand, about 85% of plant species are C_3 plants such as oat, wheat, spinach, etc. On the other hand, examples of C_4 plants include maize, sugarcane, and sorghum. Crassulacean acid metabolism (CAM) is an essential desert adaptation method preventing water loss in plants growing in a hot environment. Since the cycle was first observed in the plants belonging to family Crassulaceae, it was named as Crassulacean acid metabolism. The core of this adaptation method is in the capability of opening the stomata at nighttime while being closed at daytime to hinder transpiration water loss during the day. In warmer climates, e.g., deserts, water loss is far less in C_4 plants compared to C_3 plants, offering a stronger selective advantage to C_4 plants. CAM is a second metabolic adaptation, in which water loss is minimized along with utilizing a C_4 pathway. CAM plants' stomata remain open during the night while remaining closed during the day. Rapid growth is stinted in CAM plants relative to C_3 plants, but in desert environments, where survival is relatively important compared to rapid growth, it pays in terms of reproduction to be a CAM plant. To recap, CAM plants are C_4 plants that retain their stomata stay opened at night and closed during the hottest part of the day, maximizing water storage. Most plants in deserts are CAM. Exceptionally, some desert C_3 plants have been found such as *Rhazya stricta*, *Calotropis procera*, and *C. gigantean*, and they have high photosynthesis yield with no diminishing in photosynthetic capacity detected up to leaf temperature of 48 °C (Tezara et al. 2011; Lawson et al. 2014). This indicated that these plants have peculiar physiological adaptations enabling them to thrive where most C_3 plants cannot grow.

Lawson et al. (2014) suggested that in *Rhazya stricta* Rubisco activase (RCA) has undergone a duplication event in which one copy lost the ability to generate an isoform that have the regulatory subunit as found in other species (Salvucci et al. 2003), whereas the other has the regulatory subunit. Wild watermelon

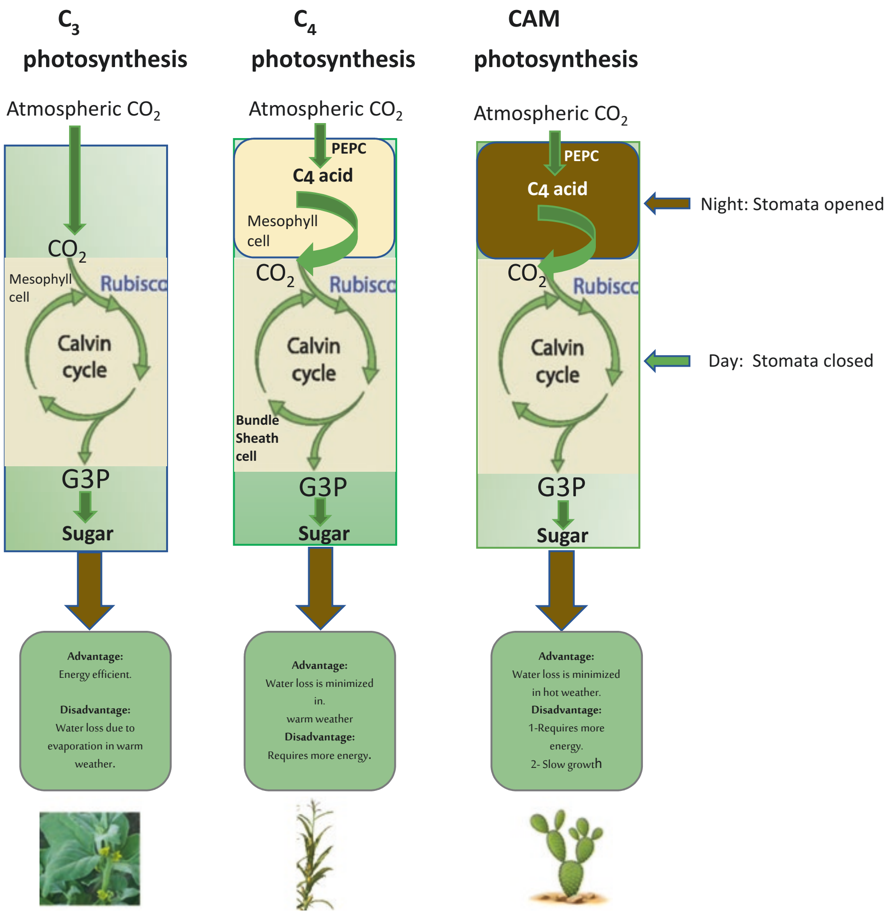

Fig. 9.4 C_3, C_4, and CAM photosynthesis. In C_3 plants, CO_2 enters the Calvin cycle by reacting with ribulose-1,5-bisphosphate to produce G3P, whereas in C_4 and CAM photosynthesis, C_4 acids aspartate and malate are the first stable, detectable intermediates of photosynthesis. The primary carboxylation is catalyzed not by Rubisco but by PEPC. The participating enzymes are found in one of the two cell types: PEPC is limited to mesophyll cells; the decarboxylases and the Calvin cycle enzymes are restricted to the bundle sheath cells. In CAM plants, at night, PEPC in the cytosol captures CO_2, and the produced C_4 acid is stored in the vacuole. During the day, the stored malate is translocated to the chloroplast and decarboxylated by NADP-malic enzyme; the released CO_2 is then fixed by Calvin cycle. *PEPC* phosphoenolpyruvate carboxylase, *Rubisco* ribulose bisphosphate carboxylase/oxygenase, *G3P* glyceraldehyde 3-phosphate

(*Citrullus lanatus* sp.) is another example of xerophyte plant that exhibits extraordinarily high drought tolerance, although it carries out C_3-type photosynthesis (Kawasaki et al. 2000). The photosynthetic apparatus of the plant stays intact under extended drought and high light intensities owing to drought tolerance mechanisms, mainly the production of a large number of drought-induced proteins (Yoshimura et al. 2008).

It is well known that the rate of photosynthesis is proportional to the chlorophyll content. The solar radiation absorbed by a leaf is largely a function of the foliar concentrations of photosynthetic pigments. Abundant sunlight and water scarcity in arid environments are specified for plants with reduced chlorophyll amount in the photosynthetic reaction center; the low concentrations of chlorophyll can directly diminish photosynthetic potential (Filella et al. 1995; Liu and Guan 2012). Several halo-xerophytes have low chlorophyll contents as an adaptive mechanism to limit solar radiation absorption, and this is compensated by increased chlorophyll stability against the prevailing stress conditions (Farghali and El-Aidarous 2014).

9.4.3.2 Osmoprotective and Osmotic Readjustment Strategies

Previous studies have revealed that xerophytes developed a structural modification of root architecture under drought stress to enhance water absorption from the soil and then switched (see Sect. 4.1.1.) their stress-resistant strategies sequentially from drought avoidance to drought tolerance through programmed induction of osmolytes and distinctive sets of defensive proteins (Yoshimura et al. 2008; Fang and Xiong 2015).

Osmolytes accumulation, also known as compatible solutes, is a powerful mechanism for maintaining water status in plants. Compatible solutes accumulated in the cytoplasm without obstructing with cellular metabolism even at elevated concentrations. They have not only a potential role in osmotic adjustment (Flowers et al. 1986; Glenn et al. 1999) but also they act as osmoprotectants by directly stabilizing proteins and membrane structures, during dehydration status, and by protecting the cell against oxidative stress as scavengers of reactive oxygen species (ROS) (Szabados and Savouré 2010). From a chemical point of view, osmolytes are diverse organic and inorganic substances including sugars such as trehalose and sucrose (Jouve et al. 2004), sugar alcohols (polyols) such as mannitol and sorbitol (Koyro 2006), some amino acids and quaternary ammonium compounds such as proline and glycine betaine (Boscaiu et al. 2009), and inorganic ions (Fang and Xiong 2015). Osmotic adjustment is one of the drought tolerance mechanisms exhibited by xerophytes.

Carbohydrates

Soluble carbohydrates, e.g., sugars and polyols, are some of the solutes that are of high compatibility for osmotic adjustment and osmoprotection. The role of carbohydrates in osmoregulation of xerophytes is the same as they do in a large number of mesophytes. There are over 100 known highly desiccation-tolerant species that are distributed among several plant orders (Gaff 1981); several plants such as *Craterostigma plantagineum* are known for massive reversible fluctuation of carbohydrates during periods of rehydration or desiccation. For example, the unusual sugar 2-octulose accumulates in developing leaves of well-hydrated plants, but it is rapidly converged into sucrose when desiccation period begins.

Gil et al. (2011) studied the variation of carbohydrates content in five halophytes growing in Mediterranean marsh to find the possible correlation between the type of carbohydrates accumulated and the plant. They found that in *Inula crithmoides*, the most abundant carbohydrates identified were the polyols *myo*inositol and glycerol. Besides its function in osmoregulation under cellular dehydration conditions, *myo*-inositol is a key component of several biochemical pathways in plants, including cell signaling and membrane biogenesis (Nelson et al. 1998), whereas glycerol is the main osmolyte in yeast and algae (Hohmann 2002; Cui et al. 2010). The closely related *Juncus acutus* and *J. maritimus* both accumulated high level of sucrose, while sorbitol was the major carbohydrate detected in *Plantago crassifolia*, which contained very low levels of the rest of sugars and polyols. Sorbitol is the osmolyte used specifically by plant of the whole Plantaginaceae family (Flowers et al. 2010). Sorbitol contents also correlated positively with high temperature and evaporation. Glucose and fructose were proved to be the carbohydrates present at higher concentrations in *Sarcocornia fruticosa*, which is probably the most salt tolerant of the studied species.

Polyol

Accumulation of polyols, whether straight chain, e.g., sorbitol and mannitol (Bieleski 1982), or cyclic polyols, e.g., *myo*inositol and its methylated derivatives (Loewus and Dicklnson 1982), is correlated with drought tolerance. They have two main functions under harsh condition: they act as osmolytes and protect cellular structures as low-molecular-weight chaperones (possibly by scavenging active oxygen), thus limiting injuries to macromolecular complexes, membranes, or processes such as photosynthesis. In addition, polyols are nonreducing sugar that may also store additional carbon under abiotic stress conditions (Paul and Cockburn 1989). Inositol is necessary for membrane biosynthesis which accounts for signaling functions in all organisms. It is also fueling the biosynthesis of other compounds that have correlation with stress tolerance such as non-cellulosic cell wall components, e.g., gums, mucilage, cell wall-located carbohydrates, and carbohydrates in glycoproteins (Loewus and Loewus 1983). Mannitol forms a substantial percentage of all assimilated CO_2 (Bieleski 1982) and serves as compatible solutes, low-molecular-weight chaperones as well as ROS scavenger (Smirnoff and Cumbes 1989).

Raffinose

Raffinose family oligosaccharides (RFOs), e.g., stachyose, raffinose, and verbascose, are soluble galactosyl-sucrose carbohydrates. Previous studies have concluded that the expression of enzymes responsible for the production of galactinol and RFOs and their intracellular accumulation in plant cells are associated with plant response to drought stress (Kaplan et al. 2007; Peters et al. 2007). Nishizawa et al. (2008) suggested that under water-deficit condition, raffinose and galactinol may act as osmoprotectants, scavenge ROS, stabilize cellular membranes, and protect cellular metabolism, especially photosynthesis, from oxidative damage associated with drought. Raffinose and related oligosaccharides are considered as important molecules of the resistance mechanism in xerophytes (Sanchez et al. 2008).

Amino Acids and Quaternary Ammonium Compounds

Amino acids, e.g., proline and quaternary ammonium compounds (QAC) such as alanine betaine, glycine betaine, and choline O-sulfate osmolytes, are zwitterions at physiological pH. Though ionic, they harbor no net charge. Their osmoprotective role in cytosol may be correlated to their peculiar chemistry (Bohnert and Jensen 1996).

Proline

Proline biosynthesis occurs by two pathways, glutamate and ornithine pathways. A positive correlation was proved between plant stress and proline accumulation. Proline plays an extremely beneficial role in plant grown under stressful conditions. Proline acts at least four major roles during stress; it acts as an excellent osmolyte, contributes majorly as an antioxidative defense molecule, and functions as molecular chaperon stabilizing protein structure and as a signaling molecule (Hayat et al. 2012). It is well known that proline safeguards plants from stress by stabilizing the mitochondrial electron transport complex II (Hamilton and Heckathorn 2001), membrane proteins (Holmström et al. 2000), and enzymes, e.g., Rubisco (Allen et al. 1997).

Proline accumulation is known to happen during water deficit. The proline biosynthetic pathway is activated, and its catabolism is halted during dehydration, whereas rehydration regulates the other opposite direction (Deuschle et al. 2001; Rentsch et al. 1996; Yoshiba et al. 1995). Unlike carbohydrates, proline content varies among species, but these differences are obviously not related to their taxonomic classification: xerophytes species from the same family or even the same genus show significantly different levels of endogenous proline (Boscaiu et al. 2009). In general, the species which accumulate more proline as a drought tolerance mechanism (e.g., *Rosmarinus officinalis* and *Stipa tenacissima*) accumulate low levels of sugars, whereas those which have high levels of sugars (e.g., *Thymus vulgaris* and *Dorycnium pentaphyllum*) have low amounts of proline indicating that any particular species normally accumulates only one type of osmolyte in significant amounts (Boscaiu et al. 2009).

Glycine Betaine

Glycine betaine (*N*, *N*, *N*-trimethylglycine) is one of the most QACs that has been extensively studied. The biosynthesis of glycine betaine (GB) happens via a two-step oxidation from choline and betaine aldehyde which are catalyzed by choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH) (Cromwell and Rennie 1953; Xu et al. 2018). Glycine betaine levels in plants vary among organs and species and increase in response to abiotic stress (Zhang et al. 2012). Glycine betaine enhances plant tolerance to abiotic stress mainly by membrane stabilization and protection of proteins and photosystem II and mitigate oxidative damage by induction of ROS-scavenging enzyme genes (Chen and Murata 2011). Occurrence of QACs, especially GB in plant community coexisting in xerophytic environment, suggests their ecophysiological role in the tolerance of plant species to abiotic stress (Piazza et al. 2014). Previous studies showed that GB accumulators, e.g., *Larrea and Baccharis* and *Grindelia* species, can develop and endure under extreme abiotic stress (Zavala and Ravetta 2002; Medeiros and Pockmand 2011). In addition, Piazza et al. (2014) suggested that GB presence in all the studied species of *Flourensia* (typically grow in xeric environment) may indicate its role in the genus tolerance to stress. Generally, the fact that QACs were present in 50% of the dominant native xerophytes studied suggests that QACs accumulation may represent a community-level adaptation in xeric environments.

Inorganic Solutes

The ability of plant to accumulate high concentrations of inorganic ions to maintain the water potential of the cell more negative than the surrounding medium is a crucial factor to determine the plant's ability to survive under water-deficit condition (Khidr et al. 2017). This adaptation was detected in many species of plants and is well known to play a role in fending against dehydration (Blum 2017). Plants grown in semiarid and arid areas have increased Cl^- concentration (Khidr et al. 2017). In addition, several xerophytes were found to have increased SO_4^{2-} concentrations during dry season. Sulfur is incorporated in a wide range of biomolecules such as cofactors and peptides (Nocito et al. 2007). Sodium accumulation in xerophytes such as *Zygophyllum xanthoxylum* plays an important ecophysiological role to enable xerophytes to adapt to extremely drought habitat. In this respect, Xi et al. (2018) demonstrated that *Z. xanthoxylum* exhibited a maximum water storage and uptake minimum water loss by accumulating Na^+ in its leaves by reducing leaf osmotic potential, downregulating transpiration, and enhancing leaf succulence. Inorganic solutes, especially Na^+, are also found to be important cellular osmoregulators in *Suaeda fruticosa* (halophyte) and *Artemisia judaica* (xerophyte). Potassium was also identified as a primary osmoticum in xerophytic plant *A. sphaerocephala* with 10.5-fold higher than proline concentration (Aba Alkhail and Moftah 2011). Potassium is a major plant macronutrient that plays important roles in stomatal behavior, enzyme activity, and drought resistance (Wang et al. 2004a).

9.4.3.3 Hormonal Regulation

Modulation of endogenous phytohormone levels is one of the most important physiological modifications to counter the harmful effect of drought. The main phytohormones include abscisic acid (ABA), gibberellic acids (GAs), cytokinins (CKs), auxins (Aux), ethylene (ET), jasmonic acid (JAs), nitric oxide (NO), salicylic acid (SA), brassinosteroids (BRs), and strigolactones (SLs). Many studies indicated that plant hormone ABA modulates plant tolerance to drought stress (Liu et al. 2003; Xiong and Zhu 2003). Accumulation of ABA in the leaf can instigate stomatal closure, hence diminishing transpiration rate, and fend against dehydration of leaf tissues and decrease leaf expansion during the early stages of soil drying (Ron et al. 2004). Several studies showed that the ABA concentration increases in guard cells when humidity is low; such increase resulted from induction of ABA biosynthesis and/or inhibition of ABA breakdown (Huang et al. 2008; Waadt et al. 2014). Additionally, ABA was found to stimulate proline biosynthesis and accumulation by increasing the activity of pyrroline-5-carboxylate reductase (P5CR) (Verslues and Bray 2006). However, the correlation between ABA endogenous level and stress tolerance is not always positive. Remarkably, the xerophytic species *Papostypa speciosa* had low ABA levels (Llanes et al. 2016). Stomatal closure has also been connected to the endogenous level of JA and its precursor (OPDA, 12-oxo-phytodienoic acid). It was suggested that plants with enhanced drought tolerance exhibited higher OPDA level which might act together with ABA to reduce stomatal aperture (Savchenko et al. 2014).

9.4.3.4 Proteome Response

Proteomic studies provide essential information about proteins in a specific sample, to explore more components of biochemical pathways and to highlight posttranslational modification (Yang et al. 2015). Although physiological and anatomical responses of xerophytes have been extensively studied, there are still little information available regarding the water-deficit-induced proteome response in these plants. Comparative proteomic analysis provided a detailed picture of functional proteins induced in xerophytes in response to drought. Late embryogenesis-abundant (LEA) protein family, heat-shock proteins (HSPs), antioxidant proteins, and ABA biosynthesis-related protein are among the most accumulated proteins in xerophytes under harsh environment.

Heat-Shock Proteins (HSPs)

Heat-shock proteins (HSPs) are ubiquitous proteins present in animal and plant cells. They originally were attributed to respond to heat shock but are now known to be a response to a wide variety of stresses (Vierling 1991). In animals and plants, five major families of HSPs are recognized as molecular chaperones according to their rough molecular weights, e.g., HSP90, HSP100, HSP60, HSP70, and small HSP (sHSP) (Gupta et al. 2010). It is well established that HSPs are responsible for protein stabilization, assist protein refolding, prevent protein aggregation, and maintain organellar precursor proteins under stress conditions (Huttner and Strasser 2012; Wang et al. 2004b). Most HSPs have critically vital chaperone functions such as three-dimensional folding of newly synthesized proteins and/or proteins damaged by stress within cells (Whitley et al. 1999). Yoshimura et al. (2008) studied the programmed proteome response of drought tolerance in wild watermelon (*Citrullus lanatus*) which shows exceptionally high drought resistance. They found that HSP70 and sHSPs are upregulated, suggesting their vital role in coping with water deficits. Akashi et al. (2011) found that 15 out of the 23 upregulated proteins (65% of the upregulated proteins) in xerophytic plant *Citrullus lanatus* were HSPs. Upregulation of many HSPs in xerophytes grown under drought condition suggests that these proteins are important for acclimation to drought and protecting cellular proteins in risk of deleterious denaturation in the presence of strong light in arid environment (Akashi et al. 2011).

Late Embryogenesis-Abundant (LEA) Proteins

Late embryogenesis-abundant (LEA) are divided into at least eight subfamilies: LEA (1–6), dehydrin, and seed maturation protein (SMP) (Finn et al. 2014). LEA proteins have been shown with crucial role in osmotic adjustment in plant cells. They are hydrophilic proteins due to high amounts of charged amino acid residue, with very high thermal stability, and they function as biological macromolecules' protector, limiting collisions between enzymes; redirect intercellular water allocation; bind to inorganic ions to prevent damage caused by drought stress; prevent excessive hydration of plant tissues; and regulate the expression of other gene via binding to nucleic acids (Hanin et al. 2011; Shao et al. 2005). Studying *Cleistogenes songorica*, a xerophyte C_4 desert plant, Muvunyi et al. (2018) identified 44 putative *LEA* genes that could have functional importance during low water availability and may be used to enhance crop resistance to abiotic stress. Expression patterns of stress-responsive proteins in *Stipa purpurea*, a highly tolerant plant to drought and cold, revealed that dehydrin was heavily expressed in leaves when relative water content decrease (Yang et al. 2015). These results indicated that dehydrin accumulation may improve drought resistance by protecting cells against dehydration.

9.4.3.5 Reactive Oxygen Species Scavenging

Reactive oxygen species (ROS) function as signaling molecules regulating many biological processes in plant (Ron et al. 2004). However, accumulation of excessive amounts of ROS can negatively affect plant cells because they halt metabolic processes and impair cellular components. To avoid oxidative damage, plants evolved a system of ROS-scavenging enzymes, e.g., ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), glutathione reductase (GR), and peroxiredoxin, to avoid damage of oxidative nature, whereas ascorbic acid, carotenoids, glutathione, and flavonoids act as nonenzymatic antioxidants (Schafer et al. 2002). Together, they form a highly efficient system to remove ROS and guard plant cells. In fact, ROS-scavenging aptitude of plant antioxidant system is one of the most important mechanisms to tolerate harsh environmental conditions. Previous studies reported that antioxidant enzymes' (SOD, CAT, POX, and GR) levels are higher in drought-tolerant plants species providing protection against oxidative stress. In this respect, Ozkur et al. (2009) found that CAT, APX, and GR activities are induced by drought in *Capparis ovata*, a xerophyte. Moreover, regulation of SOD isoenzymes (Mn SOD, Cu/Zn SOD, and Fe SOD) is proved to be an adaptive mechanism to drought-induced oxidative stress in many xerophytic plants such as *Gypsophila aucheri* (Esen et al. 2012).

9.5 Molecular Basis of Drought Resistance in Xerophytic Plants

Drought stress adaptation strategies contain ample pools of genes of stress tolerance. Discovering the genetic basis of how xerophytic plants adapt to water deficit is one of the most confronting tasks. Understanding the molecular mechanisms underlaying plants' resistance to environmental stresses is imperative for genetic engineering approaches to enhance crop performance under stress. The adaptive response of xerophytes to water deficit is a sophisticated process involving many genes and signaling pathways. The external water scarcity stimuli are perceived rapidly by sensors on the membrane, and then the signals are delivered through various signal transduction pathways; this results in the expression of drought-responsive genes that lead to physiological changes and drought adaptation (Zhu 2002). A number of secondary messengers (such as Ca^{2+}, ROS, phosphoglycerol, and ABA) and transcriptional factors play important roles in the signal transduction pathways (Xiong et al. 2002). The proteins produced from the expression of drought-induced genes are classified into three groups: (1) regulatory proteins involved in the signaling transduction pathway and transcriptional regulation mainly via phosphorylation and dephosphorylation (protein kinase, transcription factors, and protein phosphatase), (2) functional proteins that safeguard the membranes and other cellular constituents (such as LEA protein, HSPs, and antioxidant enzymes), and (3) transporter proteins that facilitate the transport of water and mineral ions across the cellular membranes (such as aquaporins) (Hirayama and Shinozaki 2010).

Shi et al. (2009) using cDNA-AFLP (amplified fragment length polymorphism) technique have identified 68 TDFs (transcript-derived fragments) as drought responsive in xerophytic desert shrub *Haloxylon ammodendron*. Fifty-seven percent of TDFs was corresponding to proteins participate in signal transduction, transcriptional regulation, stress and defense response, transport, and photosynthesis.

Shi et al. (2013) identified at least 123 genes related to drought acclimation in extreme xerophyte *Reaumuria soongarica.* Most of these genes are correlated to ABA biosynthesis and catabolic and receptor compound, such as rate-limiting enzyme 9-cis epoxycarotenoid dioxygenase (NCED) in the biosynthesis pathway and protein phosphatase 2Cs (PP2Cs), a sensor for ABA signal.

9.6 Conclusion and Future Perspective

Understanding the unique mechanisms that empower drought tolerance in xerophytes is very useful due to its potential to pinpoint key genetic elements for crop enhancements and enhanced agricultural managements. It is now known that xerophytes are characterized by complex anatomical, biochemical, and molecular adaptive mechanisms to survive in an ecosystem with scarce water recourses. Accumulation of compatible solutes (organic and inorganic molecules), proteins (HSPs and LEA), ABA-mediated regulation of stomatal opening in addition to a network of antioxidant enzymes, and compounds to scavenge toxic ROS are the main drought responses exhibited by xerophytes. These responses play a vital role in alleviating the harmful impact of drought on vital cellular constituents to maintain normal growth and stable photosynthesis under such harsh environment. Integrating information obtained from metabolomic, proteomic, and transcriptomic analysis to assess the cross talk and fill in vacancies in the regulatory networks of xerophytes response to drought is one of the most challenging tasks for researches in the coming years and is a necessity for producing drought-resistant crops.

References

Aba Alkhail MS, Moftah AE (2011) Adaptation mechanisms of some desert plants grown in central region of Saudi Arabia. Inter Res J Agric Sci Soil Sci 1:462–470

Akashi K, Yoshida K, Kuwano M, Kajikawa M et al (2011) Dynamic changes in the leaf proteome of a C3 xerophyte, *Citrullus lanatus* (wild watermelon), in response to water deficit. Planta 233:947–960

Allen DJ, McKee IF, Farage PK, Baker NR (1997) Analysis of limitations to CO_2 assimilation on exposure of leaves of two *Brassica napus* cultivars to UV-B. Plant Cell Environ 20:633–640

Ashraf M, Harris P (2013) Photosynthesis under stressful environments: an overview. Photosynthetica 51:163–190

Basu S, Ramegowda V, Kumar A, Pereira A (2016) Plant adaptation to drought stress. F1000Res 5:F1000 Faculty Rev-1554. https://doi.org/10.12688/f1000research.7678.1

Bieleski RL (1982) Sugar alcohols. In: Loewusand FA, Tanner W (eds) Plant carbohydrates I encyclopedia of plant physiology, new series, vol 13A. Springer, Berlin, pp 158–192

Blum A (2017) Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. Plant Cell Environ 40:4–10. https://doi.org/10.1111/pce.12800

Bohnert HJ, Jensen RG (1996) Strategies for engineering water-stress tolerance in plants. Trends Biotechnol 14:89–97

Boscaiu M, Mora E, Fola O, Scridon S, LLinares J, Vicente O (2009) Osmolyte accumulation in xerophytes as a response to environmental stress. Bull UASVM Hort 66(1):96–102

Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought-from genes to the whole plant. Funct Plant Biol 30:239–264

Chen TTH, Murata N (2011) Glycine betaine protects plants against abiotic stress: mechanisms and biotechnological applications. Plant Cell Environ 34:1–20

Cromwell BT, Rennie SD (1953) The biosynthesis and metabolism of betaines in plants. The estimation and distribution of glycinebetaine (betaine) in *Beta vulgaris* L. and other plants. Biochem J 55:189–192

Cui L, Chai Y, Li J, Liu H, Zhang L, Xue L (2010) Identification of a glucose-6-phosphate isomerase involved in adaptation to salt stress of *Dunaliella salina*. J Appl Phycol 22:563–568

Deuschle K, Funck D, Hellmann H, Däschner K, Binder S, Frommer WB (2001) A nuclear gene encoding mitochondrial Delta-pyrroline-5-carboxylate dehydrogenase and its potential role in protection from proline toxicity. Plant J 27:345–356

During HJ (1979) Life strategies of bryophytes: a preliminary review. Lindbergia 5:2–18

Esen AH, Özgür R, Uzilday B, Tanyolac Ö, Dinc A (2012) The response of the xerophytic plant *Gypsophila aucheri* to salt and drought stresses: the role of the antioxidant defence system. Turk J Bot 36:697–706

Fang Y, Xiong L (2015) General mechanisms of drought response and their application in drought resistance improvement in plants. Cell Mol Life Sci 72:673–689

Farghali KA, El-Aidarous AA (2014) Thermostability of chlorophylls in some native species of xerophytes. IOSR J Agr Vet Sci 6:52–65

Feller U (2006) Stomatal opening at elevated temperature: an underestimated regulatory mechanism. General Appl Plant Physiol Special Issue:19–31. https://doi.org/10.7892/boris.53995

Filella I, Serrano L, Serra J, Peñuelas J (1995) Evaluating wheat nitrogen status with canopy reflectance indices and discriminant analysis. Crop Sci 35(5):1400–1405

Finn RD, Bateman A, Clements J, Coggill P, Eberhardt RY, Eddy SR, Heger A, Hetherington K, Holm L, Mistry J et al (2014) Pfam: the protein families database. Nucleic Acids Res 42:222–230

Flowers TJ, Hajibagheri MA, Clipson NJW (1986) Halophytes. Q Rev Biol 61:313–337

Flowers TJ, Galal HK, Bromham L (2010) Evolution of halophytes: multiple origins of salt tolerance in land plants. Funct Plant Biol 37:604–612

Gaff DF (1981) The biology of resurrection plants. In: Pate S, McComb AJ (eds) The biology of australian plants. University of Western Australia Press, Nedland, pp 114–116

Gil R, Lull C, Boscaiu M, Bautista I, Lidón A, Vicente O (2011) Soluble carbohydrates as osmolytes in several halophytes from a Mediterranean salt marsh. Not Bot Horti Agrobot Cluj Napoca 39:9–17

Glenn EP, Brown JJ, Blumwald E (1999) Salt tolerance and crop potential of halophytes. Crit Rev Plant Sci 18:227–255

Goswami A, Banerjee R, Raha S (2013) Drought resistance in rice seedlings conferred by seed priming: role of the anti-oxidant defense mechanisms. Protoplasma 250:1115–1129

Gupta SC, Sharma A, Mishra M, Mishra RK, Chowdhuri DK (2010) Heat shock proteins in toxicology: how close and how far? Life Sci 86:377–384

Hamilton EW 3rd, Heckathorn SA (2001) Mitochondrial adaptations to NaCl. Complex I is protected by anti-oxidants and small heat shock proteins, whereas complex II is protected by proline and betaine. Plant Physiol 126:1266–1274

Hanin M, Brini F, Ebel C, Toda Y, Takeda S, Masmoudi K (2011) Plant dehydrins and stress tolerance: versatile proteins for complex mechanisms. Plant Signal Behav 6:1503–1509

Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, Ahmad A (2012) Role of proline under changing environments: a review. Plant Signal Behav 7(11):1456–1466. https://doi.org/10.4161/psb.21949

Hirayama T, Shinozaki K (2010) Research on plant abiotic stress responses in the post-genome era: past, present and future. Plant J 61:1041–1052

Hohmann S (2002) Osmotic stress signaling and osmoadaptation in yeasts. Microbiol Mol Biol Rev 66:300–372

Holmström KO, Somersalo S, Mandal A, Palva TE, Welin B (2000) Improved tolerance to salinity and low temperature in transgenic tobacco producing glycine betaine. J Exp Bot 51:177–185

Hu H, Xiong L (2014) Genetic engineering and breeding of drought-resistant crops. Annu Rev Plant Biol 65:715–741

Huang D, Wu W, Abrams SR, Cutler AJ (2008) The relationship of drought-related gene expression in *Arabidopsis thaliana* to hormonal and environmental factors. J Exp Bot 11:2991–3007

Hussain HA, Hussain S, Khaliq A, Ashraf U, Anjum SA, Men S, Wang L (2018) Chilling and drought stresses in crop plants: implications, cross talk, and potential management opportunities. Front Plant Sci 9:393. https://doi.org/10.3389/fpls.2018.00393

Huttner S, Strasser R (2012) Endoplasmic reticulum-associated degradation of glycoproteins in plants. Front Plant Sci 3:67

Jordaan A, Kruger H (1998) Notes on the cuticular ultrastructure of six xerophytes from Southern Africa. S Afr J Bot 64(1):82–85

Jouve L, Hoffmann L, Hausman JF (2004) Polyamine, carbohydrate, and proline content changes during salt stress exposure of Aspen (*Populus tremula* L.): involvement of oxidation and osmoregulation metabolism. Plant Biol 6:74–80

Kaplan F, Kopka J, Sung DY, Zhao W, Popp M, Porat R, Guy CL (2007) Transcript and metabolite profiling during cold acclimation of *Arabidopsis* reveals an intricate relationship of cold-regulated gene expression with modifications in metabolite content. Plant J 50:967–981

Kawasaki S, Miyake C, Kohchi T, Fujii S, Uchida M, Yokota A (2000) Responses of wild watermelon to drought stress: accumulation of an ArgE homologue and citrulline in leaves during water deficits. Plant Cell Physiol 41:864–873

Khidr ZA, Ebad FA, El-Khawaga HA (2017) Osmoregulation and antimicrobial activity of two Egyptian true xerophytes; Launaea spinosa (Forssk.) and Leptadenia pyrotechinica (Forssk.). Egypt J Desert Res 67(2):327–345

Koyro HW (2006) Effect of salinity on growth, photosynthesis, water relations and solute composition of the potential cash crop halophyte *Plantago coronopus* L. Environ Exp Bot 56:136–146

Kurek I, Change TK, Bertain SM, Madrigal A, Liu L, Lassner MW, Zhu G (2007) Enhanced thermostability of Arabidopsis Rubisco activase improves photosynthesis and growth rates under moderate stress. Plant Cell 19:3230–3241

Larcher W (1983) Physiological plant ecology. Trans. by Biederman-Thorson MA. Springer, Berlin, 303pp

Law RD, Crafts-Brandner SJ (2001) High temperature stress increases the expression of wheat leaf ribulose-1,5-bisphosphate carboxylase/oxygenase activase protein. Arch Biochem Biophys 386:261–267

Lawson T, Davey PA, Yates SA, Bechtold Y, Baeshen M, Baeshen N, Mutwakil MZ, Sabir J, Baker NR, Mullineaux PM (2014) C_3 photosynthesis in the desert plant *Rhazya stricta* is fully functional at high temperatures and light intensities. New Phytol 201:862–873

Liu N, Guan L (2012) Linkages between woody plant proliferation dynamics and plant physiological traits in southwestern North America. J Plant Ecol 5:407–416

Liu F, Jensen CR, Andersen MN (2003) Hydraulic and chemical signals in the control of leaf expansion and stomatal conductance in soybean exposed to drought stress. Funct Plant Biol 30:65–73

Llanes A, Andrade A, Alemano S, Luna V (2016) Alterations of endogenous hormonal levels in plants under drought and salinity. Am J Plant Sci 7:1357–1371

Loewus FA, Dlcklnson DB (1982) Cyclitols. In: Loewus FA, Tanner W (eds) Encyclopedia of plant physiology, new series: plant carbohydrates I, vol 13A. Springer, Berlin, pp 193–216

Loewus FA, Loewus MW (1983) Myo-inositol: Its biosynthesis and metabolism. Annu Rev Plant Physiol 34:137–161

Luo LJ (2010) Breeding for water-saving and drought-resistance rice (WDR) in China. J Exp Bot 61:3509–3517

Manavalan LP, Guttikonda SK, Tran L-SP, Nguyen HT (2009) Physiological and molecular approaches to improve drought resistance in soybean. Plant Cell Physiol 50:1260–1276

Mauseth JD (2006) Structure-function relationships in highly modified shoots of cactaceae. Ann Bot 98(5):901–926. https://doi.org/10.1093/aob/mcl133

Medeiros JS, Pockmand WT (2011) Drought increases freezing tolerance of both leaves and xylem of *Larrea tridentata*. Plant Cell Environ 34:43–51

Michael H, Clive K (2001) Xeromorphic. In: The Cambridge illustrated glossary of botanical terms. Cambridge University Press, Cambridge

Mulroy TW (1979) Spectral properties of heavily glaucous and non-glaucous leaves of a succulent rosette-plant. Oecologia 38(3):349–357. https://doi.org/10.1007/BF00345193. PMID 28309493

Muvunyi BP, Yan Q, Wu F, Min X, Yan ZZ, Kanzana G, Wang Y, Zhang J (2018) Mining late embryogenesis abundant (LEA) family genes in *Cleistogenes songorica*, a xerophyte perennial desert plant. Int J Mol Sci 19:3430

Nelson DE, Rammesmayer G, Bohnert HJ (1998) Regulation of cell-specific inositol metabolism and transport in plant salinity tolerance. Plant Cell 10:753–764

Nikita (2019) Plant adaptations: introduction and ecological classification of plant. http://www.biologydiscussion.com/plants/plant-adaptations-introduction-and-ecological-classification

Nishizawa A, Yabuta Y, Shigeoka S (2008) Galactinol and raffinose as a novel function to protect plants from oxidative damage. Plant Physiol 147:1251–1263

Nocito FF, Kancilli C, Giacomini B, Sacchi GA (2007) Sulfur metabolism and cadmium stress in higher plants. Stress 1(2):142–156

Ozkur O, Ozdemir F, Bor M, Turkan I (2009) Physiochemical and antioxidant responses of the perennial xerophyte *Capparis ovata* defense to drought. Environ Exp Bot 66:487–492

Passioura J (1997) Drought and drought tolerance. In: Drought tolerance in higher plants: genetical, physiological and molecular biological analysis. Springer, Netherlands

Paul MJ, Cockburn W (1989) Pinitol, a compatible solute in *Mesembtyanthemum crystallinum* L. J Exp Bot 40:1093–1098

Peters S, Mundree SG, Thomson JA, Farrant JM, Keller F (2007) Protection mechanisms in resurrection plant *Xerophyta viscosa* (Baker): both sucrose and raffinose family oligosaccharides (RFOs) accumulate in leaves in response to water deficit. J Exp Bot 58:1947–1956

Piazza LA, Lopez D, Silva MP, Lopez Rivilli MJ, Cantero JJ, Tourn GM, Scopel AL (2014) Characterization of quaternary ammonium compounds in *Flourensia xerophytic* communities and response to UV-B radiation. S Afr J Bot 94:14–23

Proctor MCF (2000) The bryophyte paradox: tolerance of desiccation, evasion of drought. Plant Ecol 151:41–49

Rentsch D, Hirner B, Schmelzer E, Frommer WB (1996) Salt stress-induced proline transporters and salt stress-repressed broad specificity amino acid permeases identified by suppression of a yeast amino acid permease-targeting mutant. Plant Cell 8:1437–1446

Ron M, Sandy V, Martin G, Frank VB (2004) Reactive oxygen gene network in plants. Trends Plant Sci 9:490–498

Salvucci ME, Ogren WL (1996) The mechanism of Rubisco activase: insights from studies of the properties and structure of the enzyme. Photosynth Res 47:1–11

Salvucci ME, van de Loo FJ, Stecher D (2003) Two isoforms of Rubisco activase in cotton, the products of separate genes not alternative splicing. Planta 216:736–744

Sánchez de Jiménez, Medrano L, Martinez-Barajas E (1995) Rubisco activase, a possible new member of the molecular chaperone family. Biochem 34:2826–2831

Sanchez DH, Siahpoosh MR, Roessner U, Udvardi M, Kopka J (2008) Plant metabolomics reveals conserved and divergent metabolic responses to salinity. Physiol Plant 132:209–219

Savchenko T, Kolla VA, Wang C-Q, Nasafi Z, Hicks DR, Phadungchob B, Chehab WE, Brandizzi F, Froehlich J, Dehesh K (2014) Functional convergence of oxylipin and abscisic acid pathways controls stomatal closure in response to drought. Plant Physiol 164:1151–1160

Schafer FQ, Wang HP, Kelley EE, Cueno KL, Martin SM, Buettner GR (2002) Comparing β-carotene, vitamin E and nitric oxide as membrane antioxidants. Biol Chem 383:671–681

Seki M, Umezawa T, Urano K, Shinozaki K (2007) Regulatory metabolic networks in drought stress responses. Curr Opin Plant Biol 10:296–302

Shao HB, Liang ZS, Shao MA (2005) LEA proteins in higher plants: structure, function, gene expression and regulation. Colloid Surf B 45:131–135

Shi S-Q, Shi Z, Qi L-W, Sun X-M, Jiang Z-P, Li C-X, Xiao W-F, Zhang S-G (2009) Molecular responses and expression analysis of genes in a xerophytic desert shrub *Haloxylon ammodendron* (Chenopodiaceae) to environmental stresses. Afr J Biotech 8(12):2667–2676

Shi Y, Yan X, Zhao P, Yin H, Zhao X, Xiao H, Li X, Chen G, Ma X (2013) Transcriptomic analysis of a tertiary relict plant, extreme xerophyte *Reaumuria soongarica* to identify genes related to drought adaptation. PLoS One 8(5):e63993

Smirnoff N, Cumbes OJ (1989) Hydroxyl-radical scavenging activity of compatible solutes. Phytochem 28:1057–1060

Spreitzer RJ, Salvucci ME (2002) Rubisco: structure, regulatory interactions, and possibilities for a better enzyme. Annu Rev Plant Biol 53:449–475

Szabados L, Savouré A (2010) Proline: a multifunctional amino acid. Trends Plant Sci 15:89–97

Talia Powell (2013) Water balance in plants. http://waterbalanceinplants.blogspot.co.nz/2013_06_01_archive.html

Tezara W, Colombo R, Coronel I, Marıin O (2011) Water relations and photosynthetic capacity of two species of Calotropis in a tropical semi-arid ecosystem. Ann Bot 107:397–405

Verslues PE, Bray EA (2006) Role of abscisic acid (ABA) and Arabidopsis thaliana ABA-insensitive loci in low water potential-induced ABA and proline accumulation. L Exp Bot 57:201–212

Vierling E (1991) The roles of heat shock proteins in plants. Annu Rev Plant Physiol Plant Mol Biol 42:579–620

Vinocur B, Altman A (2005) Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. Curr Opin Biotechnol 16:123–132

Waadt R, Hitomi K, Nishimura N, Hitomi C, Adams SR, Getzoff ED, Schroeder JI (2014) FRET-based reporters for the direct visualization of abscisic acid concentration changes and distribution in *Arabidopsis*. eLife 3:e01739

Wang SM, Wan CG, Wang YR, Chen H, Zhou ZY, Fu H, Sosebee RE (2004a) The characteristics of Na^+, K^+ and free proline distribution in several drought resistant plants of the Alxa Desert, China. J Arid Environ 56(3):525–539

Wang W, Vinocur B, Shoseyov O, Altman A (2004b) Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. Trends Plant Sci 9:244–252

Warming E, Balfour IB, Groom P, Vahl M (1909) Ecology of plants. Oxford University Press, London

Whitley D, Goldberg SP, Jordan WD (1999) Heat shock proteins: a review of the molecular chaperones. J Vasc Sur 29:748–751

Wise RR, Olson AJ, Schrader SM, Sharkey TD (2004) Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. Plant Cell Environ 27:717–724

Xi J-J, Chen H-Y, Bai W-P, Yang R-C, Yang P-Z, Chen R-J, Hu T-M, Wang S-M (2018) Sodium-related adaptations to drought: new insights from the xerophyte plant *Zygophyllum xanthoxylum*. Front Plant Sci 9:1678. https://doi.org/10.3389/fpls.2018.01678

Xiong L, Zhu JK (2003) Regulation of abscisic acid biosynthesis. Plant Physiol 133:29–36

Xiong L, Schumaker KS, Zhu JK (2002) Cell signaling during cold, drought, and salt stress. Plant Cell 14:165–183

Xu Z, Sun M, Jiang X et al (2018) Glycinebetaine biosynthesis in response to osmotic stress depends on jasmonate signaling in watermelon suspension cells. Front Plant Sci 9:1469

Yamori W, Hikosaka K, Way DA (2014) Temperature response of photosynthesis in C3, C4, and CAM plants: temperature acclimation and temperature adaptation. Photosynth Res 119(1–2):101–117. https://doi.org/10.1007/s11120-013-9874-6

Yang Y, Dong C, Yang S, Li X, Sun X, Yang Y (2015) Physiological and proteomic adaptation of the alpine grass *Stipa purpurea* to a drought gradient. PLoS One 10(2):e0117475

Yoshiba Y, Kiyosue T, Katagiri T, Ueda H, Mizoguchi T, Yamaguchi-Shinozaki K et al (1995) Correlation between the induction of a gene for delta 1-pyrroline-5-carboxylate synthetase and the accumulation of proline in *Arabidopsis thaliana* under osmotic stress. Plant J 7:751–760

Yoshimura K, Masuda A, Kuwano M, Yokota A, Akashi K (2008) Programmed proteome response for drought avoidance/tolerance in the root of a C3 xerophyte (wild watermelon) under water deficits. Plant Cell Physiol 49(2):226–241

Zavala JA, Ravetta DA (2002) The effect of solar UV-B radiation on terpenes and biomass production in *Grindelia chiloensis* (Asteraceae), a woody perennial of Patagonia, Argentina. Plant Ecol 161:185–191

Zeng YJ, Wang YR, Zhang JM (2010) Is reduced seed germination due to water limitation a special survival strategy used by xerophytes in arid dunes? J Arid Environ 74(4):508–511. https://doi.org/10.1016/j.jaridenv.2009.09.013

Zhang L, Gao M, Hu J, Zhang X, Wang K, Ashraf M (2012) Modulation role of abscisic acid (ABA) on growth, water relations and glycinebetaine metabolism in two maize (*Zea mays* L.) cultivars under drought stress. Inter J Mol Sci 13:3189–3202

Zhu JK (2002) Salt and drought stress signal transduction in plants. Annu Rev Plant Biol 53:247–273

Chapter 10
Ecophysiology and Response of Plants Under High Temperature Stress

Renu Khanna-Chopra and Vimal Kumar Semwal

Contents

Abstract High temperature-induced heat stress has been identified as an important abiotic stress having a detrimental effect on crop productivity and quality. Episodes of heat stress alone or combined with other environmental stresses are on the rise world over causing significantly losses in crop yield and thus reducing world food security. Heat stress effects can be mitigated by breeding thermotolerance in crop plants using various genetic approaches which requires understanding of the plant responses at physiological, biochemical and molecular level. Reproductive stage in crop plants is very sensitive to heat stress though vegetative growth is also affected. Heat stress response starts with the perception of stress and results in sensing, signal transduction and gene expression. Growth and photosynthesis are reduced, and leaf senescence is enhanced under heat stress, thus reducing biomass accumulation. Chloroplast is the major organelle influenced by heat stress. Metabolic reprogramming in chloroplast occurs in order to optimize growth and development under heat stress. Heat stress reduces grain number, grain weight and grain quality which are important commercial traits due to less assimilate availability and shorter grain growth rate and duration leading to reduced yield. Development of thermotolerance is associated with ROS, sugar and hormone signalling, expression of HSFs genes

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and activation of HSPs, enhancement in antioxidant capacity, accumulation of compatible solutes, etc. In this chapter, we discuss the current understanding of plant response to heat stress at physiological, biochemical and molecular level with emphasis on crop plants.

Keywords Heat stress · Thermotolerance · Reactive oxygen species · Heat tolerance · Heat-shock proteins · Epigenetic changes

Abbreviations

ABA	Abscisic acid
APX	Ascorbate peroxidase
AsA	Reduced ascorbic acid
CaMs	Calmodulins
CKs	Cytokinins
DHAR	Dehydroascorbate reductase
GR	Glutathione reductase
GSH	Reduced glutathione
HS	Heat stress
HSEs	Heat-shock elements
HSFs	Heat stress transcription factors
HSPs	Heat-shock proteins
PCD	Programmed cell death
POX	peroxidases
RdDM	RNA-directed DNA methylation
ROS	Reactive oxygen species
SAGs	Senescence-associated genes
SOD	Superoxide dismutase
TF	Transcription factor

10.1 Introduction

Environmental plant physiology helps us to understand the mechanisms which enable plant survival, distribution and productivity across the diverse climates of our planet. Plant systems both natural and managed experience a wide range of environmental stresses including heat stress, which is expected to increase as a consequence of global climate change. Heat stress can be defined as temperatures higher than the optimum which hamper growth and cause irreversible damage to plants. Agricultural production worldwide has been affected by changes in climate as yield reduction due to heat stress reduces global food security (Christensen and Christensen 2007). Exposure to heat stress reduces growth, development and yield as plant processes are affected at various levels of organization (Wahid et al. 2007).

Heat stress can be continual or transient varying in intensity and duration, and its effect is dependent on the stage of the plant. Although a detrimental effect of heat stress is observed both at vegetative and reproductive stages, the effect is more intense at the reproductive stage. In many parts of the world, the crops often experience heat stress at the flowering stage and/or during grain development resulting in significant loss in grain yield and quality (Prasad et al. 2017). Heat stress response starts with sensing of stress and results in signal transduction and gene expression. Sensors in many cellular apartments help in sensing changes in ambient temperature. Temperature changes increase the fluidity of membranes and cause an initiation of the lipid-based signalling cascades, followed by increased influx of calcium and changes in cytoskeletal organization. Subsequently, the adaptive mechanisms are initiated in order to provide protection against heat stress (Saidi et al. 2011). Exposure of plants to nonlethal high temperatures triggers the genetically controlled process of heat acclimation which plays a major role in plant survival facing heat stress under field conditions (Wang and Li 2006). The ability of an organism to tolerate high temperatures is often referred to as thermotolerance. Development of thermotolerance is associated with ROS, sugar and hormone signalling, expression of HSFs genes and activation of HSPs, enhancement in antioxidant capacity, accumulation of compatible solutes, etc.

Plants respond to heat stress at various levels of organization. In this chapter, we discuss the current understanding of response of plants to heat stress at the physiological, biochemical and molecular level with special emphasis on crop plants. Enhancing crop productivity in heat stress environments is an important goal in agriculture worldwide. This requires an in-depth knowledge of processes which enable plants to acclimate and adapt in order to mitigate the detrimental effects of heat stress and thus maintain productivity.

10.2 Sensing Temperature Stress in Plants

A typical heat stress response starts with the perception of stress and results in sensing, signal transduction and gene expression. Plasma membranes are the first to face and sense heat and are major heat sensing parts of the cells. The composition of lipid bilayer and the degree of its saturation dictate membrane fluidity under high temperature condition, and change in membrane fluidity is one of the initial responses of plant cells under high temperature stress (Niu and Xiang 2018). Sensing (perception) of temperature in plants is carried out through different temperature sensing devices (Fig. 10.1) which results in changes in membrane fluidity, conformational changes to proteins, disassembly of cytoskeleton, rearrangements in metabolic processes and finally expression of array of target genes (Schroda et al. 2015). Temperature changes are perceived and then transduced to nucleus where the

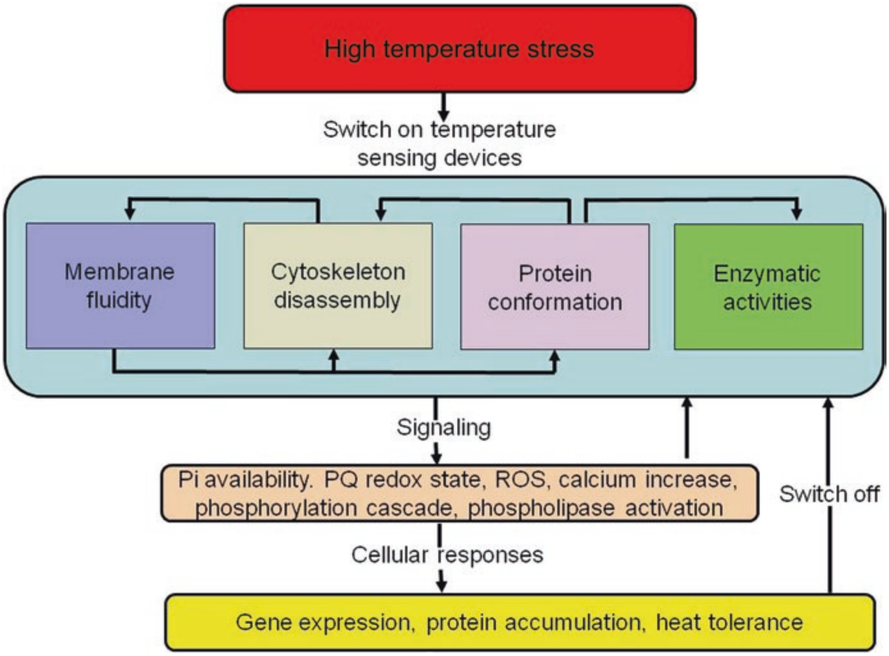

Fig. 10.1 Schematic representation of the temperature sensing machinery in plants

transcriptome is altered (Ruelland and Zachowski 2010). Sensing of temperature fluctuations by plasma membrane, temporal influx of Ca^{2+} and activation of downstream signalling pathways is a conserved response in plants (Saidi et al. 2009). The activation of Ca^{2+}-permeable channel due to high temperature or chemical treatments has been reported in moss *Physcomitrella patens*. The intensity of HS response is dependent on the magnitude of Ca^{2+} influx immediately after heat episode. Disturbing Ca^{2+} influx using chemicals blocking Ca^{2+} channels resulted in suppression of HS response and heat acclimation/thermotolerance in soybean and tobacco (Saidi et al. 2009; Ruelland and Zachowski 2010). Downstream of heat-sensitive Ca^{2+} channels calmodulins (CaMs) and kinases acts to further amplify the signal and regulate expression of transcription factors and HSPs. CaMs are known regulators of HSPs expression in plants. Heat shock leads to accelerated accumulation of CaM3 and CaM7 in *Arabidopsis*, while addition of CaM antagonists results in downregulation of *hsp26* and *hsp70* genes (Liu et al. 2005). The presence of CaM proteins is shown to enhance the DNA binding ability of HSFs to heat-shock elements (HSEs) on the promoter sites of HSPs (Bokszczanin and Fragkostefanakis 2013). *cam3* mutants exhibited reduced HSP levels and heat sensitivity, while *cam3* overexpressing plants exhibited high levels of many HSPs leading to enhanced thermotolerance in *Arabidopsis*. Hence, induction of thermotolerance in plants is controlled through Ca^{2+}-dependent activation of CaMs and kinases.

However, how heat stress perception is different from and integrated with perception of other abiotic stresses is largely unknown (Niu and Xiang 2018).

10.3 Effect of High Temperature on Physiological, Biochemical and Molecular Processes

10.3.1 Physiological Processes

10.3.1.1 Growth and Flowering

Heat stress affects plant growth, development, flowering and productivity. Heat stress can vary both in intensity and duration, and hence the plant response varies accordingly. The threshold temperatures causing mild, medium or severe heat stress vary with the crop and the stage. Most of the studies on response of plants to high temperature have been conducted in greenhouse or plant growth chambers under variable temperature combinations and hence cannot be easily compared. Plant growth is hampered by heat stress at both vegetative and reproductive stages, though susceptibility is higher at reproductive stages.

High temperatures generally reduce germination percentage and seedling emergence leading to poor stand establishment coupled with lack of seedling vigour in crops (Essemine et al. 2010). Under extreme heat stress say around 40 °C germination in wheat occurred but was inhibited in freshly harvested seeds and seedling growth was severely inhibited as embryonic cells were damaged. Heat-tolerant wheat variety showed seedling vigour coupled with higher total amylase activity of the kernels compared to a heat-susceptible variety up to 35 °C (Alka and Khanna-Chopra 1995). Wheat seeds aged for 36–40 weeks acquired the ability to germinate at 40 °C, thus breaking the thermodormancy observed in freshly harvested seeds. Heat stress can cause physiological injuries such as scorching, shedding and yellowing of leaves, growth inhibition, less biomass and damage to developing fruits leading to loss in productivity (Vollenweider and Günthardt-Goerg 2005). In wheat warm temperature such as 30 °C day/25 °C night reduces leaf area, tiller number and productive tillers and reduces biomass compared to crop growing under optimal or lower temperatures (Rahman et al. 2009). High temperature causes loss of water content and decrease in photosynthesis rate and productivity (Almeselmani et al. 2009; Ashraf and Harris 2013).

10.3.1.2 Senescence

Heat stress during grain development phase is associated with increase in chlorophyllase activity, decline in photosynthesis and photosynthetic pigments and thus enhances leaf senescence (Todorov et al. 2003). Oxidative damage of cell membranes caused by reactive oxygen species (ROS) production under heat stress is a consequence of detrimental effect on chlorophyll and photosystems (Camejo et al. 2006). Grain yield under heat stress in wheat is directly proportional to the duration of photosynthetically active leaf area duration (Chauhan et al. 2009; Shirdelmoghanloo et al. 2016).

Senescence, a programmed cell death process (PCD), is associated with the overproduction of ROS which causes oxidative stress. During leaf senescence, there are significant changes in chloroplast structure and function, damage to plasma membrane and alterations in metabolic processes (Khanna-Chopra 2012). Antioxidant defence of the leaf declines as senescence progresses, thus implying the importance of ROS in the senescence process. Several studies have emphasized the importance of oxidative stress and its management under heat stress in plants (Khanna-Chopra 2012; Hasanuzzaman et al. 2013). Heat-tolerant wheat cultivar exhibited a slower rate of monocarpic senescence coupled with lower oxidative stress and damage due to a better antioxidant defence and higher Rubisco activity than the susceptible cultivar during heat stress (Khanna-Chopra and Chauhan 2015). High diurnal temperatures also hastened flag leaf senescence in wheat coupled with decline in SOD, APX and CAT activity (Zhao et al. 2007). Reduced production of ROS coupled with a better antioxidant defence plays an important role in stress tolerance (Mittler 2006). High temperature-induced increase in ROS levels resulted in increased SAG transcripts such as senescence-related transcription factor *PeWRKY6-1*, *WRKY53* and cysteine protease homolog *SAG12*, thus promoting senescence (Miao et al. 2004; Rosenvasser et al. 2006).

Relationship between abiotic stresses and leaf senescence is the shared response to the phytohormones such as abscisic acid (ABA), cytokinins (CKs), ethylene and strigolactones (Wang et al. 2018). ABA induces H_2O_2 accumulation and enhances antioxidant defence, thus modulating the process of senescence (Jajic et al. 2015). Senescence is promoted by ethylene, ABA and strigolactones, while its initiation is delayed by CKs. The holistic picture of hormonal signalling pathways and its interplay with other regulatory factors in heat stress-induced senescence is complicated and needs more research.

Delayed senescence, or functional stay-green, results in a longer duration of grain filling period and yield stability under high temperature stress in several crops (Abdelrahman et al. 2017). Genotypes showing stay-green trait had higher yields associated with higher photosynthetic rate, reduced sterility of reproductive organs resulting in higher grain numbers. Studies on molecular markers have shown that QTLs for stay-green trait coincide with loci for drought and heat tolerance (Gous et al. 2016; Pinto et al. 2016). Hence stay-green is a desirable trait for enhancing heat tolerance in crops and needs to be understood at the biochemical and molecular level.

10.3.1.3 Reproductive Physiology

Reproductive processes in crops are very sensitive to high temperature stress. These processes generally extend over 2–3 weeks in different crop species. Reproductive stages have different optima and critical temperature thresholds, beyond which these processes are affected leading to poor seed set and reduction in yield. Temperatures between 30 and 40 °C have been identified as damaging for key reproductive processes in different crop species using growth temperatures facilities (Prasad et al. 2017). Significant reproductive damage can occur if maximum temperature is between 30 and 38 °C in cereals, 40 °C in millets, around 36 °C in oilseeds and 32–40 °C in pulses. It has been shown in many crops that heat stress influences pollen development reducing pollen viability and germination causing sterility and poor seed set (Kaushal et al. 2016). However, limited information is available on heat stress effects on female reproductive organs in most field crops.

Heat stress impacts the biochemical and nutritional aspects of anther/pollen in field crops. Heat stress increases unsaturated fatty acids in pollen exine wall, thereby making the membrane more porous in sorghum (Prasad and Djanaguiraman 2011). Reproductive organs such as tapetal cells have several fold higher mitochondrial number compared to vegetative tissue in order to meet the higher energy demand which can lead to higher ROS production. Increased production and accumulation of ROS under high temperature stress damages membrane lipids, increases membrane permeability and causes denaturation of functional proteins, thereby influencing pollen tube growth (Parrotta et al. 2016). Increased ROS level in anther/pollen correlated with heat susceptibility in wheat and sorghum (Kumar et al. 2014a, b; Prasad et al. 2017). In sorghum pollen, viability is reduced under heat stress due to reduced sucrose availability (Jain et al. 2007). Heat stress over a longer duration reduced the expression of genes involved in synthesis and degradation of starch and sugar transporters in tapetum and anther of sorghum (Jain et al. 2010). It has been observed that heat stress also affects female reproductive organs in sorghum in terms of receptivity of stigma to pollen and causes desiccation to style and damage to ovary, thereby reducing pollen tube growth and fertilization (Prasad et al. 2017).

In addition to the warmer day temperatures, rapid increase in night temperatures is also included in the climate change scenarios in the future (IPCC 2013). Growth chamber studies on the effect of increase in night temperature in wheat and rice showed that spikelet sterility is increased leading to reduction in yield (Coast et al. 2014; Narayanan et al. 2015). However, higher night temperatures under field conditions led to reduced biomass due to enhanced night respiration leading to loss of carbohydrates and resulted in reduced yield and quality in rice with minimum reduction in spikelet fertility (Bahuguna et al. 2016).

10.3.1.4 Grain Development and Yield

High temperatures are more detrimental at the reproductive stage and during grain development in many crops resulting in substantial loss in yield (Wahid et al. 2007; Prasad et al. 2017). Temperature between 20 and 24 °C is optimum for grain filling in different spring wheat cultivars, while temperatures above 35 °C can limit proper grain filling leading to shrivelling of grains, hence reducing the grain weight. In wheat high temperatures reduce assimilate translocation, grain growth rate and duration and grain setting, thereby reducing grain number, size and weight

(Akter and Islam 2017). Viswanathan and Khanna-Chopra (2001) showed that high temperature stress of 6–8 °C during grain development reduced grain growth duration and rate in wheat varieties differing in grain weight stability. The susceptible variety showed more reduction in grain growth duration, while the stable variety showed more reduction in grain growth rate under high temperature stress. The heat-tolerant variety exhibited thermotolerance in grain growth rate, starch and protein synthesis in developing grains compared to the heat-susceptible variety. Extremely high temperatures (>35 °C) during ripening can lead to reduced grain filling by inhibiting the disposition of storage materials such as starch and protein resulting in reduced final yield in rice (Yamakawa and Hakata 2010). Heat stress during kernel growth in maize affects kernel size and weight and determines whether kernels at the tip will fill even after successful pollination. Temperatures during grain filling above 40 °C affect kernel growth and filling and hasten grain maturation, leading to yield loss in maize (Wilhelm et al. 1999).

Wheat can be exposed to heat stress throughout the growth period or terminal heat stress, i.e. during grain growth period. Patil et al. (2008) found a wide variation in heat tolerance both continual and terminal in *T. aestivum* and *T. durum* genotypes. High biomass production and grains m^{-2} contributed towards heat tolerance in yield under both heat stress environments. High grain yield and grains per unit area correlated with photothermal quotient under both heat stress environments as high temperature is often associated with high radiation. Under continual but moderate heat stress environment, grain weight is maintained although grain number is reduced in wheat genotypes. *T. aestivum* genotypes performed better than *T. durum* genotypes under terminal heat stress environment, while *T. durum* showed specific adaptation to continual moderate heat stress.

Grain legume productivity and quality is reduced if crop experiences high temperature stress during reproductive development and grain filling phases (Sehgal et al. 2018). Severe losses in legume grain yield can occur if temperatures exceed the optimum range of 10–36 °C. Grain development is susceptible to heat stress as tapetum layer is disintegrated, thereby reducing nutrition to microspores causing dehiscence of anthers. High temperatures cause reduction in both pod number and grain weight resulting in reduced grain yield. Grain weight is reduced due to less carbohydrate availability and shorter grain filling duration (Farooq et al. 2017).

10.3.2 Effect of Temperature Stress on Biochemical Processes

10.3.2.1 Photosynthesis

Photosynthesis, the key process determining productivity, is very sensitive to high temperature stress. Heat-tolerant plants often retain the ability to maintain leaf gas exchange and CO_2 assimilation rates under heat stress (Wahid et al. 2007). Mild heat stress influences leaf water relations, decreases stomatal conductance and intercellular CO_2 concentration and thereby decreases net photosynthesis

(Greer and Weedon 2012). Photochemical reactions and carbon metabolism are sensitive to heat stress (Wise et al. 2004). High temperatures decrease net assimilation due to decrease in photosynthesis rate and increase in dark and photorespiration rates. Calvin-Benson cycle enzymes are heat sensitive. Loss in photosynthesis correlated with decrease in Rubisco activity under moderate heat stress (Law and Crafts-Brandner 1999). Rubisco enzyme is stable under heat stress, but Rubisco activase is heat labile causing loss of Rubisco activity at high temperatures (Salvucci and Crafts-Brandner 2004; Sharkey 2005). Photorespiratory activity increases because oxygenase activity of Rubisco increases, while the carboxylase activity declines due to higher specificity and solubility of O_2 compared to CO_2 of Rubisco (Jordan and Ogren 1984). Heat-stressed leaves retain the capacity for electron transport and RuBP regeneration (Crafts-Brandner and Law 2000). In various species, lower expression of Rubisco per unit leaf area has been reported under high temperature stress which is concomitant with decrease in protein content (Sage and Kubien 2007).

Heat-stressed plants show lesser chlorophyll accumulation due to either reduced chlorophyll synthesis or accelerated degradation or both. The enzymes of chlorophyll biosynthetic pathway are inhibited by high temperature (Dutta et al. 2009). Thermotolerant tomato genotypes exhibited higher chlorophyll *a*/*b* ratio and lower chlorophyll/carotenoids ratio compared to susceptible genotypes under high temperature stress indicating its importance in heat stress tolerance (Camejo et al. 2005). In developed leaves, chlorophyll a and b degradation was higher leading to senescence compared to young leaves under heat stress (Karim et al. 1999).

High temperatures reduce PSII activity considerably as it is thermolabile (Camejo et al. 2005). Heat stress induces release of Mn atoms due to dissociation of manganese-stabilizing protein at oxygen-evolving complex and damages D1 and/or the D2 proteins of the PS II reaction centre. This leads to an imbalance between electron flows from oxygen-evolving complex towards the accepter side of PSII in the direction of PSI reaction centre under heat stress (Allakhverdiev et al. 2008). Loss of photosynthetic activity at very high temperatures is attributed to the inactivation of the acceptor side of PSII and reduced electron transport in the chloroplast (Allakhverdiev et al. 2008). Compared to PSII, PSI activity is more heat stable. PSI activity is stimulated and cyclic electron flow around PSI is increased under moderate heat stress, thus generating ATP which appears to be an adaptive process enabling dissipation of excess energy and maintaining active CO_2 fixation (Mathur et al. 2014).

Hence, heat stress damages the oxygen-evolving complex, PSII reaction centre components, Rubisco activity and system generating ATP in plants. The ability of plants to acclimate and recover from damages of heat stress depends on the balance between PSII damage and repair in vivo (Allakhverdiev et al. 2008). An important aspect of PSII repair is the de novo synthesis of DI protein damaged due to ROS, which also influences the repair process. The adaptive processes triggered by membrane-linked sensors such as synthesis of compatible solutes and stress proteins alleviate ROS-induced inhibition of repair of photosynthetic machinery and thus contribute towards the acclimation process (Mathur et al. 2014).

10.3.2.2 ROS Generation and Antioxidant Defence

Under optimal environmental conditions, cellular equilibrium is obtained by a coordinated and highly regulated balance among several metabolic pathways that exist in diverse organelles. However, under HS this balance may get disturbed because different enzymes have different temperature optimum. Heat stress is associated with impairments in chloroplastic and mitochondrial functions leading to accelerated production of ROS (Pospíšil 2016). ROS, viz. $^1O_2$, H_2O_2, $O_2^{\bullet-}$ and $HO^{\bullet}$, are toxic molecules causing oxidative damage to proteins, DNA and lipids (Pospíšil 2016; Foyer 2018). During heat stress, accelerated production of ROS is well documented and these reactive species can be produced in different parts of cell importantly in membranes by NADPH oxidases and subcellular locations (chloroplasts, mitochondria, peroxisomes, etc.) during photosynthesis, respiration and other processes (summarized in Fig. 10.2). An intimate relationship exists between HS response and ROS-mediated damage.

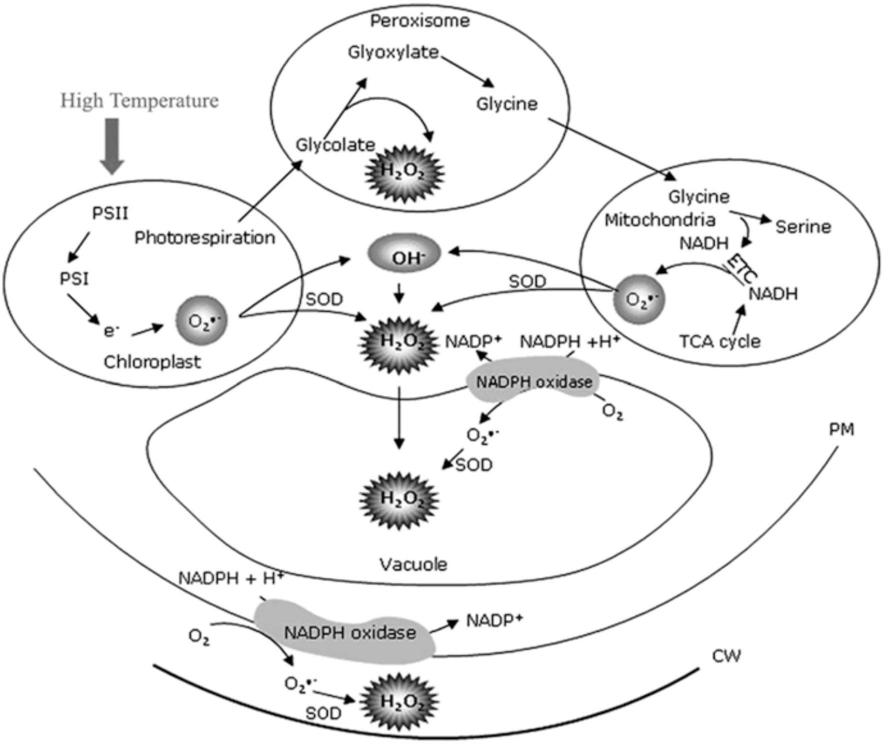

Fig. 10.2 Various intracellular sources of ROS in a plant cell during high temperature. *CW* cell wall, *ETC* electron transport chain, H_2O_2 hydrogen peroxide, OH^- hydroxyl radical; $O2^-$ superoxide ion, *PS* photosystems I and II, *PM* plasma membrane, *SOD* superoxide dismutase, *TCA* tricarboxylic acid cycle

Acquired thermotolerance (Heat acclimation) is a major protective mechanism in plants. Plants are static life forms, with insufficient capacity to thermoregulate that depends on the availability of water, and prompt acclimatization to temperature fluctuations is imperative for their viability. Differential acclimation treatments showed different heat stress responses. Gradual increase in ambient temperature (gradual increase from 22 to 45 °C in 6 h) was more effective in terms of plant survival, compared to a stepwise acclimation (38 °C) and recovery (22 °C) (Larkindale and Vierling 2008). The capability of plant acclimatization to usually damaging high temperatures is a primitive and conserved dynamic reaction. Heat stress-induced oxidation is expressed in membrane damage through peroxidation of membrane lipids (Larkindale and Knight 2002) and damage to DNA and proteins (Awasthi et al. 2015). Heat acclimation results in the elevation in expression of genes encoding ROS-scavenging enzymes during heat acclimation and heat shock (Rizhsky et al. 2002; Pospíšil 2016). Heat acclimation is mediated through balancing cellular biochemical processes that can protect from oxidative stress under HS (Bergmüller et al. 2003; Larkindale and Huang 2004). Several studies have indicated that HSFs are involved in sensing of ROS especially during heat stress and acclimation (Suzuki and Katano 2018).

It has been reported that enhanced activities of ROS-scavenging enzymes and increased biosynthesis of antioxidants contribute to plants' tolerance to HS and heat acclimation is achieved through enhancing antioxidant response (Wahid et al. 2007; Awasthi et al. 2015). Transcriptome changes in response to HS have been reported by many groups in the last decade, and a large number of transcripts exhibited differential expression under HS and acclimation compared to no stressed plants (Rizhsky et al. 2002; Busch et al. 2005; Schramm et al. 2006; Kilian et al. 2007; Larkindale and Vierling 2008). Upregulation of major HSFs and HSPs gene families, viz. HSP101, HAP70 and small HSPs, has been reported under HS in all of the above-listed studies. The transcripts of other gene families that increase dramatically under HS include dehydration-responsive element-binding protein (DREB2) TF family and ASCORBATE PEROXIDASE2 (APX2). Expression of APX2 is enhanced under HS and is regulated by HSFA2 (Schramm et al. 2006). Specific activities of different antioxidative defence enzymes are well known to respond to HS and provided defence by scavenging ROS. Increased transcript level and/or net activities of superoxide dismutase (SOD), peroxidase (POX), ascorbate peroxidase (APX) and catalase (CAT) have been reported in several plants including *Brassica juncea*, wheat, grapes, cotton, maize, grasses, bean, tomato, lilium and others (Dat et al. 1998; Sairam et al. 2006; Scandalios et al. 2003; Ye et al. 2000; Jiang and Huang 2001; Huang et al. 2003; Rivero et al. 2004; Wang and Li 2006; Yin et al. 2008; Kaur et al. 2009; Gur et al. 2010; Lin et al. 2010; Khanna-Chopra and Chauhan 2015).

The role of different ROS-scavenging enzymes in heat acclimation and HS tolerance is evaluated by several groups by using overexpressing transgenics or knockout mutants. Overexpression of single antioxidant protein gene or two genes simultaneously resulted in enhanced thermotolerance under highly defined controlled environment conditions. Only few studies conducted on mature plants reported positive impact on yield or other related traits (Shafi et al. 2015). By using whole-genome microarrays, it has already been reported that acquired thermotolerance is highly complex and multigenic trait involving multiple gene regulation processes. Knockdown or overexpression of a single gene may result in altered expression of other related genes. Overexpression of wheat MnSOD in *Brassica*, superoxide reductase (SOR) *Pyrococcus furiosus* in *Arabidopsis* and cytosolic Cu/Zn SOD isolated from *Avicennia marina* in rice conferred tolerance to HS (Prashanth et al. 2008; Gusta et al. 2009; Im et al. 2009). Wang et al. (2006) reported that overexpressing cAPX in tomato resulted in enhanced thermotolerance. Overexpression of both APX and MnSOD resulted in abiotic stress tolerance including HS in tall fescue and other plants (Wang et al. 2007; Lee et al. 2007). In addition, increased levels of SOD and APX due to overexpression might interact with other ROS-responsive enzymes and increase their HS tolerance (Lee et al. 2007). Rice mutants deficient in both cytosolic APX1 and APX2 showed normal growth under control condition but increased levels of ROS, membrane damage, higher AsA levels and CAT activity under abiotic stresses. The increase in total antioxidant capacity under abiotic stresses in APX double mutant rice is indicative of the importance of diverse antioxidant machineries in plants (Rosa et al. 2010). Knockdown of one of the ROS-scavenging enzymes may result in enhanced activities of other antioxidative enzymes, increased biosynthesis of antioxidant metabolites such as ascorbic acid and maintenance of higher AsA/DHA ratio (Rosa et al. 2010).

The activities of ROS-scavenging enzymes under HS are regulated through calcium, ethylene, ABA and SA signalling pathways (Larkindale and Huang 2004). *Arabidopsis* mutants defective in SA, ABA, ethylene and ROS signalling pathways exhibited a decline in both the capacity for heat acclimation and basal thermotolerance (Larkindale et al. 2005; Suzuki and Mittler 2006).

Proteins are the most sensitive macromolecules in the cells as they are subjected to denaturation very rapidly after heat episodes. The stability of protein synthesizing machinery is very essential for survival during prolonged heat exposure. Heat stress is known to cause structural changes to proteins in plants (Anderson and Padhye 2004), and so the stability of enzymes during extremes of environmental conditions such as very high temperatures can be considered as an adaptive character of plants. Brock (1967) reported that structural and functional stability of various enzymes is essential for the survival of thermophiles under very high temperatures. The in vitro heat stress stability is also reported for some proteins of higher plants as in temperature-tolerant and adaptive weed plant *Chenopodium murale* which is a highly heat stable chloroplastic Cu/Zn SOD exhibiting activity even after 100 °C treatment (Khanna-Chopra and Sundaram 2004). N-terminal sequence analysis of this novel protein showed a unique pattern of amino acids. Heat stable SOD and APX are also reported in cytosol, chloroplast and mitochondria of *Chenopodium album* (Khanna-Chopra et al. 2011; Khanna-Chopra and Semwal 2011). Carter and Thornburg (2000) reported the thermostability of a MnSOD in floral organs of *Nicotiana* species. The thermostability of other important antioxidant defence enzymes APX and CAT was higher in *Vinca* than in sweet pea leaf extracts (Anderson and Padhye 2004). These heat stable forms may be playing important role in basal as well as acquired thermotolerance and survival of these plants in very high temperatures.

Antioxidant enzymes are essential components of plant defence under HS-mediated oxidative stress. Under HS upregulation of enzyme activities and enhanced transcript levels of ROS-scavenging enzymes is reported by many groups. They are known to be essential for heat acclimation process in plants.

Antioxidant metabolites such as reduced ascorbic acid (AsA) and reduced glutathione (GSH) are very important for regulating ROS levels through direct or indirect scavenging under abiotic stresses (Foyer 2018). In maize GSH and hence total glutathione content increased under heat stress, thereby emphasizing its importance for heat stress tolerance and ROS management (Dash and Mohanty 2002). Maintenance of high reduced/oxidized (GSH/GSSG) ratio under HS lead to enhanced thermotolerance in wheat and maize (Kocsy et al. 2004a, b). The scavenging of H_2O_2 by GSH is facilitated by increased GR activity in mustard under HS (Dat et al. 1998). In many crop plant homologues of GSH, hydroxymethylglutathione (hmGSH) is also present which has serine in place of glycine. Increased synthesis/accumulation of GSH is the characteristic of heat-stressed plants. HS and cold stress induced increase in GSH, and reduced hmGSH synthesis was higher in heat-tolerant genotypes compared to the susceptible genotypes (Kocsy et al. 2000, a). Increase in GSH levels is an early response in thermal stress. Heat-shock-treated maize roots exhibited increase in GSH content and decrease in cysteine content due to increased GSH biosynthesis (Nieto-Sotelo and Ho 1986). Only heat-tolerant maize genotypes and not the susceptible genotypes exhibited increase in GSH content under HS at 40 °C for 3 days (Szalai et al. 2009). Maintaining high GSH/GSSG ratio either by increased GSH biosynthesis or recycling through GSSG reduction is essential for the protection of plants from abiotic stresses that induced oxidative stress in plants. GSH biosynthesis is influenced by HS and oxidative stress in plants, and manipulation of GSH biosynthesis enhanced abiotic stress tolerance (Sirko et al. 2004; Szalai et al. 2009). Manipulation of proline synthesis effects not only the GSH concentrations but also the levels of other antioxidants, for example, genetic manipulation of proline synthesis in soybean plants, also affected GSH concentrations under drought and heat stress combination indicating towards the competitive use of glutamate, the common precursor for proline and GSH biosynthesis (Kocsy et al. 2005). Li et al. (2010) also reported increase in GSH content both during high temperature stress and acclimation to chilling stress. Increased GSH/GSSG ratio was reported in lily plants, which was linked to enhanced heat stress tolerance (Yin et al. 2008). *Arabidopsis* mutants defective in GSH biosynthesis *cad2-1* (mutants of γ-glutamylcysteine synthetase gene) have shown strong decrease in basal thermotolerance, reduced heat acclimation capacity and increased TBARS content (Larkindale et al. 2005).

Most eukaryotic organisms and all higher plants produce ascorbic acid (AaA), a powerful, water-soluble scavenger of ROS (Foyer 2018). AsA has the ability to donate electrons in both types of biochemical reactions involving or not involving enzymes; hence, it is the most powerful antioxidant compound. AsA is mainly present in photosynthetic organelles such as chloroplasts. High concentration (as 50 mM) of AsA has been reported in stroma. Reduced pool of AsA in cells is maintained by dehydroascorbate reductase (DHAR) and glutathione reductase (GR) during AsA-GSH pathway as observed in transformed plants overexpressing GR. AsA content increased in grape plants acclimated to high or low temperatures (Li et al. 2010). However, most ascorbic acid biosynthetic genes were downregulated during heat stress (40 °C) in tomato fruits as revealed by gene expression analysis (Ioannidi et al. 2009). Mutants defective in AsA biosynthesis *vtc-1*, *vtc-2* (mutants of GDP-mannose phosphorylase gene) and *vtc-4* (mutants of ʟ-galactose 1-P phosphatase gene) have shown reduced capacity to heat acclimation. *Arabidopsis vtc-1* and *vtc-2* have reduced basal thermotolerance and heat acclimation capacity than the non-transformed plants and showed massive membrane damage when subjected to direct HS (Larkindale et al. 2005). *vtc2-1* has greater thermoinduced photon emission and increased lipid peroxidation at high temperatures (Havaux et al. 2003). In contrast, the increased levels of AsA in transgenic potato plants overexpressing ʟ-gulono-γ-lactone oxidase (GLOase) gene resulted in increased tolerance to oxidative stress imposed by methyl viologen or salt stress (Hemavathi et al. 2010).

Tocopherols are lipid-soluble antioxidants present in different plant cells and are essential for scavenging of ROS and lipid radicals (Kruk et al. 2005). α-tocopherol has the highest antioxidant capacity among the four isomers that have been reported in plant cells. Lipid peroxidation is an inherent feature of HS, and tocopherols prevent the HS-induced chain reaction of lipid autoxidation, making it a powerful lipid radical trap (Sadiq et al. 2019). Bergmüller et al. (2003) showed that HS and other abiotic stress-induced ROS generation lead to increase in the amounts of α-tocopherol and γ-tocopherol in wild-type plants and γ-tocopherol in *vte4-1* mutant (mutant of tocopherol cyclase gene which lacks α-tocopherol). Chlorophyll content and photosynthesis rate were similar in nonmutant and *vte4-1* mutant under HS indicating that α-tocopherol can be replaced functionally by γ-tocopherol in *vte4-1* under HS (Giacomelli et al. 2003).

Carotenoids are lipid-soluble antioxidants that have many functions in plant cells besides protecting from HS-induced oxidative stress (Kim et al. 2018). The role of monoterpene (a carotenoid compound) was already reported at elevated temperature and oxidative stress (Peñuelas and Munné-Bosch 2005; Ahmad et al. 2009). Mutants of *Arabidopsis npq1-2* (mutants of violaxanthin deepoxidase gene) with reduced capacity of violaxanthin synthesis showed decreased capacity for heat acclimation and thermotolerance (Larkindale et al. 2005).

From all of the above-cited studies, it can be concluded that antioxidants are the major components of HS tolerance and are the functional and essential parts of acquired thermotolerance in plants. ROS are central signalling molecules of heat and other abiotic stresses. However, other components of heat acclimation also act parallel and are as important as the antioxidant defence system.

10.3.2.3 Accumulation of Compatible Solutes

Increased accumulation of compatible organic solutes also can result in enhanced thermotolerance. These solutes have a role in the protection of enzymes and protein complexes against heat-induced inactivation (Yang et al. 2007). Transgenic tobacco overexpressing genes coding for betaine-aldehyde dehydrogenase (BADH) showed enhanced ability to synthesize glycinebetaine and enhanced photosynthesis during high temperature stress. Accumulation of low-molecular-weight osmolytes also protects cells during excessive water loss during high temperature stress by maintaining an appropriate cellular turgor (Yang et al. 2007). Proline is the major osmoprotectant that accumulates in plants in response to abiotic stresses including HS. Proline plays multifaceted roles in plants as an amino acid, osmolyte, antioxidant and chaperone (Kaushal et al. 2011). Increased thermotolerance with high proline accumulation has been reported in many plants. However, different studies suggest differential responses of plants with high proline accumulation and HS tolerance. *Arabidopsis* plants overexpressing Δ(1)-pyrroline-5-carboxylate synthetase 1 (*AtP5CS1*) gene accumulated high levels of proline under HS not leading to enhanced thermotolerance (Lv et al. 2011).

10.3.2.4 Secondary Metabolites Under Heat Stress

Secondary metabolites in plants are derivatives of primary metabolites, are produced due to various physiological changes and environmental cues and have long-term effects on plants under changing environments (Zandalinas et al. 2017). Secondary metabolites are classified in three major groups based on their biosynthetic pathways: (I) nitrogen-containing compounds such as cyanogenic glycosides, alkaloids and glucosinolates; (II) phenolic compounds such as flavonoids and phenylpropanoids; and (III) terpenes such as isoprenoids (Ashraf et al. 2018). High temperature stress influences plant secondary metabolism. In fact, Verma and Shukla (2015) observed that secondary metabolites biosynthesis is correlated with increasing temperatures in plants. HS resulted in a marked decline in photosynthesis and enhanced levels of ginsenosides in *Panax quinquefolius* (Jochum et al. 2007). In tomato HS leads to enhanced levels of phenolic secondary metabolites (Rivero et al. 2001). High temperature resulted in enhanced biosynthesis of ginsenosides in hairy roots of *Panax ginseng* (Yu et al. 2005). In addition, overexpression of *b*-carotene hydroxylase (*chyB*) gene in *Arabidopsis* resulted in enhanced thermotolerance due to enhanced biosynthesis of zeaxanthin and protection of membranes from oxidative damage (Meiri et al. 2010). Expression of violaxanthin biosynthesis genes was upregulated, and zeaxanthin biosynthesis genes were downregulated in heat-sensitive plant spinach, while in relatively heat-tolerant plants such as rice and wheat, the upregulation of genes involved in biosynthesis of violaxanthin, antheraxanthin and zeaxanthin is reported under HS (Yan et al. 2016). Hence, apart from their commercial values as pharmaceuticals, flavours and additives, plant secondary metabolites play an important role in heat and other abiotic stress tolerance in plants.

10.3.3 Molecular Effects

10.3.3.1 Heat-Shock Proteins and Transcription Factors

Induction of heat-shock proteins (HSPs) under HS is a well-known response in higher plants (Kotak et al. 2007; Suzuki and Katano 2018). HSPs are known to act as molecular chaperones for protein folding and disassembly under HS. The HSP gene network in plants is very complex, and many of the HSP families play the role of functional proteins involved in growth and development. Although almost all HSPs show induction after heat stress in plants, there is still no specific information on their exact role/function in plant survival under HS. The major HSP groups are HSP100/clpB, HSP90/HtpG, HSP70/DnaK, HSP60/GroEL and small HSPs (sHsps) (Kotak et al. 2007). Although it is well known that accumulation of HSPs is a conserved response in plants, variation in the levels of HSPs accumulation has been documented among/within plant species under HS. The variation in HSPs accumulation in plants is genetic and correlated with HS tolerance (Barua et al. 2003). Elevated levels of HSPs are essential for heat acclimation and thermotolerance in plants.

HSP 100 or HSP100/ClpB specifically has been reported essential for the onset of heat acclimation in plants and other organisms (Hong and Vierling 2000; Lee et al. 2005). The role of HSP 101 in acquisition of thermotolerance is reported in *Arabidopsis hot1* mutants (mutation in HSP 101 gene). The *hot1* plants were thermosensitive in terms of hypocotyl elongation, while transformation of *hot1* plants with HSP 101 gene resulted in restoration of thermotolerance of *hot1* mutants similar to nonmutant plants (Hong and Vierling 2000). Suppression/defects in HSP101 gene expression using antisense suppression, co-suppression or mutants and knockouts plants exhibited serious defects in heat acclimation/thermotolerance (Queitsch et al. 2000; Nieto-Sotelo et al. 2002), indicating that HSP101 protein is essential for plant survival under heat stress. HS results in heat-shock granule (HSG) formation in cytoplasm. The presence of these high-molecular-weight complexes has been shown to be important for the survival of cells subjected to heat stress. Smykal et al. (2000) have shown that these complexes are predominantly composed of LMW HSPs, HSP 40 and HSP 70. These granules have shown a chaperone-like activity. The 90 amino acids long C-terminal domain of LMW HSPs (α-crystallin domain) is conserved among higher plants. This complex family of HSPs plays vital roles in various subcellular locations in plants including protections from HS. The various subcellular locations where sHSPs are found include cytosol, mitochondria, chloroplast, nucleus, endoplasmic reticulum and peroxisomes, where they mainly exist in the form of oligomers (>8 monomers) in a functional state (Yang et al. 2019). Chloroplast and mitochondrial small HSPs known as csHSPs and mHSPs, respectively, are known to protect electron transfer machinery in these organelles under HS. It has been reported that differential accumulation of csHSPs was correlated to the heat tolerance of photosystems in ecotypes of *Chenopodium album* through protecting photosynthetic proteins from HS-induced oxidative stress (Downs et al. 1999; Barua et al. 2003). Constitutive overexpression of sHSPs in chloroplast and mitochondria resulted in enhanced thermotolerance in tomato and tobacco (Sanmiya et al. 2004; Neta-Sharir et al. 2005; Guo et al. 2007). sHSPs are important in developmental programs and especially important in the protection of thermosensitive tissues such as anthers in tomato (Giorno et al. 2010) and cork oak somatic embryos (Puigderrajols et al. 2002). In different rice cultivars, expression of 20 kDa sHSP was selective in HS-tolerant varieties, while other HSPs were expressed in all varieties studied (Iqbal et al. 2010).

Heat stress transcription factors (HSFs) are the central regulons of HS transcriptome expression in plants. Plant have many HSFs coding gene classified into three major evolutionary classes known as A, B and C (Kotak et al. 2007). The *N*-terminal domain of all HSFs is essential for binding to the heat stress promoter elements (HSEs) specifically. HSEs are recognized as repeated palindromic motifs (5′-AGAAnnTTCT-3′), upstream of transcription initiation site of HSPs and many other HS-inducible genes. *LpHsfA1* and *AtHsfA2* have been widely studied and considered master regulators of HS-induced transcriptome in tomato and *Arabidopsis*, respectively. Overexpression of theses TF genes resulted in enhanced thermotolerance, while mutants of these genes exhibited serious defects in acquired thermotolerance (Mishra et al. 2002; Charng et al. 2007; Nishizawa et al. 2007; Ogawa et al. 2007).

Overexpression of HSPs and HSFs in different plant species resulted in enhanced thermotolerance. Transgenic plants showed significantly enhanced thermotolerance in different physiological processes including photosynthesis (Neta-Sharir et al. 2005; Xue et al. 2010), antioxidant defence (Panchuk et al. 2002) and increased seedling survival or seed germination rates after imposition of HS. Due to different initial growth temperatures (18–25 °C for *Arabidopsis*), thermotolerance assay temperatures and time periods (35–49 °C for 1 h to 5 days in *Arabidopsis*), it is difficult to compile and conclude from present-day literature on heat-tolerant transgenic plants. Many reports have shown altered expression of many other HSPs and/or stress-related genes in plants overexpressing HSFs and HSPs or knockout plants (Panchuk et al. 2002; Sakuma et al. 2006; Charng et al. 2007; Yokotani et al. 2008). Whole-genome microarray studies during heat stress also showed altered expression of more than 4000 genes during heat acclimation in *Arabidopsis* (Larkindale and Vierling 2008). Some of the studies were conducted with heat acclimation (Panchuk et al. 2002; Charng et al. 2007; Yokotani et al. 2008) before heat stress, thus showing enhanced survival rates of overexpressing plants and decreased capacity to acclimate in knockout plants (Sakuma et al. 2006; Charng et al. 2007). Specific parameters were taken as a measure of thermotolerance in different transgenics; however, growth and seed yield-related parameters were not reported. Constitutive, ectopic or stress-induced expression of single HSP and HSF gene led to enhanced thermotolerance under highly defined conditions only in model plants, which could not be transformed to agronomically important heat-tolerant crops due to highly complex genetic response of plants to heat stress.

Major oxidative stress-responsive genes such as APX are controlled by HSFs (Suzuki and Mittler 2006). HSF overexpressing transgenic *Arabidopsis* exhibited a novel heat-responsive isozyme of APX (Panchuk et al. 2002). In *Arabidopsis,* H_2O_2

accumulated due to HS is essential for sustained expression of HSPs. Many genes such as HsfA4a, Zat 12, RbohD and MAPK3 are associated with H_2O_2 signalling in plants and are also responsive to other abiotic stresses resulting in enhanced production of H_2O_2. Interestingly HSFs are now being considered as potential redox-sensing molecules in plants. HsfA4a and HsfA8 are now being considered as major TFs that might also act as a H_2O_2 and redox sensor in *Arabidopsis* (Miller and Mittler 2006).

Besides HSFs, many other potential regulons are now being increasingly implicated in acquired thermotolerance including DREB family and WRKY TFs. DREB2A, a transcription regulating mainly dehydration-responsive genes, is reported to be a regulator of HSFA3 in *Arabidopsis* (Sakuma et al. 2006). These results indicate that there is an HSF-mediated crosstalk between heat and other abiotic stress signalling, for example, HS-mediated upregulation of DREB gene family member LeDREB1 in tomato (Frank et al. 2009). Recently, it was shown that HS-induced inhibition of phosphorylation of DREB2A resulted in enhanced thermotolerance in *Arabidopsis* (Mizoi et al. 2019). Overexpression of some of these families may result in enhanced thermotolerance and knockdown in severe loss in heat acclimation and basal heat tolerance (Sakuma et al. 2006; Hong et al. 2009; Li et al. 2009). In addition, bZIP Tfs are also being implicated in heat stress tolerance. The overexpression of bZIP-type TF ABF3 involved in ABA signalling imparts HS tolerance in *Arabidopsis* (Kim et al. 2004). However, knockdown of bZIP28 gene in *Arabidopsis* resulted in severe chlorosis and decreased expression of HSP genes, and retransformation of these plants with full ORF of bZIP28 resulted in regaining of thermotolerance (Gao et al. 2008). Multiprotein binding factor 1c (MBF1c) is also reported recently to be the regulator of thermotolerance in *Arabidopsis*. MBF1c accumulates rapidly and is localized to nucleus during heat stress, and MBF1c knockout plants showed decreased basal and acquired thermotolerance (Suzuki et al. 2008).

Heat tolerance is a complex response of plants involving mainly, but not limited to, HSFs and HSPs and other TFs. Beyond these, other signalling pathways and other biochemical and molecular changes also influence acquisition of thermotolerance in plants. For example, mutants disrupting calcium, salicylic acid, ethylene, abscisic acid and hydrogen peroxide signalling pathways exhibited defects in heat acclimation despite accumulating sufficient amounts of HSPs (Larkindale et al. 2005). Spraying plants with these signalling molecules resulted in enhanced thermotolerance with or without the corresponding increase in HSP levels (Larkindale and Knight 2002). Hence, HS response in plants is a highly complex process involving more than 20 different HSFs, other TFs and signalling networks. TFs are responsible for the regulation of gene expression of HSPs and other defence proteins. HSPs are important for cellular maintenance during HS and acting as chaperones in protein folding and play other multitudes of functions in heat acclimation process.

10.3.3.2 Transcriptome Changes Under High Temperature Stress

Heat stress response is a multigenic trait, and many genes exhibited altered expression under HS in plants. Whole-genome sequence information of model plant *Arabidopsis* and many other crops like rice, wheat, chickpea and pigeon pea has a significant impact on genome-wide functional analysis of HS-responsive genes in plants. Whole-genome expression studies are performed using microarray analysis and next-generation sequencing (NGS) data. After the discovery of these gene expression analysis technologies, a significant number of studies have been reported in model plants as well as crops under heat stress. Microarray studies under HS in *Arabidopsis*, wheat, maize, soybean and rice revealed an altered expression of many genes (Table 10.1, Busch et al. 2005; Larkindale and Vierling 2008; Hu et al. 2009; Mittal et al. 2009; Sarkar et al. 2009; Singh et al. 2010; Bita et al. 2011; Chauhan et al. 2011; Khurana et al. 2011; Mangelsen et al. 2011; Zhang et al. 2012a, b; Jung et al. 2013).

Whole-genome expression studies in *Arabidopsis* exhibited that majority of the genes responsive to heat stress are regulated by HsfA1a/HsfA1b (Busch et al. 2005). Mittal et al. (2009) further proved the same in transcriptome of rice. Microarray analysis of Hsfs in various tissues of rice including shoot, root and panicles demonstrated the role of OsHsfA2a in regulation of HS transcriptome in all the tissues (Chauhan et al. 2011). Heat stress-induced early flowering in *Arabidopsis* is also regulated through heat-responsive genes in the absence of photoperiodic effects (Balasubramanian et al. 2006). Microarray studies in barley under heat stress revealed that heat stress differentially regulated gene expression at the seedling stage compared to the reproductive stage (Oshino et al. 2011). Similarly, Qin et al. (2008) revealed that short-term heat stress altered expression of higher number of genes compared to prolonged heat stress.

Next-generation sequencing (NGS) is a highly robust tool for gene expression analysis. NGS involves sequencing of whole transcriptome. The NGS technologies available are Roche 454 (based on pyrose-sequencing), Illumina/HiSeq and sequencing using oligonucleotide ligation and detection (SoLiD). NGS technologies have been used as a tool for gene expression analysis under abiotic/biotic stresses in plants (Varshney et al. 2009). Using Illumina sequencing of heat stress-responsive transcriptome exhibited the differential expression of many genes in *Arabidopsis* and other plants (Table 10.1, Gulledge et al. 2012; Li et al. 2013). Majority of the genes upregulated were *Hsfs* and *Hsps* coding genes together with some stress-responsive transcription factors and metabolic genes. NGS has also been successfully used to identify HS-regulated small miRNAs and sRNAs involved in heat tolerance in model plants and crops (Xin et al. 2010; Jeong et al. 2011; Yu et al. 2011; Barrera-Figueroa et al. 2012; Chen et al. 2012). Hence, the revolution in the form of microarray and NGS technologies contributed towards a better understanding of genome-wide changes in response to HS in plants.

Table 10.1 Summary of some of the transcriptomics studies of plants using microarray and next-generation sequencing tools under high temperature stress

Plant	Technique used and effects on gene expression	References
Rice	Microarray analysis under heat stress at 40 °C for 20 min to 8 h exhibited upregulation of many transcription factor families including *Hsfs*, *NAC*, *AP2/ERF*, *WRKY*, *MYB*, C_2H_2 and many *hsp* genes, cellulose biosynthesis genes	Zhang et al. (2012a, b)
Rice	2-week-old seedling stressed at 42 °C for 10 h root microarray exhibited upregulation of *Hsfs*, *Hsp70*, *HSP90*, *HSP100* and *sHSPs* families	Hu et al. (2009)
Rice	Microarray analysis of 10-day-old seedlings stressed at 42 °C resulted in upregulation of *sHAPs*, *hspP30*, *hsp90*, *hsp* and *cytochrome P450* genes	Mittal et al. (2009)
Rice	2-week-old seedlings subjected to heat stress at 37 °C for 1 h exhibited a twofold increase in 710 genes including *Hsfs*, *bZIP* TFs and *hsps*	Jung et al. (2013)
Arabidopsis	Illumina RNA-Seq of *Arabidopsis* cDNA library prepared from plants subjected to heat stress revealed *SR45a* mediated alternate splicing of heat-induced transcribed genes	Gulledge et al. (2012)
Arabidopsis	RNA-Seq analysis of heat-stressed transgenic *Arabidopsis* constitutively overexpressing tomato *hsf SIHsfA3* revealed upregulation of many *hsp* genes families leading to enhance thermotolerance	Li et al. (2013)
Arabidopsis	Microarray studies on *Arabidopsis* seedlings under heat stress with and without acclimations revealed the essential role of *hsp101*, *hsp110*, *Hsfs* and *APX2* in heat acclimation	Larkindale and Vierling (2008)
Wheat	Microarray study on wheat seedlings at the flowering stage subjected to heat stress at 37 °C or 42 °C for 2 h showed upregulation of *hps*, transporters and signalling molecules in developing wheat flowers	Khurana et al. (2011)
Wheat	Using Affymetrix wheat genome array of 10-day-old seedlings stressed at 40 °C for 1 h with and without acclimation, it was revealed that many genes involved in hormone, calcium and sugar signalling differently expressed apart from upregulation of *Hsfs* and *hsps*	Qin et al. (2008)
Wheat	Microarray study on wheat seedlings at the flowering stage subjected to heat stress at 37 °C or 42 °C for 2 h showed upregulation of *hsps*, *Hsfs*, *bZIP* TFs and calmodulins	Chauhan et al. (2011)
Barley	Using microarray of developing barley seeds heat-stressed for 0.5–6 h revealed upregulation of 958 genes and downregulation of 1122 genes. Hsfs and hsps genes upregulated, while genes related to storage compound synthesis and cell growth were downregulated	Mangelsen et al. (2011)
Tomato	Microarray studies on heat stress-tolerant and susceptible varieties showed that long-term heat stress tolerance in tolerant genotype was due to constitutive expression of *hsps* compared to the susceptible genotype which showed lower expression of *hsps* after 2 h of stress	Bita et al. (2011)

(continued)

Table 10.1 (continued)

Plant	Technique used and effects on gene expression	References
Tomato	Microarray analysis of heat-stressed developing tomato microspores showed upregulation of *Hsfs*, *hsps* and antioxidant defence-related genes	Frank et al. (2009)
Banana	RNA-Seq analysis of cDNA library of 6-week-old banana seedlings subjected to lethal heat stress at 55 °C for 2 h with or without acclimation showed genes related to *Hsfs*, *hsps*, ROS-scavenging and fatty acid metabolism were significantly upregulated in heat-acclimated plants compared to directly stressed plants	Vidya et al. (2018)

10.3.3.3 Epigenetic Regulation of High Temperature Stress

Apart from the various genetic, biochemical and physiological regulation of HS responses in plants, a lot of work has been done towards the understanding of epigenetic regulation of HS response. Epigenetic changes are transgenerational adaptive responses of plants which include changes through DNA methylation, histone chaperones, histone modifications, histone variants, small RNAs and long noncoding RNAs.

DNA Methylation

DNA methylation is a process of addition of methyl group to cysteine bases of DNA. Methylation of DNA defends genome from selfish DNA elements (transposons and retrotransposons) and regulates gene expression through transcriptional gene silencing (Liu et al. 2015b). DNA methylation is differentially regulated by HS in different plants. Heat stress enhanced DNA methylation and homologous recombination in *Arabidopsis* (Boyko et al. 2010). Several genes related to genome methylation, viz. domains regulated methyltransferase-2 (DRM2), nuclear RNA polymerase-1 (NRPD-1) and NRPE1, are known to be upregulated under HS in *Arabidopsis* (Naydenov et al. 2015). Enhanced DNA methylation under HS is known in trees and crops in addition to model plants (Table 10.2). Heat-tolerant cultivars of Brassica exhibited lower levels of genome methylation compared to the heat-susceptible genotypes under HS (Gao et al. 2014). Heat-induced hypomethylation of genome is attributed to lower expression of genes involved in DNA methylation like DRM1 and DRM3 in cotton (Min et al. 2014). Popova et al. (2013) reported that *Arabidopsis* mutants defective in DNA methylation exhibited declined basal thermotolerance and RNA-directed DNA methylation (RdDM) is essential for plants' survival under high temperature stress. Mutants of chromomethylase 2 *crm2* showed improved thermotolerance, while *nrpd2* mutants are reported to be hypersensitive to HS (Pandey et al. 2016). These studies showed that DNA methylation plays an important role in heat stress response in plants.

Table 10.2 Summary of some studies on epigenetic regulations involved in heat stress responses in plants

Plant	Epigenetic responses	References
Arabidopsis	• DNA methylation • Histone acetylation • miRNAs interference • Histone chaperones modifications • Upregulation of epigenetic regulators • siRNAs • ATP-dependent chromatin remodelling • CAF-1-dependent chromatin assembly complex	Pecinka et al. (2010) Mlynarova et al. (2007) Singh et al. (2014) Boyko et al. (2010) Liu et al. (2015a) Zhang et al. (2012a, b) Weng et al. (2014)
Rice	• DNA methylation • Hypomethylation at CHG site	Ou et al. (2012) Folsom et al. (2014)
Wheat	• miRNAs • Long noncoding RNAs	Xin et al. (2010) Xin et al. (2011)
Maize	• Genome hypermethylation • Histone modifications • Histone variants	Wang et al. (2015) Eichten and Springer (2015)
Barley	• miRNAs	Kruszka et al. (2014)
Cotton	• DNA methylation • Histone modifications	Min et al. (2014)
Brassica sp.	• DNA methylation • miRNAs • Chloroplast small RNAs (csRNAs)	Bilichak et al. (2015) Wang et al. (2011) Yu et al. (2013)
Grapevine	• Transgenerational stress memory inheritance of DNA methylation	Baránek et al. (2015)
Cork oak	• DNA methylation • Histone modifications	Correia et al. (2013)
Nicotiana benthamiana	• siRNAs	Andika et al. (2013)

Histone Modifications, Chaperons and Variants

Covalent modifications to histone tails via acetylation, methylation, ubiquitination, phosphorylation, carbonylation, sumoylation and glycosylation are affected by HS in plants. HSF1 transcription factor-mediated acetylation of histones H3/4 and H3K4 methylation results in the initiation of transcription in unicellular alga *Chlamydomonas* under HS (Strenkert et al. 2011). Acetylation of histone H3 declined under HS in cork oak (Correia et al. 2013). Downregulation of histomethyltransferase gene and histone monoubiquitination genes is reported under heat stress in cotton anthers (Min et al. 2014). However, the exact role of histone covalent modifications remains to be studied in plant heat stress tolerance. Histone chaperones play an essential role in nucleosome assembly during replication and transcription. H3-H4 and H2A-H2B chaperones are classified based on their preference for binding to histones. Chromatin assembly factor 1 (CAF1) is essential for the formation of chromatin assembly complex for replication and transcription.

Mutants lacking CAF-1 exhibited heat sensitivity and lost the recovery capacity after exposure to HS (Pecinka et al. 2010). CAF-1-dependent chromatin assembly complex plays an important role in the protection of germ line from heat-induced epigenetic changes (Pecinka et al. 2010). In addition, the variants of histones H2A, viz. H2A.Z containing nucleosome, are reported to be involved in heat sensing (Kumar and Wigge 2010). However, more studies are needed to pinpoint the roles of individual histone modifications and histone variants in heat tolerance.

Small RNAs

Small noncoding RNAs typically 18–30 nucleotide strands are known to regulate gene expression differentially under HS in plants. The two major classes of small RNAs present in the plants are MicroRNAs (miRNAs) and small interfering RNAs (siRNAs). Several miRNAs responsive to heat stress are conserved in plants which are regulated differentially during HS in different plants. Several families of miRNAs are known to respond to HS in *Arabidopsis* and other crop plants including miR156, miR159, miR160, miR162, miR167, miR168, miR169, miR171, miR408, miR827 families, etc. (Zhong et al. 2013; Kumar et al. 2014a, b; Liu et al. 2015b). Several HS-responsive miRNAs also respond to other abiotic stresses like drought (Ballen-Taborda et al. 2013; Liu et al. 2015b). Hence, miRNAs are components of regulatory networks for heat and other abiotic stresses in plants. siRNAs are 24 nucleotides of small RNAs and are the products of repetitive sequences in genome which are major sites of DNA methylation via RdDM pathway. Many siRNAs are known to be affected under heat stress in plants. siRNAs are major posttranscriptional gene silencing (PTGS) components. PTGS pathways are induced through sense transgene (S-PTGS), antisense transgene (A-PTGS), inverted repeat transgene (IR-PTGS) and virus replication (VIGS). Heat stress results in the initiation of S-PTGS and A-PTGS in plants (Zhong et al. 2013). Chloroplast small RNAs (csRNAs) are also responsive to HS, and many csRNAs silence the target chloroplast genes under heat stress.

Epigenetic or transgenerational changes in the DNA are adaptive responses against environmental cues. Heat stress leads to transgenerational changes in plants (Boyko et al. 2010; Liu et al. 2015b; Pandey et al. 2016). Heat-induced methylation of DNA, changes in histones, etc. may lead to the diverse phenotypic plasticity during long-term evolution in plants.

10.4 Conclusions and Future Research

Climatic models have predicted the warming of earth by 1.5–4 °C by the end of the twenty-first century with a significant impact on agricultural productivity and thus diminishing world food security (IPCC 2013). A rise of one degree in temperature is predicted to reduce wheat production by 6%. In order to maintain food security and agricultural production in the future, it is necessary to understand the response of plants to heat stress and stress combinations so that appropriate strategies can be planned to breed stress-tolerant crop plants. Air temperatures higher than the optimum threshold for longer period cause irreversible damage to plants and thus cause heat stress (Teixeira et al. 2013). Heat stress is often associated with increase in soil temperature and loss of moisture resulting in drought stress and consequently water stress to plants. Hence, heat stress effects on plant growth and productivity may be aggravated due to accompanied drought stress. Heat stress response starts with the perception of stress and results in sensing, signal transduction and gene expression. HS influences both the source and sink capacity of the plant. Growth and photosynthesis are reduced, and leaf senescence is enhanced under HS, thus reducing the source availability. Chloroplast is the major organelle influenced by heat stress. Plants adapt and acclimate to heat stress in order to survive and reproduce by altering the metabolism considerably in chloroplast which results in the breakdown of chlorophyll, ROS generation, enhancing antioxidant defence and turnover of proteins involved in carbon assimilation. Stay-green character is a desirable trait in crops under heat stress and helps in maintaining higher yield. Heat stress also reduces source availability and sink capacity by reducing both grain number and grain weight, thus influencing important commercial traits, i.e. grain yield and quality. An important strategy of crop plants growing under field is to acquire thermotolerance by exposure to episodes involving gradual increase in high temperatures and involves induction of several plant processes. Heat acclimation involves upregulation of antioxidant defence, induction of HSFs, HSPs and major changes in the transcriptome of plants. Studies done using *Arabidopsis* mutants have shown that important players involved in the development and maintenance of acquired thermotolerance include HSPs, ABA, ROS and SA pathways. Identification of high temperature-tolerant germplasm of different crops and its further transfer to high-yielding varieties with the help of conventional breeding programs and marker-assisted selection will help in better understanding of the genetic and physiological basis of heat tolerance in crops. Effort is needed to identify germplasm in different crops having tolerance to heat stress and heat stress and drought combination specifically during flowering and grain development so that crops can be bred tolerant to stresses occurring together.

References

Abdelrahman M, El-Sayed M, Jogaiah S, Burritt DJ, Lam-Son Phan T (2017) The "STAY-GREEN" trait and phytohormone signaling networks in plants under heat stress. Plant Cell Rep 36:1009–1025

Ahmad P, Jaleel CA, Azooz MM, Nabi G (2009) Generation of ROS and non-enzymatic antioxidants during abiotic stress in plants. Bot Res Intern 2:11–20

Akter N, Islam MR (2017) Heat stress effects and management in wheat. A review. Agron Sustain Dev 37:37

Alka P, Khanna-Chopra R (1995) Influence of temperature on germination, seedling growth and amylase activity in wheat varieties differing in temperature tolerance. Indian J Exp Biol 33:775–779

Allakhverdiev SI, Kreslavski VD, Klimov VV, Los DA, Carpentier R, Mohanty P (2008) Heat stress: an overview of molecular responses in photosynthesis. Photosynth Res 98:541–550

Almeselmani M, Deshmukh PS, Sairam RK (2009) High temperature stress tolerance in wheat genotypes: role of antioxidant defense enzymes. Acta Agron Hung 57:1–14

Anderson JA, Padhye SR (2004) Protein aggregation, radical scavenging capacity, and stability of hydrogen peroxide defense systems in heat-stressed vinca and sweet pea leaves. J Am Soc Hortic Sci 129:54–59

Andika IB, Sun L, Xiang R, Li J, Chen J (2013) Root-specific role for Nicotiana benthamiana RDR6 in the inhibition of Chinese wheat mosaic virus accumulation at higher temperatures. Mol Plant Microbe Interact 26:1165–1175

Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: an overview. Photosynthetica 51:163–190

Ashraf MA, Iqbal M, Rasheed R, Hussain I, Riaz M, Arif MS (2018) Environmental stress and secondary metabolites in plants: an overview. In: Plant metabolites and regulation under environmental stress. Academic, Cambridge, pp 153–167

Awasthi R, Bhandari K, Nayyar H (2015) Temperature stress and redox homeostasis in agricultural crops. Front Environ Sci 3:11. https://doi.org/10.3389/fenvs.2015.00011

Bahuguna RN, Solis CA, Shi W, Jagadish KSV (2016) Post-flowering night respiration and altered sink activity account for high night temperature-induced grain yield and quality loss in rice (*Oryza sativa*). Physiol Plant 159:59–73. https://doi.org/10.1111/ppl.12485

Balasubramanian S, Sureshkumar S, Lempe J, Weigel D (2006) Potent induction of Arabidopsis thaliana flowering by elevated growth temperature. PLoS Genet 2:106

Ballen-Taborda C, Plata G, Ayling S, Rodriguez-Zapata FB, Lopez-Lavalle LA, Duitama J (2013) Identification of cassava microRNAs under abiotic stress. Int J Genomic 2013:857–986

Baránek M, Čechová J, Raddová J, Holleinová V, Ondrušíková E, Pidra M (2015) Dynamics and reversibility of the DNA methylation landscape of grapevine plants (*Vitis vinifera*) stressed by in vitro cultivation and thermotherapy. PLoS One 10(5):0126638

Barrera-Figueroa BE, Gao L, Wu ZG, Zhou XF, Zhu JH, Jin HL, Liu RY, Zhu JK (2012) High throughput sequencing reveals novel and abiotic stress-regulated microRNAs in the inflorescences of rice. BMC Plant Biol 12:132

Barua D, Downs CA, Heckathorn SA (2003) Variation in chloroplast small heat shock protein function is a major determinant of variation in thermotolerance of photosynthetic electron transport among ecotypes of *Chenopodium album*. Funct Plant Biol 30:1071–1079

Bergmüller E, Porfirova E, Dőrmann P (2003) Characterization of an Arabidopsis mutant deficient in γ-tocopherol methyltransferase. Plant Mol Biol 52:1181–1190

Bilichak A, Ilnytskyy Y, Woycicki R, Kepeshchuk N, Fogen D, Kovalchuk I (2015) The elucidation of stress memory inheritance in *Brassica rapa* plants. Front Plant Sci 6:5

Bita CE, Zenoni S, Vriezen WH, Mariani C, Pezzotti M, Gerats T (2011) Temperature stress differentially modulates transcription in meiotic anthers of heat-tolerant and heat-sensitive tomato plants. BMC Genomics 12:384

Bokszczanin KL, Fragkostefanakis S (2013) Solanaceae pollen thermotolerance initial training network (SPOT-ITN) consortium and perspectives on deciphering mechanisms underlying plant heat stress response and thermotolerance. Front Plant Sci 4:315. https://doi.org/10.3389/fpls.2013.00315

Boyko A, Blevins T, Yao Y, Golubov A, Bilichak A, Ilnytskyy Y (2010) Transgenerational adaptation of *Arabidopsis* to stress requires DNA methylation and the function of dicer-like proteins. PLoS One 5:9514

Brock TD (1967) Life at high temperature. Science 158:1012–1019

Busch W, Wunderlich M, Schoffl F (2005) Identification of novel heat shock factor-dependent genes and biochemical pathways in *Arabidopsis thaliana*. Plant J 41:1–14

Camejo D, Jiménez A, Alarcón JJ, Torres W, Gómez JM, SSevill F (2006) Changes in photosynthetic parameters and antioxidant activities following heat-shock treatment in tomato plants. Funct Plant Biol 33:177–187

Camejo D, Rodríguez P, Morales MA, Dell'amico JM, Torrecillas A, Alarcón JJ (2005) High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. J Plant Physiol 162:281–289

Carter C, Thornburg RW (2000) Tobacco Nectarin I. Purification and characterization as germ-like manganese superoxide dismutase implicated in the defense of floral reproductive tissues. J Biol Chem 275:26726–36733

Charng YY, Liu HC, Liu NY, Chi WT, Wang CN, Chang SH, Wang TT (2007) A heat inducible transcription factor, HsfA2, is required for extension of acquired thermotolerance in *Arabidopsis*. Plant Physiol 143:251–262

Chauhan H, Khurana N, Agarwal P, Khurana P (2011) Heat shock factors in rice (*Oryza sativa* L.) genome-wide expression analysis during reproductive development and abiotic stress. Mol Genet Genomics 286:171–187

Chauhan S, Srivalli S, Nautiyal AR, Khanna-Chopra R (2009) Wheat cultivars differing in heat tolerance show a differential response to monocarpic senescence under high temperature stress and the involvement of serine proteases. Photosynthetica 47(4):536–547

Chen L, Ren Y, Zhang Y, Xu J, Sun F, Zhang Z, Wang Y (2012) Genome-wide identification and expression analysis of heat-responsive and novel microRNAs in Populus tomentosa. Gene 504:160–165

Christensen JH, Christensen OB (2007) A summary of the PRUDENCE model projections of changes in European climate by the end of this century. Clim Chang 81:7–30. https://doi.org/10.1007/s10584-006-9210-7

Coast O, Ellis RH, Murdoch AJ, Quiñones C, KSV J (2014) High night temperature induces contrasting responses for spikelet fertility spikelet tissue temperature, flowering characteristics and grain quality in rice. Funct Plant Biol 42:149–161

Correia B, Valledor L, Meijon M, Rodriguez JL, Dias MC, Santos C (2013) Is the interplay between epigenetic markers related to the acclimation of cork oak plants to high temperatures? PLoS One 8:53543

Crafts-Brandner SJ, Law RD (2000) Effect of heat stress on the inhibition and recovery of the ribulose-1,5-bisphosphate carboxylase/oxygenase activation state. Planta 212:67–74

Dash S, Mohanty N (2002) Response of seedlings to heat stress in cultivars of wheat: growth temperature-dependent differential modulation of photosystem 1 and 2 activity, and foliar antioxidant defense capacity. J Plant Physiol 159:49–59

Dat JF, Lopez-Delgado H, Foyer CH, Scott IM (1998) Parallel changes in H_2O_2 and catalase during thermotolerance induced by salicylic acid or heat acclimation in mustard seedlings. Plant Physiol 116:1351–1357

Downs CA, Rayen SL, Heckathorn SA (1999) The chloroplast small heat-shock protein: evidence for a general role in protecting photosystem-II against oxidative stress and photoinhibition. J Plant Physiol 155:477–487

Dutta S, Mohanty S, Tripathy BC (2009) Role of temperature stress on chloroplast biogenesis and protein import in pea. Plant Physiol 150:1050–1061

Eichten SR, Springer NM (2015) Minimal evidence for consistent changes in maize DNA methylation patterns following environmental stress. Front Plant Sci 6:308

Essemine J, Ammar S, Bouzid S (2010) Impact of heat stress on germination and growth in higher plants: physiological, biochemical and molecular repercussions and mechanisms of defence. J Biol Sci 10:565–572

Farooq M, Nadeem F, Gogoi N, Ullah A, Alghamdi SS, Nayyar H (2017) Heat stress in grain legumes during reproductive and grain-filling phases. Crop Pasture Sci 68:985–1005. https://doi.org/10.1071/CP17012

Folsom JJ, Begcy K, Hao X, Wang D, Walia H (2014) Rice fertilization-independent endosperm1 regulates seed size under heat stress by controlling early endosperm development. Plant Physiol 165:238–248

Foyer CH (2018) Reactive oxygen species, oxidative signaling and the regulation of photosynthesis. Environ Exp Bot 154:134–142

Frank G, Pressman E, Ophir R, Altman L, Shaked R, Freedman M, Shen S, Firon M (2009) Transcriptional profiling of maturing tomato (*Solanum lycopersicum* L.) microspores reveals the involvement of heat shock proteins, ROS scavengers, hormones and sugars in the heat stress response. J Exp Bot 60:3891–3908

Gao G, Li J, Li H, Li F, Xu K, Yan G (2014) Comparison of the heat stress induced variations in DNA methylation between heat-tolerant and heat-sensitive rapeseed seedlings. Breed Sci 64:125–133

Gao H, Brandizzi F, Benning C, Larkin RM (2008) A membrane-tethered transcription factor defines a branch of the heat stress response in *Arabidopsis thaliana*. Proc Natl Acad Sci U S A 105:16398–16403

Giacomelli L, Masi A, Ripoll DR, Lee MJ, Van Wijk KJ (2003) *Arabidopsis thaliana* deficient in two chloroplast ascorbate peroxidases shows accelerated light induced necrosis when levels of cellular ascorbate are low. Plant Mol Biol 65:627–644

Giorno F, Wolters-Arts M, Grillo S, Scharf K-D, Vriezen WH, Mariani C (2010) Developmental and heat stress-regulated expression of HsfA2 and small heat shock proteins in tomato anthers. J Exp Bot 61:453–462

Gous PW, Hickey L, Christopher JT, Franckowiak J, Fox GP (2016) Discovery of QTL for stay-green and heat-stress in barley (*Hordeum vulgare*) grown under simulated abiotic stress conditions. Euphytica 207:305–317

Greer DH, Weedon MM (2012) Modelling photosynthetic responses to temperature of grapevine (*Vitis vinifera* cv. Semillon) leaves on vines grown in a hot climate. Plant Cell Environ 35:1050–1064

Gulledge AA, Roberts AD, Vora H, Patel K, Loraine AE (2012) Mining Arabidopsis thaliana RNA-seq data with integrated genome browser reveals stress-induced alternative splicing of the putative splicing regulator SR45a. Am J Bot 99:219–231

Guo SJ, Zhou HY, Zhang XS, Li XG, Meng QW (2007) Overexpression of *CaHSP26* in transgenic tobacco alleviates photoinhibition of PS-II and PS-I during chilling stress and low irradiance. J Plant Physiol 164:126–136

Gur A, Demirel U, Őzden M, Kahraman A, Copur O (2010) Diurnal gradual heat stress affects antioxidant enzymes, praline accumulation and some physiological components in cotton (*Gossypium hirsutum* L.). Afr J Biotechnol 9:1008–1015

Gusta LV, Benning NT, Wu G, Luo X, Liu X, Gusta ML, McHughen A (2009) Superoxide dismutase: an all-purpose gene for agri-biotechnology. Mol Breed 24:103–115

Hasanuzzaman M, Nahar K, Alam MDM, Roychowdhury R, Fujita F (2013) Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plant. Int J Mol Sci 14:9643–9684

Havaux M, Lütz C, Grimm B (2003) Chloroplast membrane photostability in chlP transgenic tobacco plants deficient in tocopherols. Plant Physiol 132:300–310

Hemavathi, Upadhyaya CP, Akula N, Young KE, Chun SC, Kim DH, Park SW (2010) Enhanced ascorbic acid accumulation in transgenic potato confers tolerance to various abiotic stresses. Biotechnol Lett 32:321–330

Hong B, Ma C, Yang Y, Wang T, Yamaguchi-Shinozaki K, Gao J (2009) Over-expression of AtDREB1A in chrysanthemum enhances tolerance to heat stress. Plant Mol Biol 70:231–240

Hong SW, Vierling E (2000) Mutants of *Arabidopsis thaliana* defective in the acquisition of tolerance to high temperature stress. Proc Natl Acad Sci U S A 97:4392–4397

Hu WH, Hu GC, Han B (2009) Genome-wide survey and expression profiling of heat shock proteins and heat shock factors revealed overlapped and stress specific response under abiotic stresses in rice. Plant Sci 176:583–590

Huang SZ, Tang XJ, Zhang L, Fu JR (2003) Thermotolerance and activity of antioxidative enzymes in Lotus seed. J Plant Physiol Mol Biol 29:421–424

Im YJ, Ji M, Lee A, Killens R, Grunden AM, Boss WF (2009) Expression of *Pyrococcus furiosus* superoxide reductase in *Arabidopsis* enhances heat tolerance. Plant Physiol 151:893–904

Ioannidi E, Kalamaki MS, Engineer C, Peteraki I, Alexandrou D, Mellidou I, Giovannonni J, Kanellis AK (2009) Expression profiling of ascorbic acid-related genes during tomato fruit development and ripening and in response to stress conditions. J Exp Bot 60:663–678

IPCC (2013) Working group I contribution to the IPCC fifth assessment report climate change: the physical science basis, summary for policymakers. http://www.climatechange2013.org/images/report/WG1AR5SPMFINAL.pdf (verified 20.06.16)

Iqbal N, Farooq S, Arshad R, Hameed A (2010) Differential accumulation of high and low molecular weight heat shock proteins in basmati rice (*Oryza sativa* L.) cultivars. Genet Resour Crop Evol 57:65–70

Jain M, Chourey PS, Boote KJ, Allen LH (2010) Short-term high temperature growth conditions during vegetative-to-reproductive phase transition irreversibly compromise cell wall invertase-mediated sucrose catalysis and microspore meiosis in grain sorghum (*Sorghum bicolor*). J Plant Physiol 167:578–582

Jain M, Prasad PVV, Boote KJ, Allen LH, Chourey PS (2007) Effects of season-long high temperature growth conditions on sugar-to-starch metabolism in developing microspores of grain sorghum (*Sorghum bicolor* L. Moench). Planta 227:67–79

Jajic I, Sarna T, Strzalka K (2015) Senescence, stress, and reactive oxygen species. Plan Theory 4:393–411

Jeong DH, Park S, Zhai J, Gurazada SG, De Paoli ED, Meyers BC, Green PJ (2011) Massive analysis of rice small RNAs: mechanistic implications of regulated microRNAs and variants for differential target RNA cleavage. Plant Cell 23:4185–4207

Jiang YW, Huang BG (2001) Effects of calcium on antioxidant activities and water relations associated with heat tolerance in two cool-season grasses. J Exp Bot 52:341–349

Jochum GM, Mudge KW, Thomas RB (2007) Elevated temperatures increase leaf senescence and root secondary metabolite concentration in the understory herb *Panax quinquefolius* (Araliaceae). Am J Bot 94:819–826

Jordan DB, Ogren WL (1984) The CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase dependence on ribulose 1,5-bisphosphate concentration, pH and temperature. Planta 161:308–313

Jung KH, Ko HJ, Nguyen MX, Kim SR, Ronald P, An G (2013) Genome-wide identification and analysis of early heat stress responsive genes in rice. J Plant Biol 55:458–468

Karim MA, Fracheboud Y, Stamp P (1999) Photosynthetic activity of developing leaves is less affected by heat stress than that of developed leaves. Physiol Plant 105:685–693

Kaur P, Ghai N, Sangha MK (2009) Induction of thermotolerance through heat acclimation and salicylic acid in *Brassica* species. Afr J Biotechnol 8:619–625

Kaushal N, Bhandari K, Siddique KH, Nayyar H (2016) Food crops face rising temperatures: an overview of responses, adaptive mechanisms, and approaches to improve heat tolerance. Cogent Food Agric 2:1134380

Kaushal N, Gupta K, Bhandhari K, Kumar S, Thakur P, Nayyar H (2011) Proline induces heat tolerance in chickpea (*Cicer arietinum* L.) plants by protecting vital enzymes of carbon and antioxidative metabolism. Physiol Mol Biol Plants 17(3):203

Khanna-Chopra R (2012) Leaf senescence and abiotic stresses share reactive oxygen species-mediated chloroplast degradation. Protoplasma 249:469–481

Khanna-Chopra R, Chauhan S (2015) Wheat cultivars differing in heat tolerance show a differential response to oxidative stress during monocarpic senescence under high temperature stress. Protoplasma 252(5):1241–1251. https://doi.org/10.1007/s00709-015-0755-z

Khanna-Chopra R, Jajoo A, Semwal VK (2011) Chloroplast and mitochondria contain multiple heat stable isozymes of SOD and APX in leaves and inflorescence in *Chenopodium album*. Biophys Biochem Res Commun 412:522–525

Khanna-Chopra R, Semwal VK (2011) Superoxide dismutase and ascorbate peroxidase are constitutively more thermotolerant than other antioxidant enzymes in *Chenopodium album*. Physiol Mol Biol Plants 17(4):339–346

Khanna-Chopra R, Sundaram S (2004) Heat-stable chloroplastic Cu/Zn superoxide dismutase in *Chenopodium murale*. Biochem Biophys Res Commun 320:1187–1192

Khurana P, Chauhan H, Khurana N (2011) Characterization and expression of high temperature stress responsive genes in bread wheat. J Genet Plant Breed 47:S94–S97

Kilian J, Whitehead D, Horak J, Wanke D, Weinl S, Batistic O, D'Angelo C, Bornberg-Bauer E, Kudla J, Harter K (2007) The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. Plant J 50:347–363

Kim HS, Ji CY, Lee CJ, Kim SE, Park SC, Kwak SS (2018) Orange: a target gene for regulating carotenoid homeostasis and increasing plant tolerance to environmental stress in marginal lands. J Exp Bot 69(14):3393–3400

Kim S, Kang JY, Cho DI, Park JH, Kim SY (2004) ABF2, an ABRE-binding bZIP factor is an essential component of glucose signaling and its over-expression affects multiple stress tolerance. Plant J 40:75–87

Kocsy G, Kobrehel K, Szalai G, Duviau MP, Buzás Z, Galiba (2004a) Thioredoxin and glutathione as abiotic stress tolerance markers in maize. Environ Exp Bot 52:101–112

Kocsy G, Laurie R, Szalai G, Szilágyi V, Simon-Sarkadi L, Galiba G, de Ronde JA (2005) Genetic manipulation of praline levels affects antioxidants in soybeans subjected to simultaneous drought and heat stresses. Physiol Plant 124:227–235

Kocsy G, Szalai G, Sutka J, Páldi E, Galiba G (2004b) Heat tolerance together with heat stress-induced changes in glutathione and hydroxymethyl glutathione levels is affected by chromosome 5A of wheat. Plant Sci 166:451–458

Kocsy G, Szalai G, Vágújfalvi A, Stéhli L, Orosz G, Galiba G (2000) Genetic study of glutathione accumulation during cold hardening in wheat. Planta 210:295–301

Kotak S, Larkindale J, Lee U, von Koskull-Doring P, Vierling E, Scharf KD (2007) Complexity of the heat stress response in plants. Curr Opin Plant Biol 10:310–316

Kruk J, Hollander-Czytko H, Oettmeier W, Trebst A (2005) Tocopherol as singlet oxygen scavenger in photosystem-II. J Plant Physiol 162:749–757

Kruszka K, Pacak A, Swida-Barteczka A, Nuc P, Alaba S, Wroblewska Z (2014) Transcriptionally and post-transcriptionally regulated microRNAs in heat stress response in barley. J Exp Bot 65:6123–6135

Kumar RR, GGoswam S, Gadpayle KA, Singh K, Sharma SK, Singh GP, Pathak H, Rai RD (2014a) Ascorbic acid at pre-anthesis modulate the thermotolerance level of wheat (Triticum aestivum) pollen under heat stress. J Plant Biochem Biotechnol 23:293–306

Kumar RR, Pathak H, Sharma SK, Kala YK, Nirjal MK, Singh GP, Goswami S, Rai RD (2014b) Novel and conserved heat-responsive microRNAs in wheat (*Triticum aestivum* L.). Funct Integr Genomics 15(3):323–348. https://doi.org/10.1007/s10142-014-0421-0

Kumar SV, Wigge PA (2010) H2A.Z-containing nucleosomes mediate the thermosensory response in *Arabidopsis*. Cell 140:136–147

Larkindale J, Hall JD, Knight MR, Vierling E (2005) Heat stress phenotypes of *Arabidopsis* mutants implicate multiple signaling pathways in the acquisition of thermotolerance. Plant Physiol 138:882–897

Larkindale J, Huang B (2004) Thermotolerance and antioxidant systems in *Agrostis stolonifera*: involvement of salicylic acid, abscisic acid, calcium, hydrogen peroxide and ethylene. J Plant Physiol 161:405–413

Larkindale J, Knight MR (2002) Protection against heat stress-induced oxidative damage in *Arabidopsis* involves calcium, abscisic acid, ethylene and salicylic acid. Plant Physiol 128:682–695

Larkindale J, Vierling E (2008) Core genome response involved in acclimation to high temperature. Plant Physiol 146:748–761

Law R, Crafts-Brandner SJ (1999) Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase/oxygenase. Plant Physiol 120:173–182

Lee SH, Ahsan N, Lee KW, Kim DH, Lee DG, Kwak SS, Kwon SY, Kim TH, Lee BH (2007) Simultaneous overexpression of both Cu/Zn superoxide dismutase and ascorbate peroxidase in transgenic tall fescue plants confers increased tolerance to a wide range of abiotic stresses. J Plant Physiol 164:1626–1638

Lee U, Wie C, Escobar M, Williams B, Hong SW, Vierling E (2005) Genetic analysis reveals domain interactions of Arabidopsis Hsp100/ClpB and cooperation with the small heat shock protein chaperone system. Plant Cell 17:559–571

Li Y, Liu Y, Zhang J (2010) Advances in the research on the AsA-GSH cycle in horticultural crops. Front Agric China 4:84–90

Li Z, Zhang L, Wang A, Xu X, Li J (2013) Ectopic overexpression of slhsfa3, a heat stress transcription factor from tomato, confers increased thermotolerance and salt hypersensitivity in germination in transgenic Arabidopsis. PLoS One 8(1):54880. https://doi.org/10.1371/journal.pone.0054880

Li ZS, Fu Q, Huang W, Yu D (2009) Functional analysis of an Arabidopsis transcription factor *WRKY25* in heat stress. Plant Cell Rep 28:683–693

Lin K-H, Huang H-C, Lin C-Y (2010) Cloning, expression and physiological analysis of broccoli catalase and Chinese cabbage ascorbate peroxidase gene under heat stress. Plant Cell Rep 29:575–593

Liu F, Wang W, Sun X, Liang Z, Wang F (2015a) Conserved and novel heat stress-responsive microRNAs were identified by deep sequencing in *Saccharina japonica* (*Laminariales, Phaeophyta*). Plant Cell Environ 38(7):1357–1367. https://doi.org/10.1111/pce.12484

Liu HT, Sun DY, Zhou RG (2005) Ca_2+ and AtCaM3 are involved in the expression of heat shock protein gene in Arabidopsis. Plant Cell Environ 28(10):276–1284

Liu J, Feng L, Li J, He Z (2015b) Genetic and epigenetic control of plant heat responses. Front Plant Sci 6:267

Lv WT, Lin B, Zhang M, Hua XJ (2011) Proline accumulation is inhibitory to Arabidopsis seedlings during heat stress. Plant Physiol 156(4):1921–1933

Mangelsen E, Kilian J, Harter K, Jansson C, Wanke D, Sundberg E (2011) Transcriptome analysis of high-temperature stress in developing barley caryopses: early stress responses and effects on storage compound biosynthesis. Mol Plant 4:97–115

Mathur S, Agrawal D, Jajoo A (2014) Photosynthesis: response to high temperature stress. J Photochem Photobiol 137:116–126

Meiri D, Tazat K, Cohen-Peer R, Farchi-Pisanty O, Aviezer-Hagai K, Avni A (2010) Involvement of *Arabidopsis* ROF2 (FKBP65) in thermotolerance. Plant Mol Biol 72:191–203

Miao Y, Laun TM, Zimmermann P, Zentgraf U (2004) Targets of WRKY53 transcription factor and its role during leaf senescence in *Arabidopsis*. Plant Mol Biol 55:853–867

Miller G, Mittler R (2006) Could heat shock transcription factors function as hydrogen peroxide sensors in plants. Ann Bot 98:279–288

Min L, Li Y, Hu Q, Zhu L, Gao W, Wu Y (2014) Sugar and auxin signaling pathways respond to high-temperature stress during anther development as revealed by transcript profiling analysis in cotton. Plant Physiol 164:1293–1308

Mishra SK, Tripp J, Winkelhaus S, Tschiersch B, Theres K, Nover L, Scharf KD (2002) In the complex family of heat stress transcription factors, HsfA1 has a unique role as master regulator of thermotolerance in tomato. Genes Dev 16:1555–1567

Mittal D, Chakrabarti S, Sarkar A, Singh A, Grover A (2009) Heat shock factor gene family in rice: genomic organization and transcript expression profiling in response to high temperature, low temperature and oxidative stresses. Plant Physiol Biochem 47:785–795

Mittler R (2006) Abiotic stress, the field environment and stress combination. Trends Plant Sci 11:15–19

Mizoi J, Kanazawa N, Kidokoro S, Takahashi F, Qin F, Morimoto K, Shinozaki K, Yamaguchi-Shinozaki K (2019) Heat-induced inhibition of phosphorylation of the stress-protective transcription factor DREB2A promotes thermotolerance of Arabidopsis thaliana. J Biol Chem 294(3):902–917

Mlynarova L, Nap JP, Bisseling T (2007) The SWI/SNF chromatin-remodeling gene *AtCHR12* mediates temporary growth arrest in *Arabidopsis thaliana* upon perceiving environmental stress. Plant J 51:874–885

Narayanan S, Prasad PVV, Fritz AK, Boyle DL, Gill BS (2015) Impact of high night time and high daytime temperature stress on winter wheat. J Agron Crop Sci 201:206–218

Naydenov M, Baev V, Apostolova E, Gospodinova N, Sablok G, Gozmanova M (2015) High-temperature effect on genes engaged in DNA methylation and affected by DNA methylation in *Arabidopsis*. Plant Physiol Biochem 87:102–108

Neta-Sharir I, Isaacson T, Lurie S, Weiss D (2005) Dual role for tomato heat shock protein 21: protecting photosystem ii from oxidative stress and promoting color changes during fruit maturation. Plant Cell 17:1829–1838

Nieto-Sotelo J, Ho THD (1986) Effect of heat shock on the metabolism of glutathione in maize roots. Plant Physiol 82:1031–1035

Nieto-Sotelo J, Martínez LM, Ponce G, Cassab GI, Alagón A, Meeley RB, Ribaut JM, Yang R (2002) Maize HSP101 plays important roles in both induced and basal thermotolerance and primary root growth. Plant Cell 14:1621–1633

Nishizawa A, Yabuta Y, Yoshida E, Maruta T, Yoshimura K, Shigeoka S (2007) *Arabidopsis* heat shock transcription factor A2 as a key regulator in response to several types of environmental stress. Plant J 48:535–547

Niu Y, Xiang Y (2018) An overview of biomembrane functions in plant responses to high-temperature stress. Front Plant Sci 9:915. https://doi.org/10.3389/fpls.2018.00915

Ogawa D, Yamaguchi K, Nishiuchi T (2007) High level expression of Arabidopsis *HsfA2* gene confers not only increased thermotolerance but also salt/osmotic stress tolerance and enhanced callus growth. J Exp Bot 58:3373–3383

Oshino T, Miura S, Kikuchi S, Hamada K, Yano K, Watanabe M, Higashitani A (2011) Auxin depletion in barley plants under high-temperature conditions represses DNA proliferation in organelles and nuclei via transcriptional alterations. Plant Cell Environ 34:284–290

Ou X, Zhang Y, Xu C, Lin X, Zang Q, Zhuang T, Jiang L, von Wettstein D, Liu B (2012) Transgenerational inheritance of modified DNA methylation patterns and enhanced tolerance induced by heavy metal stress in rice (*Oryza sativa* L.). PLoS One 7(9):41143

Panchuk II, Volkov RA, Schŏffl F (2002) Heat stress- and heat shock transcription factor-dependent expression and activity of ascorbate peroxidase in *Arabidopsis*. Plant Physiol 129:838–853

Pandey G, Sharma N, Pankaj SP, Prasad M (2016) Chromatin-based epigenetic regulation of plant abiotic stress response. Curr Genomics 17(6):490–498

Parrotta L, Faleri C, Cresti M, Cai G (2016) Heat stress affects the cytoskeleton and the delivery of sucrose synthase in tobacco pollen tubes. Planta 243:43–63

Patil RV, Chinnusamy V, Chauhan S, Ruwali KN, Pandey HN, Khanna-Chopra R (2008) Heat stress tolerance in *T. aestivum* and *T. durum* wheat genotypes under continual and terminal heat stress environments. J Plant Biol 34:1–10

Pecinka A, Dinh HQ, Baubec T, Rosa M, Lettner N, Mittelsten Scheid O (2010) Epigenetic regulation of repetitive elements is attenuated by prolonged heat stress in *Arabidopsis*. Plant Cell 22:3118–3129

Peñuelas J, Munné-Bosch S (2005) Isoperanoids: an evolutionary pool for photoprotection. Trends Plant Sci 10:166–169

Pinto RS, Lopes MS, Collins NC, Reynolds MP (2016) Modelling and genetic dissection of stay-green under heat stress. Theor Appl Genet 129:2055–2074

Popova OV, Dinh HQ, Aufsatz W, Jonak C (2013) The RdDM pathway is required for basal heat tolerance in *Arabidopsis*. Mol Plant 6:396–410

Pospíšil P (2016) Production of reactive oxygen species by photosystem II as a response to light and temperature stress. Front Plant Sci 7:1950. https://doi.org/10.3389/fpls.2016.01950

Prasad PVV, Bheemanahalli R, Jagdish SK (2017) Field crops and the fear of heat stress-opportunities, challenges and future directions. Field Crops Res 200:114–121. https://doi.org/10.1016/j.fcr.2016.09.024

Prasad PVV, Djanaguiraman M (2011) High night temperature decreases leaf photosynthesis and pollen function in grain sorghum. Funct Plant Biol 38:993–1003

Prashanth SR, Sadhasivam V, Parida A (2008) Over expression of cytosolic copper/zinc superoxide dismutase from a mangrove plant Avicennia marina in Indica rice var Pusa Basmati-1 confera abiotic stress tolerance. Transgenic Res 17:281–291

Puigderrajols P, Jofre A, Mir G, Pla M, Verdaguer D, Huguet G, Molinas M (2002) Developmentally and stress-induced small heat shock proteins in cork oak somatic embryos. J Exp Bot 53:1445–1452

Qin D, Wu H, Peng H, Yao Y, Ni Z, Li Z, Zhou C, Sun Q (2008) Heat stress-responsive transcriptome analysis in heat susceptible and tolerant wheat (Triticum aestivum L.) by using Wheat Genome Array. BMC Genomics 9:432

Queitsch C, Hong SW, Vierling E, Lindquest S (2000) Heat shock protein 101 plays a crucial role in thermotolerance in *Arabidopsis*. Plant Cell 12:479–492

Rahman MA, Chikushi J, Yoshida S, Karim AJMS (2009) Growth and yield components of wheat genotypes exposed to high temperature stress under control environment. Bangladesh J Agric Res 34:361–372

Rivero RM, Ruiz JM, Romero L (2004) Oxidative metabolism in tomato plants subjected to heat stress. J Hortic Sci Biotechnol 79:560–564

Rivero RM, Ruiz JM, Garcı́a PC, López-Lefebre LR, Sánchez E, Romero L (2001) Resistance to cold and heat stress: accumulation of phenolic compounds in tomato and watermelon plants. Plant Sci 160(2):315–321

Rizhsky L, Liang H, Mittler R (2002) The combined effect of drought stress and heat shock on gene expression in tobacco. Plant Physiol 130:1143–1151

Rosa SB, Caverzan A, Teixeira FK, Lazzarotto F, Silveira JAG, Ferreira-Silva SL, Abreu-Neto J, Margis R, Margis-Pinheiro M (2010) Cytosolic APX knockdown indicates an ambiguous redox response in rice. Phytochemistry 71:548–558

Rosenvasser S, Mayak SET, Friedman H (2006) Increase in reactive oxygen species (ROS) and in senescence-associated gene transcript (SAG) levels during dark-induced senescence of Pelargonium cuttings, and the effect of gibberellic acid. Plant Sci 170:873–879

Ruelland E, Zachowski A (2010) How plant sense temperature. Environ Exp Bot 69:225–232

Sadiq M, Akram NA, Ashraf M, Al-Qurainy F, Ahmad P (2019) Alpha-tocopherol-induced regulation of growth and metabolism in plants under non-stress and stress conditions. J Plant Growth Regul 1:16

Sage RF, Kubien DS (2007) The temperature response of C3 and C4 photosynthesis. Plant Cell Environ 30:1086–1106

Saidi Y, Finka A, Goloubinoff P (2011) Heat perception and signalling in plants: a tortuous path to thermotolerance. New Phytol 190:556–565. https://doi.org/10.1111/j.1469-8137.2010.03571

Saidi Y, Finka A, Muriset M, Bromberg Z, Weiss YG, Maathuis FJM, Goloubinoff P (2009) The heat shock response in moss plant is regulated by specific calcium permeable channels in plasma membrane. Plant Cell 21:2829–2843

Sairam RK, Srivatava GC, Saxsena DC (2006) Increased antioxidant activity under elevated temperatures: a mechanism of heat stress tolerance in wheat genotyped. Biol Plant 43:245–251

Sakuma Y, Maruyama K, Osakabe Y, Qin F, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2006) Functional analysis of an *Arabidopsis* transcription factor, DREB2A, involved in drought-responsive gene expression. Plant Cell 18:1292–1309

Salvucci ME, Crafts-Brandner SJ (2004) Relationship between the heat tolerance of photosynthesis and the thermal stability of Rubisco activase in plants from contrasting thermal environments. Plant Physiol 134:1460–1470

Sanmiya K, Suzuki K, Egawa Y, Shono M (2004) Mitochondrial small heat shock protein enhances thermotolerance in tobacco plants. FEBS Lett 557:265–268

Sarkar NK, Kim YK, Grover A (2009) Rice sHsp genes: genomic organization and expression profiling under stress and development. BMC Genomics 10:393

Scandalios JG, Acevedo A, Ruzsa S (2003) Catalase gene expression in response to chronic high temperature stress in maize. Plant Sci 156:103–110

Schramm F, Larkindale J, Kiehlmann E, Englich G, Walch D, von Koskull-Doring P (2006) The heat stress transcription factor HsfA2 serves as a regulatory amplifier of a subset of genes in the heat stress response in *Arabidopsis*. Plant Mol Boil 60:759–772

Schroda M, Hemme D, Mühlhaus T (2015) The *Chlamydomonas* heat stress response. Plant J 82:466–480. https://doi.org/10.1111/tpj.12816

Sehgal A, Sita K, Siddique KHM, Kumar R, Bhogireddy S, Varshney RK, HanumanthaRao B, Nair RM, Prasad PVV, Nayyar H (2018) Drought or/and heat-stress effects on seed filling in food crops: impacts on functional biochemistry, seed yields, and nutritional quality. Front Plant Sci 9:1705. https://doi.org/10.3389/fpls.2018.01705

Shafi A, Chauhan R, Gill T, Swarnkar MK, Sreenivasulu Y, Kumar S, Kumar N, Shankar R, Ahuja PS, Singh AK (2015) Expression of SOD and APX genes positively regulates secondary cell wall biosynthesis and promotes plant growth and yield in Arabidopsis under salt stress. Plant Mol Biol 87(6):615–631

Sharkey TD (2005) Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. Plant Cell Environ 28:269–277

Shirdelmoghanloo H, CCozzolin D, Lohraseb I, Collins NC (2016) Truncation of grain filling in wheat (*Triticum aestivum*) triggered by brief heat stress during early grain filling: association with senescence responses and reductions in stem reserves. Funct Plant Biol 43:919–930

Singh A, Singh U, Mittal D, Grover A (2010) Genome-wide analysis of rice ClpB/HSP100, ClpC and ClpD genes. BMC Genomics 11:95

Singh P, Yekondi S, Chen PW, Tsai CH, Yu CW, Wu K (2014) Environmental history modulates *Arabidopsis* pattern-triggered immunity in a histone acetyltransferase1-dependent manner. Plant Cell 26:2676–2688

Sirko A, Blaszczyk A, Liszewska F (2004) Overproduction of SAT and/or OASTL in transgenic plants: a survey of effects. J Exp Bot 55:1881–1888

Smykal P, Hrdy I, Pechan PM (2000) High-molecular-mass complexes formed in vivo contain smHSPs and HSP70 and display chaperone-like activity. Eur J Biochem 267:2195–2207

Strenkert D, Schmollinger S, Sommer F, Schulz-Raffelt M, Schroda M (2011) Transcription factor-dependent chromatin remodeling at heat shock and copper-responsive promoters in *Chlamydomonas reinhardtii*. Plant Cell 23:2285–2301

Suzuki N, Bajad S, Shuman J, Shulaev V, Mittler R (2008) The transcriptional co-activator MBF1c is a key regulator of thermotolerance in *Arabidopsis thaliana*. J Biol Chem 283:9269–9275

Suzuki N, Katano K (2018) Coordination between ROS regulatory systems and other pathways under heat stress and pathogen attack. Front Plant Sci 9:490. https://doi.org/10.3389/fpls.2018.00490

Suzuki N, Mittler R (2006) Reactive oxygen species and temperature stress: a delicate balance between signaling and destruction. Physiol Plant 126:45–51

Szalai G, Kellős T, Galiba G, Kocsy G (2009) Glutathione as an antioxidant and regulatory molecule in plants under abiotic stress conditions. Plant Growth Regul 28:66–80

Teixeira EI, Fischer G, Velthuizen HV, Walter C, Ewert F (2013) Global hotspots of HS on agricultural crops due to climate change. Agric Meteorol 170:206–215

Todorov DT, Karanov EN, Smith AR, Hall MA (2003) Chlorophyllase activity and chlorophyll content in wild type and eti 5 mutant of Arabidopsis thaliana subjected to low and high temperatures. Biol Plant 46:633–636

Varshney RK, Nayak SN, May GD, Jackson SA (2009) Next-generation sequencing technologies and their implications for crop genetics and breeding. Trends Biotechnol 27(9):522–530

Verma N, Shukla S (2015) Impact of various factors responsible for fluctuation in plant secondary metabolites. J Appl Res Med Aromat Plants 2(4):105–113. https://doi.org/10.1016/j.jarmap.2015.09.002

Vidya SM, Kumar HV, Bhatt RM, Laxman RH, Ravishankar KV (2018) Transcriptional profiling and genes involved in acquired thermotolerance in Banana: a non-model crop. Sci Rep 8(1):10683

Viswanathan C, Khanna-Chopra R (2001) Effect of heat stress on grain growth, starch synthesis and protein synthesis in grains of wheat (*Triticum aestivum* L.) varieties differing in grain weight stability. J Agron Crop Sci 186:1–10

Vollenweider P, Günthardt-Goerg MS (2005) Diagnosis of abiotic and biotic stress factors using the visible symptoms in foliage. Environ Pollut 137:455–465

Wahid A, Gelani S, Ashraf M, Foolad MR (2007) Heat tolerance in plants: an overview. Environ Exp Bot 61:199–223

Wang L, Yu X, Wang H, Lu YZ, De Ruiter M, Prins M (2011) A novel class of heat-responsive small RNAs derived from the chloroplast genome of Chinese cabbage (*Brassica rapa*). BMC Genomics 2:289

Wang LJ, Li SH (2006) Thermotolerance and related antioxidant enzyme activities induced by heat acclimation and salicylic acid in grape (*Vitis vinifera L.*). Plant Growth Regul 48:137–144

Wang P, Zhao L, Hou H, Zhang H, Huang Y, Wang Y, Li H, Gao F, Yan S, Li L (2015) Epigenetic changes are associated with programmed cell death induced by heat stress in seedling leaves of *Zea mays*. Plant Cell Physiol 56(5):965–976

Wang QL, Chen JH, He NY, Guo FQ (2018) Metabolic reprogramming in chloroplasts under heat stress in plants. Int J Mol Sci 19:1–22

Wang Y, Wisniewski M, Meilan R, Cui M, Fuchigami L (2006) Transgenic tomato (*Lycopersicon esculentum*) overexpressing cAPX exhibits enhanced tolerance to UV-B and heat stress. J Appl Hortic 8:87–90

Wang Y, Wisniewski M, Meilan R, Uratsu SL, Cui M, Dandekar A, Fuchigami L (2007) Ectopic expression of Mn-SOD in *Lycopersicon esculentum* leads to enhanced tolerance to salt and oxidative stress. J Appl Hortic 9:3–8

Wilhelm EP, Mullen RE, Keeling PL, Singletary GW (1999) Heat stress during grain filling in maize: effects on kernel growth and metabolism. Crop Sci 39:1733–1741

Wise RR, Olson AJ, Schrader SM, Sharkey TD (2004) Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. Plant Cell Environ 27:717–724

Xin M, Wang Y, Yao Y, Song N, Hu Z, Qin D (2011) Identification and characterization of wheat long non-protein coding RNAs responsive to powdery mildew infection and heat stress by using microarray analysis and SBS sequencing. BMC Plant Biol 11:61

Xin M, Wang Y, Yao Y, Xie C, Peng H, Nil Z, Sun Q (2010) Diverse set of microRNAs are responsive to powdery mildew infection and heat stress in wheat (*Triticum aestivum* L.). BMC Plant Biol 10:123

Xue Y, Peng R, Li X, Zha D, Yao Q (2010) Over-expression of heat shock protein gene *hsp26* in *Arabidopsis thaliana* enhances heat tolerance. Biol Plant 54:106–111

Yamakawa H, Hakata M (2010) Atlas of rice grain filling-related metabolism under high temperature: joint analysis of metabolome and transcriptome demonstrated inhibition of starch accumulation and induction of amino acid accumulation. Plant Cell Physiol 51:795–809

Yan J, Yu L, Xuan J, Lu Y, Lu S, Zhu W (2016) De novo transcriptome sequencing and gene expression profiling of spinach (*Spinacia oleracea* L.) leaves under heat stress. Sci Rep 6:19473

Yang S, Na Y, Im S, Jo J, Nguyen TD, Kim JS, Choi DW (2019) PtsHSP19. 6, a small heat-shock protein from the marine red alga *Pyropia tenera* (Rhodophyta), aggregates into granules and enhances heat tolerance. J Appl Phycol 31:1–9

Yang X, Wen X, Gong H, Lu Q, Yang Z, Tang Y, Liang Z, Lu C (2007) Genetic engineering of the biosynthesis of glycinebetaine enhances thermotolerance of photosystem II in tobacco plants. Planta 225:719–733

Ye LA, Gao HY, Zou Q (2000) Responses of antioxidant systems and xanthophyll cycle in phaseolus vulgaris to combined stress of high irradiance and high temperature. Photosynthetica 38:205–210

Yin H, Chen Q, Yi M (2008) Effects of short-term heat stress on oxidative damage and response of antioxidant system in *Lilium longiflorum*. Plant Growth Regul 54:45–54

Yokotani N, Ichikawa T, Kondou Y, Matsui M, Hirochika H, Iwabuchi M, Oda K (2008) Expression of rice heat stress transcription factor OshsfA2e enhances tolerance to environmental stresses in transgenic *Arabidopsis*. Planta 227:957–967

Yu K, Niranjana Murthy H, Hahn E, Paek K (2005) Ginsenoside production by hairy root cultures of *Panax ginseng*: influence of temperature and light quality. Biochem Eng J 23:53–56

Yu X, Wang H, Lu Y, Ruiter M, Cariaso M, Prins M, Tunenn AV, He Y (2011) Identification of conserved and novel microRNAs that are responsive to heat stress in Brassica rapa. J Exp Bot 63(2):1025–1038

Yu X, Yang J, Li X, Liu X, Sun C, Wu F (2013) Global analysis of cis-natural antisense transcripts and their heat-responsive nat-siRNAs in *Brassica rapa*. BMC Plant Biol 13:208

Zandalinas SI, Sales C, Beltrán J, Gómez-Cadenas A, Arbona V (2017) Activation of secondary metabolism in citrus plants is associated to sensitivity to combined drought and high temperatures. Front Plant Sci 7:1954. https://doi.org/10.3389/fpls.2016.01954

Zhang X, Li J, Liu A, Zou J, Zhou X, Xiang J, Rerksiri W, Peng Y, Xiong X, Chen X (2012a) Expression profile in rice panicle: insights into heat response mechanism at reproductive stage. PLoS One 7(11):49652. https://doi.org/10.1371/journal.pone.0049652

Zhang X, Zhang X, Singh J, Li D, Qu F (2012b) Temperature-dependent survival of *Turnip crinkle virus*-infected *Arabidopsis* plants relies on an RNA silencing-based defense that requires DCL2, AGO2, and HEN1. J Virol 86:6847–6854

Zhao H, Dai T, Jing Q, Jiang D, Cao W (2007) Leaf senescence and grain filling affected by post anthesis high temperatures in two different wheat cultivars. Plant Growth Regul 51:149–158

Zhong SH, Liu JZ, Jin H, Lin L, Li Q, Chen Y (2013) Warm temperatures induce transgenerational epigenetic release of RNA silencing by inhibiting siRNA biogenesis in *Arabidopsis*. Proc Natl Acad Sci 110:9171–9176

Chapter 11
Adaptation and Tolerance of Wheat to Heat Stress

Suresh and Renu Munjal

Contents

Abstract Temperature is one of the most important abiotic factors affecting yield of crop plants. Every crop species needs an optimum temperature to show its maximum potential. If the temperature is raised above a critical limit, it may cause irreversible damage to plants. When the temperature is raised beyond a certain limit for period long enough which can cause an irreversible damage to plants, it is called high temperature stress. The effect of high temperature is still more severe for cold-loving plants like wheat. This crop needs a temperature of 12–30 °C to give maximum yield. But in recent years, the increasing temperature is causing serious threat to wheat production. Wheat breeders are facing a dilemma in recent years when on one side the demand of wheat is increasing every year due to increasing population and on second side production is decreasing due to rising temperature. Heat stress causes damage at both morphological and cellular level. It may cause adverse alterations in plant growth, development, cellular and physiological processes, and yield.

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In wheat heat stress particularly at grain filling stage is more harmful. Due to high temperature, reactive oxygen species are generated which is harmful for plants. In their defense, plants try to cope up with heat stress by using mechanism of avoidance or tolerance. In avoidance mechanism, plant completes its life before the onset of stress and never faces the stress. Tolerance mechanism includes alteration in plant metabolism by producing compatible solutes that are able to organize heat response proteins and cellular structures which help in maintaining cell turgor. Morphologically, plant can alter its aerial and root parts which avoid overheating of plant. In wheat, heat-tolerant genotypes try to cool their canopy by increasing uptake of water from soil. In recent time, various biotechnological tools have helped in the identification of genes associated with heat tolerance in plants. Many genes controlling expression of heat response proteins (HRPs) are now tagged. In the present chapter, we have tried to discuss various adaptation mechanisms used by wheat to protect it from heat stress at morphological, cellular, physiological, and molecular level.

Keywords Heat stress · Wheat · Adaptation · Tolerance · Heat response proteins (HRPs)

11.1 Introduction

Plants are the base of life on this planet. Every individual is dependent on plants for their food directly or indirectly. But like other organisms, plants too need an appropriate environment under which these can give their maximum potential. The environment includes both biotic and abiotic components. When any of these components hamper in life cycle of plants, plants are said to be under stress. This stress may be due to biotic or abiotic causes. Insect, pathogens, and weeds are the major factor of biotic stress, while nutrient, temperature, water, etc. come under abiotic stress. About 50% of all yield losses in crop plants are generally caused by most of abiotic stresses (Rodríguez et al. 2006). These stresses cause alteration in plant biology at morphological, physiological, biochemical, and molecular level (Wang et al. 2001; Bita and Gerats 2013). At present time high temperature stress is causing serious challenges in crop production. The term heat stress is commonly used to denote the condition in which temperatures rise above the optimum for a period which can cause irreversible damage in plant growths and yield (Wahid et al. 2007). On an average, global ambient temperatures have increased by 0.13 °C per decade since 1950 (IPCC 2007). The temperature is expected to rise further by the rate of 0.2 °C per decade in the coming years. With this rate, average temperature will be about 5.8 °C more at the end of this century (De Costa 2011). This stress is very unpredictable in nature and depends on both intensity and duration of high temperature. Emission of large amount of greenhouse gases (GHGs) and deforestation are the main causes of this rise in temperature. In previous 40 years, along with GHGs, the concentration of CO_2 is also increased manifold. Although this increase in ambient CO_2 concentration has increased yield of maize and soybean, reverse trend is observed in case of wheat and rice (Lobell et al. 2011). Among these two crops, wheat (*Triticum* spp.) is even more prone to heat stress as it is a cool-season crop. It is one of the most important staple foods globally. It is cultivated in almost every country of the world. The genus *Triticum* includes three cultivated species with different chromosome numbers, i.e., diploid (*T. monococum*), tetraploid (*T. durrum*), and hexaploid (*T. aestivum*). Out of these three, bread wheat (*T. aestivum*) is cultivated in more areas. Wheat is a good source of both carbohydrate and protein. Although wheat productivity has increased manifold in past, the demand of wheat is increasing day by day due to growing population. The world population will increase by 23% reaching 9.6 billion in 2050. About 880 million ton wheat will be required to feed such a huge population (IIWBR 2015). This demand can be fulfilled by increasing yielding potential of wheat under both normal and stress environment. Temperature is one of the most limiting factors in wheat production. This crop requires a low temperature for most of vegetative phase, after which a slow rise in temperature is needed for ample flowering and grain formation. But due to global warming, this low temperature period is shrinking which in turns leads to reduction in wheat yield as it has been already reported in many countries (Alexander et al. 2006; Hennessy et al. 2008). The high temperature stress can further decrease the yield potential of wheat genotypes in the near future. Under such situations, it is very important to study the effects of rising temperature on various stages of wheat. This knowledge then can be used to breed genotypes which are suitable for high temperature environment.

11.2 Interface of Wheat Under Heat Stress

Wheat is an annual C_3, cool temperature-loving plant belonging to Poaceae family. This crop is very sensitive to elevated temperature. About 13.5 million ha of wheat grown in India faces heat stress at some stage of life cycle (Joshi et al. 2007). The optimum temperature for this crop ranges from 12 to 22 °C which is particularly important for grain filling stage (Farooq et al. 2011). Every 1 °C increase above this mean temperature decreases wheat yield by about 10% (Gibson and Paulsen 1999). When wheat is exposed to high temperature, the plant shows accelerated senescence leading to decreased chlorophyll content of leaves. This leads to lower CO_2 assimilation and increased photorespiration due to which shrunken grains are formed (Farooq et al. 2011; Tashiro and Wardlaw 1990). Every stage of this crop is adversely affected when temperature rises beyond a certain limit. According to a laboratory study, the germination of wheat seed is positively correlated with temperature but within the limit of 10–30 °C (Buriro et al. 2011). The temperature above and below this range may lead to poor germination. But in India, germination is not a problem because here wheat is cultivated as a *rabi* season crop. In this country, *khariff* season crops are late planted due to late onset of monsoon which in turn leads to late harvesting. Due to this wheat sowing is postponed up to mid-December. Wheat requires a long period (about 145 days) to complete its life cycle from seed to seed, but due to this late planting, reproductive phase faces high temperature (>30 °C). This creates heat-shock response which is triggered by even a few days of high air temperatures, particularly when the temperature exceeds 32 °C during seed formation (Blumenthal et al. 1994; Stone and Nicolas 1994). As grain yield is a complex trait, it depends on a number of contributing traits. Leaves are the primary source of photosynthesis in plants from where starch translocate to grains. Under temperature stress, plant height is reduced leading to reduction of specific leaf weight (SLW), leaf width, and ultimately total dry weight (Sing 2009). At cellular level photosynthesis is affected due to production of reactive oxygen species (ROS) mainly hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\bullet -}$), and hydroxyl ion ($OH^{\bullet}$) (Schoffl et al. 1999). These ROS are main cause of membrane disintegration due to which chlorophyll loss occurs leading to premature leaf senescence in wheat (Blum and Ebercon 1981). The breakdowns of thylakoid membrane also severely affect photosystem II (PS II) of photosynthesis reaction (Al-Khatib and Paulsen 1999). Photosynthesis is also reduced due to inactivation of enzyme Rubisco, an important enzyme of photosynthetic reaction (Xu et al. 1995). Secondly, rate of carboxylation of Rubisco is reduced, while its oxidase activity upregulated (Salvucci and Crafts-Brandner 2004). Overall the duration of grain filling is reduced due to which lesser number of grains is developed. Also the grains are found to be shriveled due to forced maturity (Hütsch et al. 2019). At elevated temperature, water uptake is also affected causing severe drought problems. This in turn makes the situations more severe as transpiration is affected due to which canopy temperature increases. Nutrient uptake is also reduced which is one of the major factors leading to shriveled grains of low quality.

11.3 Adaptation Mechanism in Wheat for Heat Tolerance

Plants are living organism, but they cannot run away from stress area. But like other organisms, they also have some mechanism to protect themselves from stress like high temperature. It is evident that when there is uniform heat stress, some plants perform better than others due to their inherent mechanisms. This ability of plants to survive, grow, and maintain their optimum productivity under high temperature stress is called heat tolerance (Wahid et al. 2007). There are a large number of morphological, physiological, and biochemical mechanism of heat tolerance adopted by wheat plant.

11.3.1 Escape Mechanism

Plant can maintain their potential either by escape mechanism or by giving a true resistant response to high temperature. In the escape mechanism, plant never faces the heat stress as plant completes its life cycle before the onset of stress. Earliness of wheat genotypes uses this mechanism. Wheat genotypes of short duration can avoid the devasting effect of terminal heat stress. Fast emergence of seedlings and early ground cover by leaves are traits which can be used as selection criteria for earliness (Cossani and Reynolds 2012). Tolerance mechanism either helps in reduction of absorption of harmful solar radiations or protects the plant from these radiations by minimizing their effect on functioning of plants. In wheat folding of leaves, presence of small hairs on leaves and stem waxiness are the key traits which reduce absorption of solar radiations (Bonos and Murphy 1999). For these traits, synthetic wheat and triticale represents good source of genetic variability and exhibit minimum amount of yield reduction under abiotic stresses (Suresh et al. 2018). Under stress conditions, days to heading, days to maturity, plant height, number of effective tillers per plant, and biological yield are important yield attributing parameters. Flag leaf and awn have also proved as affective traits for high temperature tolerance in wheat.

11.3.2 Physiological Trait Adaptations

At physiological level, cell membrane is perhaps most susceptible to rising temperature. Wheat tries to cope up with high temperature stress by maintaining cell membrane integrity (Blum and Ebercon 1981). A tolerant genotype has capacity to protect its membrane from disintegration and thus avoid the leakage of electrolytes. Thus membrane stability can be an important criterion for selection of thermotolerant genotypes (Dhanda and Munjal 2006, 2012). Stability of cell membrane can be accessed by studying osmotic potential of a cell. As the main cause of membrane breakdown is ROS produced due to oxidative stress, tolerant plant has capacity to maintain cool canopy by enhanced transpiration. The plants having lower canopy temperature even under high temperature can be selected as heat-tolerant genotypes (Hütsch et al. 2019). The decreased conductivity of stomata is another cause of reduced photosynthesis under elevated temperature as it halts in the process of transpiration. The process of transpiration is very crucial for plants because it affects a number of physiological processes like water and nutrient uptake, photosynthesis, and maintenance of canopy temperature. As the temperature rises beyond a critical limit, transpiration is stopped adversely affecting all these processes. But heat-tolerant genotype has the ability to maintain higher rate of stomatal conductance at anthesis and grain filling stage under late sown conditions (Pooja and Munjal 2019). Stomatal conductance has a positive correlation with transpiration rate, which is directly linked with cooling of plants and maintenance of water balance in plant.

Some nondestructive methods like canopy temperature (CT) which in turn is negative correlation with transpiration can be used for evaluation of genotypes under heat and drought stress (Munjal and Rana 2003; Munjal and Dhanda 2016). Normalized difference vegetation index (NDVI) which measures the greenness of plant canopy and thus chlorophyll content also exhibit the same trend with respect to different growth stages (Singh and Jaiswal 2013). Wheat genotypes having higher NDVI values will have more chlorophyll content resulting in greater photosynthetic activity and exhibit tolerance to heat stress (Sharma et al. 2018). Stay green nature of delayed senescence of foliage is another important trait associated with stable yield of plants under abiotic stress conditions (Thomas and Ougham 2014). Stay green genotypes exhibit delayed loss of chlorophyll and remain greener even after anthesis. These genotypes have higher photosynthetic assimilation in the late stages of plant development and can utilize nutrients and moisture more efficiently at this stage which contributes to increased crop yield (Harris et al. 2007; Munjal and Dhanda 2016). In wheat, stay green can be used as a criterion for heat tolerance as there is significant variability among wheat genotypes for this trait. Temperature also affects plants indirectly by causing drought stress. To cope up with this situation, plant can adjust their root parameters such that it can absorb more water from soil. Genotypes with cooler canopy and stable yield have higher water use efficiency (WUE) and nutrient use efficiency (NUE) (Singh et al. 2017). Overall a tolerant genotype has higher photosynthesis, transcription, stem reserve mobilization, and water and nutrient use efficiency.

11.3.3 Biochemical Trait Adaptations

At biochemical level, plants start producing specific protein under high temperature stress; these proteins are called heat-shock proteins (HSPs; Lindquist and Craig 1988). Based on molecular weight, there are five categories of HSPs, namely, HSP100s, HSP90s, HSP70s, HSP60s, and the small HSPs (Waters 2013; Sharma et al. 2015; Comastri et al. 2018). Production of HSPs increases in heat-tolerant genotypes as compared to susceptible ones which protect the newly formed proteins from degradation due to high temperature (Maestri et al. 2002; Rampinoa et al. 2009). HSPs also help in translocation of more proteins to the mature grains and thus maintain the bread making quality of wheat (Blumenthal et al. 1991). In case of abiotic stress, production of ROS causes oxidative damage to DNA and proteins in plants which subsequently leads to destruction of functionality of enzymes (Gill and Tuteja 2010). In fact expression of genes coding for HSPs is directly regulated by production of ROS (Volkov et al. 2006). For scavenging the ROS, plants have evolved several antioxidant mechanisms to prevent damages to cells. Several antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and guaiacol peroxidase (POX) and peroxiredoxins (Prxs) are the most important to cope up with oxidative stress (Caverzan et al. 2016). Under multiple abiotic stress conditions, another group of protein, i.e., late embryogenesis abundant (LEA) proteins, are accumulated in plant. These proteins are extremely hydrophilic in nature and allows for a more efficient acquisition of plants to desiccation stabilizing protein and membrane (Battaglia et al. 2008).

11.4 Role of Signaling Molecule in Heat Stress Adaptations

Signal transduction is a mechanism by which signal from environment is received by a cell, in response to which a chain of intracellular reactions starts which at last activate several genes. Every type of abiotic stress causes a change in osmotic condition in cell which acts as signal and bound to receptors present on cell membrane (Zhu 2016). When temperature rises beyond a critical limit, it leads to change in fluidity of plasma membrane which in turn leads to formation of phosphatidic acid (PA) and phosphatidylinositol 4, 5-bisphosphate (PIP2). These molecules act as signal for G-protein-coupled receptor; a heterotrimeric transmembrane protein is the most common type of receptors (Mishkind et al. 2009). Within a cell, it activates a series of proteins which are called second messenger. Some of these messengers cross the nuclear membrane and activate genes associated with heat tolerance. In wheat, heat stress leads to dissociation of chaperon molecules from heat-shock transcription factors (HSFs). Now these HSFs bind heat response elements (HREs) which in turn activate heat response genes (HRGs) (Zhu 2016). In general when there is no stress, bZIP28, a common transcription factor (bound to membrane of endoplasmic reticulum), remains bound to chaperone BIP and thus prevents its movement to nucleus. Once the heat stress occurs, the interaction of bZIP28 and BIP is destabilized leading to dissociation of these molecules. Free molecules of bZIP28 then moved to nucleus where it activates various genes associated with heat tolerance (Abhinandan et al. 2018). When elevated temperature generates ROS in plant cell, HSP 70 and HSP 90 which are present in cell in low amount and bound to TF, HsfA1 destabilized. HsfA1 is free now and can enter in nucleus and activates heat-shock protein coding gene (Ohama et al. 2017). In another pathway, oxidative stress leads to formation of free cytosolic Ca^{2+} which activate another transcription element, DREB2A (Zhang et al. 2012). These all pathway helps in overexpression of HSPs which protects proteins from misfolding. This type of response can also be induced by exogenous application of salicylic acid (SA). Stimulation of genes by SA produces antioxidants which reduces oxidative damage in wheat under heat, drought, and saline conditions (Noreen et al. 2017; Fardus et al. 2018).

11.5 Genetic Adaptation of Wheat to Heat Stress

The heredity component of every individual represents its genotype. It is genotype, environment and their interaction which generate a particular phenotype. So, plant's reaction to any stress like temperature stress is governed by its gene. Only certain gene overexpresses during high temperature and provides a tolerance reaction against high temperature. In general heat-tolerant genotypes have 5% more transcriptomes under stress as compared to non-stress condition (Saidi et al. 2011). In wheat, the chromosomes 3A and 3B contain most of genes associated with heat tolerance (Xu et al. 1996; Ni et al. 2017). In recent years modern techniques such as marker and QTL analysis, functional genomics, transcriptomics, and proteomics have helped researchers in identification of major genes important under abiotic stress conditions. In case of wheat, an F-box gene *TaFBA1* has been identified, which overexpresses during drought conditions and protects the plant cells from harmful effect of ROS (Zhou et al. 2014). When this gene was transformed in tobacco explant, resulting transgenic plants were more stable at temperature above optimum (Li et al. 2018). Similarly, overexpression of wheat genes *WRKY1* and *WRKY33* in transgenic Arabidopsis led to higher degree of thermotolerance (He et al. 2016). In another study, Comastri et al. (2018) mapped four heat-shock protein genes of *sHSP26* family; three on short arm of chromosome 4A and one on 4B. These genes are upregulated under stress condition and help in acquisition of thermotolerance to wheat. Transcriptomic analysis has revealed that as the stress period starts, genes related to flag leaf and grains are overexpressed which helps in maintaining stable yield over wide environment (Su et al. 2019). From this study, three genes, namely, *TaFBR1*, *TaFBR2*, and *TaFBR3*, associated with flavonoid biosynthesis pathway were identified.

These all represent a brief account of genetic mechanism by which plants try to cope up with abiotic stresses. Although a large number of genes are also identified in wheat and related species, still there is hope to find out more genes regulating tolerance mechanism under stress environment.

11.6 Adaptation for High Night Temperature

Wheat is very intolerant to high temperature beginning from germination to maturity. Both day and night temperatures are important when discussing about effect of temperature on this crop. When the day and night temperature exceed 32 and 27 °C, germination is inhibited and if the stress occurred at from anthesis to maturity grain yield and quality is severely affected (Al-Khatib and Paulsen 1990; Reynolds et al. 2000). In case of some cereals like rice, an increase in one degree night temperature about 10% reductions in grain yield is recorded (Peng et al. 2004). This situation may be more severe as the night temperature is expected to increase faster than day temperature in the coming year (Sillmann et al. 2013). When the night temperature exceeds 14 °C, it can cause 32 and 11% reduction in photosynthesis at seedling and late anthesis stage, respectively (Prasad et al. 2008). At seedling stage, tolerant genotypes grow faster and try to produce more leaf area so that they can maintain their canopy cooler at night. But at terminal stage, leaves start drying due to which it cannot maintain canopy temperature. Wheat genotypes possessing awns are more stable under fluctuating night temperature (Blum 1986). At higher night temperature, respiration is increased due to which grain size is reduced. So plants which can maintain their respiration rate in dark hours can tolerate this stress. These plants do not waste their extra energy for cooling of their canopy. Stem reserve mobilization may be the most important trait to select genotypes with tolerance to high night temperature (Garcia et al. 2015). There is still very less knowledge of mechanisms by which night temperature stress can be managed.

11.7 Future Prospects

The demand of wheat is increasing day by day as the population is increasing. Although the productivity of wheat has increased many fold in past century but at present time there is a need to develop genotypes which can perform better under the changing climate conditions. This can be achieved by getting more knowledge about the mechanisms by which wheat plant can cope up with high temperature. Traditional mutational studies and modern tools like markers are quite helpful in the identification of genes associated with heat tolerance. Further allelic variations can be studied using target-induced local lesions in genome (TILLING). Recently most of wheat genome has been sequenced. Now there is a great need to narrow out sequences to genes which are responsible for important biochemical and physiological processes under biotic and abiotic stress conditions. In conclusion varietal development program under heat stress can be achieved with advance knowledge of genes associated with thermotolerance.

References

Abhinandan K, Skori L, Stanic M, Hickerson NMN, Jamshed M, Samuel MA (2018) Abiotic stress signaling in wheat—an inclusive overview of hormonal interactions during abiotic stress responses in wheat. Front Plant Sci 9:1–25

Alexander LV, Zhang X, Peterson TC et al (2006) Global observed changes in daily climate extremes of temperature and precipitation. J Geophys Res Atmos 111:1–22

Al-Khatib K, Paulsen GM (1990) Photosynthesis and productivity during high temperature stress of wheat genotypes from major world regions. Crop Sci 30(5):1127–1132

Al-Khatib K, Paulsen GM (1999) High-temperature effects on photosynthetic processes in temperate and tropical cereals. Crop Sci 39:119–125

Battaglia M, Olvera-Carrillo Y, Garciarrubio A, Campos F, Covarrubias AA (2008) The enigmatic LEA proteins and other hydrophilins. Plant Physiol 148:6–24

Bita CE, Gerats T (2013) Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat tolerance crops. Front Plant Sci 4:273

Blum A (1986) The effect of high temperature stress on wheat leaf and ear photosynthesis. J Exp Bot 37(1):111–118

Blum A, Ebercon A (1981) Cell membrane stability as a measure of drought and heat tolerance in wheat. Crop Sci 21(1):43–47

Blumenthal CS, Batey IL, Bekes F, Wrigley CW, Barlow EWR (1991) Seasonal changes in wheat grain quality associated with high temperature during grain filling. Aust J Agric Res 42:21–30

Blumenthal C, Wrigley C, Batey I, Barlow E (1994) The heat-shock response relevant to molecular and structural changes in wheat yield and quality. Funct Plant Biol 21:901–909

Bonos SA, Murphy JA (1999) Growth responses and performance of Kentucky bluegrass under summer stress. Crop Sci 39(3):770–774

Buriro M, Oad FC, Keerio MI, Tunio S, Gandahi AW, Hassan SW, Oad SM (2011) Wheat seed germination under the influence of temperature regimes. Sarhad J Agric 27(4):539–543

Caverzan A, Casassola A, Brammer SP (2016) Antioxidant responses of wheat plants under stress. Genet Mol Biol 39(1):1–6

Comastri A, Janni M, Simmonds J, Uauy C, Pignone D, Nguyen HT, Marmiroli N (2018) Heat in wheat: exploit reverse genetic techniques to discover new alleles within the *Triticum durum sHsp26* family. Front Plant Sci 9:1337

Cossani CM, Reynolds MP (2012) Physiological traits for improving heat tolerance in wheat. Plant Physiol 160(4):1710–1718

De Costa WAJM (2011) A review of the possible impacts of climate change on forests in the humid tropics. J Nat Sci Found 39:281–302

Dhanda SS, Munjal R (2006) Inheritance of cellular thermo tolerance in bread wheat. Plant Breed 125:557–564

Dhanda SS, Munjal R (2012) Heat tolerance in relation to acquired thermotolerance for membrane lipids in bread wheat. Field Crops Res 135:30–37

Fardus J, Matin MA, Hasanuzzaman M, Hossain MA, Hasanuzzaman M (2018) Salicylic acid-induced improvement in germination and growth parameters of wheat under salinity stress. J Anim Plant Sci 28:197–207

Farooq M, Bramley H, Palta JA, Siddique KHM (2011) Heat stress in wheat during reproductive and grain-filling phases. Crit Rev Plant Sci 30:1–17

Garcia GA, Dreccer MF, Miralles DJ, Serrago RA (2015) High night temperatures during grain number determination reduce wheat and barley grain yield: a field study. Glob Chang Biol 21:4153–4164

Gibson LR, Paulsen GM (1999) Yield components of wheat grown under high temperature stress during reproductive growth. Crop Sci 39(6):1841–1846

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 48:909–930

Harris K, Subudhi PK, Borrell A, Jordan D, Rosenow D, Nguyen H, Mullet J (2007) Sorghum stay-green QTL individually reduce post-flowering drought-induced leaf senescence. J Exp Bot 58:327–338

He GH, Xu JY, Wang YX, Liu JM, Li PS, Ming C, Ma YZ, Xu ZS (2016) Drought-responsive WRKY transcription factor genes TaWRKY1 and TaWRKY33 from wheat confer drought and/or heat resistance in Arabidopsis. BMC Plant Biol 16:116

Hennessy K, Fawcett R, Kirono D et al (2008) An assessment of the impact of climate change on the nature and frequency of exceptional climatic events. CSIRO and Bureau of Meteorology, Aspendale

Hütsch BW, Jahn D, Schubert S (2019) Grain yield of wheat (*Triticum aestivum* L.) under long-term heat stress is sink-limited with stronger inhibition of kernel setting than grain filling. J Agron Crop Sci 205:22–32

IIWBR (2015) Vision 2050. ICAR-Indian Institute of Wheat and Barley Research, Karnal

IPCC (2007) The physical science basis. In: Solomon S et al (eds) Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Joshi AK, Mishra B, Chatrath R, Ferrara GO, Singh RP (2007) Wheat improvement in India: present status, emerging challenges and future prospects. Euphytica 157:431–446

Li Q, Wang W, Wang W, Zhang G, Liu Y, Wang Y, Wang W (2018) Wheat F-Box protein gene *TaFBA1Is* involved in plant tolerance to heat stress. Front Plant Sci 9:521

Lindquist S, Craig E (1988) The heat-shock proteins. Annu Rev Genet 22:631–677

Lobell DB, Schlenker W, Costa-Roberts J (2011) Climate trends and global crop production since 1980. Science 333:616–620

Maestri E, Klueva N, Perrotta C et al (2002) Molecular genetics of heat tolerance and heat shock proteins in cereals. Plant Mol Biol 48:667–681

Mishkind M, Vermeer JEM, Darwish E, Munnik T (2009) Heat stress activates phospholipase D and triggers PIP2 accumulation at the plasma membrane and nucleus. Plant J 60:10–21

Munjal R, Dhanda SS (2016) Assessment of drought resistance in Indian wheat cultivars for morphophysiological traits. Ekin J Crop Breed Genet 2(1):74–81

Munjal R, Rana RK (2003) Evaluation of physiological traits in wheat (*Triticum aestivum* L.) for terminal high temperature tolerance. In: Proceedings of the tenth international wheat genetics symposium, classical and molecular breeding, Poestum, Italy, vol 2, pp 804–805

Ni Z, Li H, Zhao Y, Peng H, Hu Z, Xin M, Sun Q (2017) Genetic improvement of heat tolerance in wheat: recent progress in understanding the underlying molecular mechanisms. Crop J 6:32–41

Noreen S, Fatima K, Athar HUR, Ahmad S, Hussain K (2017) Enhancement of physio-biochemical parameters of wheat through exogenous application of salicylic acid under drought stress. J Anim Plant Sci 27:153–163

Ohama N, Sato H, Shinozaki K, Yamaguchi-Shinozaki K (2017) Transcriptional regulatory network of plant heat stress response. Trends Plant Sci 22:53–65

Peng S, Huang J, Sheehy JE, Laza RC, Visperas RM, Zhong X (2004) Rice yields decline with higher night temperature from global warming. Proc Nat Acad Sci 101:9971–9975

Pooja, Munjal R (2019) Heat tolerant wheat genotypes for late sown conditions identified on the basis of physiological traits. J Agrometeorol 21(1):97–100

Prasad PVV, Staggenborg SA, Ristic Z (2008) Impacts of drought and/or high temperature stress on physiological, developmental, growth and yield processes of crop plants. In: Ahuja LM et al. Responses of crops to limited water: understanding and modeling water stress effects on plant growth processes. Advances in agricultural modeling series, USA, p. 301–355

Rampinoa P, Mita G, Pataleo S et al (2009) Acquisition of thermotolerance and HSP gene expression in durum wheat (*Triticum durum* Desf.) cultivars. Environ Exp Bot 66:257–264

Reynolds MP, Delgado MI, Gutiérrez-Rodrígez M et al (2000) Photosynthesis of wheat in a warm, irrigated environment I. Genetic diversity and crop productivity. Field Crops Res 66(1):37–50

Rodríguez M, Canales E, Borroto CJ et al (2006) Identification of genes induced upon water-deficit stress in a drought-tolerant rice cultivar. J Plant Physiol 163:577–584

Saidi Y, Finka A, Goloubinoff P (2011) Heat perception and signaling in plants: a tortuous path to thermotolerance. New Phytol 190:556–565

Salvucci ME, Crafts-Brandner SJ (2004) Mechanism for deactivation of Rubisco under moderate high temperature stress. Physiol Plant 122(4):513–519

Schoffl F, Prandl R, Reindl A (1999) Molecular responses to high temperature stress. In: Shinozaki K et al (eds) Molecular responses to cold, drought, heat and salt stress in higher plants. KRG. Landes Co, Austin, pp 81–98

Sharma D, Mamrutha HM, Gupta VK, Tikari R, Singh R (2015) Association of SSCP variants of HSP genes with physiological and yield traits under heat stress in wheat. Res Crops 16:139–146

Sharma D, Jaiswal JP, Singh NK, Chauhan A, Gahtyari NC (2018) Developing a selection criterion for terminal heat tolerance in bread wheat based on various mopho-physiological traits. Int J Curr Microbiol Appl Sci 7(7):2716–2726

Sillmann J, Kharin VV, Zhang X, Zwiers FW, Bronaugh D (2013) Climate extremes indices in the CMIP5 multimodel ensemble: part 1. Model evaluation in the present climate. J Geophys Res Atmos 118:1716–1733

Sing S (2009) Variation in physiological traits for thermotolerance in wheat. Indian J Plant Physiol 14:407–412

Singh P, Jaiswal JP (2013) Assessment of genetic diversity in bread wheat (*Triticum aestivum* L. em. Thell), genotypes based on agromorphological traits using Mahalanobis 'D^2' statistic. Environ Ecol 31(2A):679–682

Singh H, Kumar SN, Ramawat N, Harit RC (2017) Response of wheat varieties to heat stress under elevated temperature environments. J Agrometeorol 19:17–22

Stone PJ, Nicolas ME (1994) Wheat cultivars vary widely in their responses of grain yield and quality to short periods of postanthesis heat stress. Aust J Plant Physiol 21:887–900

Su P, Jiang C, Qin H, Hu R, Feng J, Chang J, Yang G, He G (2019) Identification of potential genes responsible for thermotolerance in wheat under high temperature stress. Genes 10:174–189

Suresh, Bishnoi OP, Behl RK (2018) Use of heat susceptibility index and heat response index as a measure of heat tolerance in wheat and triticale. Ekin J Crop Breed Genet 4(2):39–44

Tashiro T, Wardlaw IF (1990) The response to high temperature shock and humidity prior to and during the early stages of grain development in wheat. Aust J Plant Physiol 17:551–561

Thomas H, Ougham H (2014) The stay-green trait. J Exp Bot 65:3889–3900

Volkov RA, Panchuk II, Mullineaux PM, Schöffl F (2006) Heat stress induced H_2O_2 is required for effective expression of heat shock factors in Arabidopsis. Plant Mol Biol 61:733–746

Wahid A, Gelani S, Ashraf M, Foolad M (2007) Heat tolerance in plants: an overview. Env Exp Bot 61:199–223

Wang WX, Vinocur B, Shoseyov O, Altman A (2001) Biotechnology of plant osmotic stress tolerance: physiological and molecular considerations. Acta Hortic 560:285–292

Waters ER (2013) The evolution, function, structure, and expression of the plant *sHSPs*. J Exp Bot 64:391–403

Xu Q, Paulsen AQ, Guikema JA et al (1995) Functional and ultrastructural injury to photosynthesis in wheat by high temperature during maturation. Environ Exp Bot 35(1):43–54

Xu R, Sun Q, Zhang S (1996) Chromosomal location of genes for heat tolerance as measured by membrane thermostability of common wheat cv. Hope. Hereditas 18:1–3

Zhang L, Zhao G, Jia J, Liu X, Kong X (2012) Molecular characterization of 60 isolated wheat MYB genes and analysis of their expression during abiotic stress. J Exp Bot 63:203–214

Zhou SM, Sun XD, Yin SH et al (2014) The role of the F-box gene *TaFBA1* from wheat (*Triticum aestivum* L.) in drought tolerance. Plant Physiol Biochem 84:213–223

Zhu JK (2016) Abiotic stress signaling and responses in plants. Cell 167:313–324

Chapter 12
High-Temperature Tolerance of Flowers

Satisha Hegde, Yui Umekawa, Etsuko Watanabe, and Ichiro Kasajima

Contents

Abstract Similar to the other crops, production of floricultural plants (crops for ornamental purposes) is susceptible to high temperature. High temperature changes flowering time, causing problems in the schedule of shipment to the market.

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Consistent with the idea of plant adaptation to climate, induction of long-day spring flowers (*Arabidopsis*/thale cress) is accelerated by high temperature, whereas induction of short-day autumn flowers (*chrysanthemum*) is delayed by high temperature. High temperature also reduces flower size and causes paler petal colors (e.g. *chrysanthemum*, rose, and Eustoma) and fruit skin colors (e.g. grape and apple), thus decreasing the quality of flowers and fruits. The reasons for high-temperature caused disorders are not necessarily clear, but high temperature influences part of gene expressions involved in flowering time (*FT*, *Flowering Locus T*) and pigment synthesis (such as *CHS*, *chalcone synthase*). High-temperature-tolerant cultivars are identified or selected in floricultural and pomological (fruit) crops. High-temperature effects could be alternatively attenuated by shading or supplementation of magnesium. Heat is sometimes required for flowers: some plant species generate heat in flowers by themselves. Petal color affects flower temperature. Relationships between flower and heat in these various aspects are illustrated by photographs and illustrations of the representative studies in this research field.

Keywords Extreme temperature · Flowering habit · Flower coloration · Heat stress

12.1 Introduction: High Temperature Affects Floricultural Production

The global temperature is gradually rising by 0.02 °C every year (Berkeley Earth 2019). High atmospheric temperatures caused by global warming will be a great risk for production of most crops, but the effects of high temperature on crop production and breeding of high-temperature tolerant cultivars have just started to be widely studied in recent years. In the present report, we will focus on the effect of high temperature on the production of flowers (floriculture), to discuss necessary solutions to overcome adverse effects of future high temperature on flower production. The number of reference papers is limited on this topic, but representative papers will be reviewed in precision to learn high-temperature response and tolerance of flowers. Reference photographs of flowers will be also cited from representative papers, as long as copyright permission is given from the publishers.

High temperature affects both quality and quantity of flower production. As for the quantity of flower production, short period (3 days) of very high temperature (35 °C maximum for 6 h each day) during early flowering period was enough to reduce flower yield of pyrethrum (*Tanacetum cinerariifolium*). *Pyrethrum* flower is the source of the production of pyrethrin, a natural insecticide. In addition to the yield of flowers, pyrethrin content in the flower (achene) is also reduced by heat stress, causing the problem of unstable pyrethrin production in the main producer country Australia (Suraweera et al. 2016). Reduction of the number of flowers is also observed in groundnut (*Arachis hypogaea* cultivar ‘ICGV 86015’): the number of flowers decreases as the day temperature is raised from 28 to 48 °C (Prasad et al. 2000).

As for the quality of flowers, flower diameter is reduced by 16% and petal number is reduced by 23% in rose (*Rosa* sp., cultivars 'M4-4', 'J06-20-14-3', '97/7-2', 'Red Fairy', 'Sweet Chariot', 'Vineyard Song', 'Old Blush', and 'Little Chief'), only by 1-h heat shock at 44 °C. Although severe heat shock will be better for estimation of heat tolerance, heat-tolerant trait of rose is heritable (Liang et al. 2017). The shape of freesia (*Freesia refracta* cultivar 'Blue Heaven') inflorescence is affected by high temperature. Juvenile plants of freesia generated from corms are usually chilled at 10 °C. When juvenile plants are treated at 24 °C for 1, 2, or 3 weeks, abnormal (malformed) inflorescences are formed on mature plants, and the ratio of abnormal inflorescences rises with the longevity of heat stress at 24 °C. Abnormal inflorescences have different (vertical) angles of flower stalks or form aberrant flowers at the base of inflorescence (Fig. 12.1). The formation of abnormal inflorescences is correlated with faster development of floral meristems (Motozu et al. 2000).

Heat stress affects floral scent (fragrance) as well. The production of phenylpropanoid-based volatiles was reduced in petunia (*Petunia* × *hybrida*) flowers (cultivars 'P720' and 'Blue Spark') when day/night temperature was raised from 22 °C/16 °C to 28 °C/22 °C (Cna'ani et al. 2015). Floral scent will not be important for petunia as an ornamental flower, but decrease of floral scent is critical for excellently fragrant species such as sweet pea, freesia, and fragrant rose. Other damages to flowers by heat stress include decoloration of petals and altered time of flowering. These topics will be described in the other sections of this chapter. Heat stress causes sterility in flowers (Yang et al. 2009; Ishimaru et al. 2016; Hakata et al. 2017; Zhang et al. 2018), but this is not within the focus of the present chapter. Interestingly, heat does not always have negative influences on flower production. When rose cultivars 'Meirutral' and 'Meidanclar' are grown at the day/night

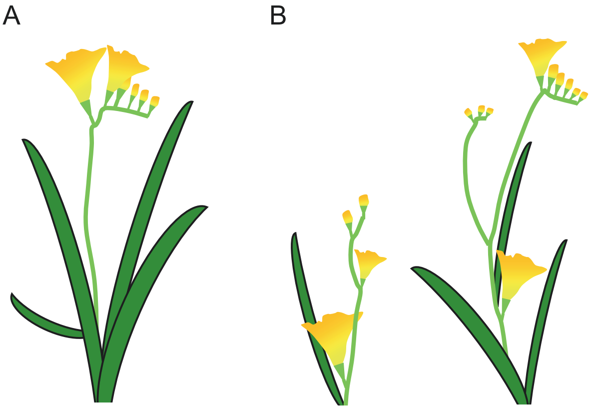

Fig. 12.1 Abnormal inflorescence of freesia. (**a**) Normal inflorescence. (**b**) Abnormal inflorescences. These figures illustrate data in Motozu et al. (2000)

temperature of 24 °C/18 °C or 29 °C/24 °C, longevity of open flowers was increased, and the ratio of bud drop was decreased at higher temperature. Most notably, flower longevity was increased from 2 to 9 days and bud drop was decreased from 61 to 5% in 'Meirutral', when plants were heated at green-bud stage. 'Meidanclar' also enjoyed similar effects of high temperature, but malformed flowers were increased in this cultivar. Although high temperature induces smaller flowers, high temperature is beneficial for some rose cultivars (Monteiro et al. 2001). Such benefits of high temperature should be also remembered to promote flower production under high temperature. After listing heat effects to flowers, we will also review physiological or chemical treatments and genetic approaches to alleviate heat damages.

12.2 High-Temperature Response of Long-Day and Short-Day Plants

12.2.1 Long-Day Plant

The time required from germination to reproductive growth (flowering) is the important trait for plants to survive in the environment (Song et al. 2015). Flowering time is principally regulated by the length of light and dark conditions in a day (photoperiod), although regulation of flowering time is much more complicated. Thale cress (*Arabidopsis thaliana*) is a "facultative" long-day plant: thale cress flowers much earlier under long-day conditions than under short-day conditions. Studies of thale cress have demonstrated that abiotic stresses also control time of flowering, in addition to photoperiod. The reason for the response of flowering time to abiotic stresses is considered that plants try to generate seeds before they are fatally damaged by stresses (Takeno 2016).

Temperature is one of such environmental stresses that accelerate flowering in thale cress. Thale cress flowering is accelerated by high temperature (Song et al. 2015). Here, we will review how thale cress plants sense temperatures. Plants sense both temperature and photoperiod by the same mechanism. Protein called "Phytochrome B" usually senses the "quality" of light, i.e. the ratio between red light and far-red light. Also wave lengths of lights, Phytochrome B also senses the temperature through its temperature-dependent reversion from the active "Pfr state" to the inactive "Pr state" (Fig. 12.2; Legris et al. 2016; Kreslavski et al. 2018). Thus, Phytochrome B is considered to work as a temperature sensor by this conformational change. Phytochromes interact with phytochrome-interacting factors (PIFs), the transcriptional factor proteins with the basic helix-loop-helix (bHLH) DNA binding domain. PIF4 protein is actually reported to be involved in acceleration of flowering by high temperature in thale cress: flowering is no longer accelerated in the *pif4* mutant of thale cress which lack the function of PIF4, under high temperature (Kumar et al. 2012).

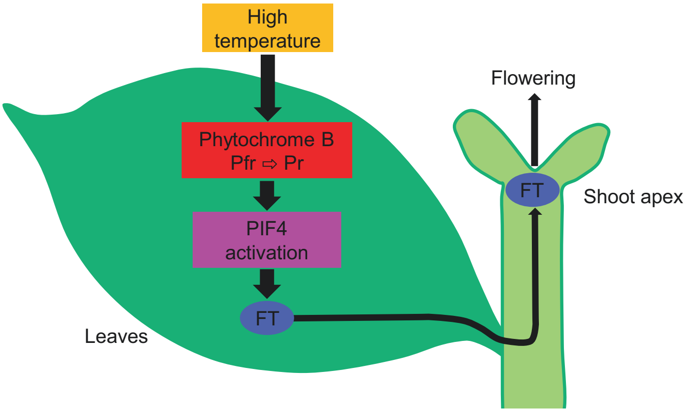

Fig. 12.2 Activation of FT by high temperature in thale cress: schematic representation

The expression of the *FT* (*Flowering Locus T*) gene, encoding florigen, takes place in the vascular tissues of leaves, and the *PIF4* gene is also expressed in the same tissues. In "chromatin immuno-precipitation" assay, PIF4 protein binds to the promoter DNA region of the *FT* gene. This indicates that heat-activated Phytochrome B activates PIF4, which enhances expression of the *FT* gene (Kumar et al. 2012). Here, florigen is the master regulator that transmits flowering-inducing stimuli in higher plants (Tsuji 2017). The *FT* gene of thale cress and the *Heading Date 3a* (*Hd3a*) gene of cultivated rice (*Oryza sativa*) encode phosphatidylethanolamine binding-like proteins, which are the realities of florigen (Kardailsky et al. 1999; Kobayashi et al. 1999; Kojima et al. 2002).These proteins are expressed in leaves and then translocated to shoot apices via the phloem and promote flowering in shoot apices (Corbesier et al. 2007; Tamaki et al. 2007).

High temperature also accelerates the heat-stress responsive pathway, e.g. upregulation of heat shock proteins (HSPs) which help the folding of proteins, and HSPs are related to flowering as well. Once HSPs are activated, plants can adapt to the secondary heat stresses. This is called "adaptation to heat stress." HSP90 is highly induced during adaptation of thale cress. HSP90 is quite abundant in normal temperature to help the protein folding. Mutation in the *HSP90* gene affects a variety of "quantitative life-history traits," including delay of flowering, reduction of total seed set, and increase in morphological diversity (Sangster et al. 2007, 2008). Then, HSP90 might regulate the flowering time by modulating several proteins. Candidates of such target proteins of HPS90 are an F-box protein ZTL involved in photoperiod regulation (Kim et al. 2011) and Heat Shock Transcription Factor A1 (HSFA1) involved in high-temperature tolerance together with HSP90 (Yamada et al. 2007). In summary, Phytochrome B and PIF would regulate high-temperature-induced change of flowering time through regulation of the expression of the *FT* gene in the vein of leaves (Fig. 12.2), and HPS will also influence this response.

12.2.2 Short-Day Plant

Data indicate that flowering induction of short-day plants such as chrysanthemum responds to high temperature oppositely from long-day plants such as thale cress. *Chrysanthemum* is the most popular cut flower in Japan: it occupies more than one-third of cut flower production, followed by rose, carnation, Gerbera, Statice, Eustoma, and gentian. Chrysanthemum is produced in many areas of Japan but is most produced in warm or semi-tropical areas such as Aichi and Okinawa (http://www.e-stat.go.jp/SG1/estat/Pdfdl.do?sinfid=000031665471). *Chrysanthemum* also occupies 18% of all sales of ornamental plants in Japan (http://www.maff.go.jp/e/policies/agri/attach/pdf/index-5.pdf#search=%27chrysanthemum+production+data%27). Chrysanthemum originates in East Asia and first cultivated in China. Data on the response of short-day plants to high temperature is practically restricted to chrysanthemum, but the other species may respond to high temperature in the same way.

Carvalho et al. (2005) reported high-temperature response of chrysanthemum cultivar ‘Reagan Improved’. They test cultivated chrysanthemum under 15, 18, 21, or 24 °C and compared flower traits. As in the other reports, they observed smaller but larger number of flowers per plant at higher temperatures. They also reported that the pink color of the petal was lighter (paler) at higher temperatures, similar to the other reports. On the other hand, they did not observe great difference in flowering time (days from the start of short-day treatment to anthesis). This range (15–24 °C) of moderate stimulus will not have significant effect on the induction of chrysanthemum flowering.

An interesting survey was performed on the response of *chrysanthemum* cultivar ‘Bright Golden Anne’ to high temperature by Karlsson et al. (1989). They changed day temperature and night temperature independently from 10 to 30 °C. Clear difference in flowering time was observed in this wide range of temperatures (Fig. 12.3a). The optimum temperature for shortest flowering time of *chrysanthemum* is both day and night temperatures of 18 °C, which requires 60 days to flowering. The flowering time becomes longer when temperatures are more different from this optimum level. The flowering time is even 120 days, the double of the shortest case at high temperatures such as day temperature of 30 °C and night temperature of 26 °C. The “total flower area” per plant was also measured in their analysis. This is the output of the balance between flower size and flower number, but the optimum temperatures are day temperature of 20 °C and night temperature of 16 °C, at which temperature the flower area is 300 cm^2 (Fig. 12.3b). This value is also much affected by high temperature, for example, the values is more than halved (less than 150 cm^2) at day temperature of 28 °C and night temperature of 22 °C. Virtually no flower is generated at both day and night temperatures of 30 °C. Light intensity also matters. The above data were obtained at light intensity (photosynthetic photon flux, PPF) of 15 mol day^{-1} m^{-2}. Flowering is delayed, and flower area is reduced in darker conditions.

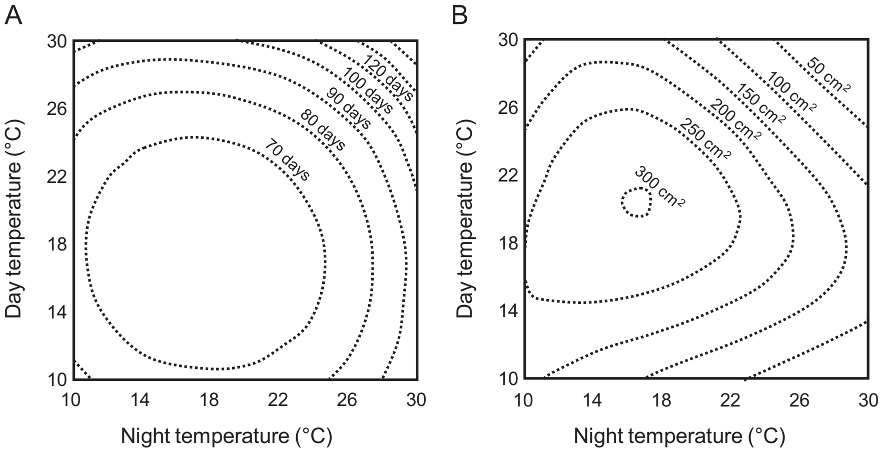

Fig. 12.3 Response of chrysanthemum to high temperature (1). Days needed to anthesis from the start of short day (**a**) and total flower area per plant (**b**), shown as the function of day temperature and night temperature. Data were acquired for plants grown in PPF of 15 mol day^{-1} m^{-2}. These figures illustrate data in Karlsson et al. (1989). (**a**) Expression inductions (in short-day condition) of the *AP3*/*AG*/*SEP*/*PI* homologs was analyzed every week at 20 or 30 °C. (**b**) Expression induction of the *CsFTL3* gene was analyzed every week at 20 or 30 °C. Data were cited from Nakano et al. (2013) under the Creative Commons CC-BY conditions

Genetic analysis of the generally observed flowering retardation of chrysanthemum at high temperature was performed on the cultivar 'NIFS-3' (Nakano et al. 2013). In *chrysanthemum* shoot apices, expressions of meristem identity genes *SOC1* (*Suppressor of Overexpression of Constans 1*), *LFY* (*Leafy*), *AP1* (*Apetala 1*), and *FUL* (*Fruitful*) and floral homeotic genes *AP3* (*Apetala 3*), *AG* (*Agamous*), *SEP* (*Sepallata*), and *PI* (*Pistillata*) are induced within 3 weeks in short-day condition at 20 °C. Expression inductions of four *SOC1*/*LFY*/*AP1*/*FUL* homologs were not significantly affected by high temperature at 30 °C, although expression inductions of two *AP1*/*FUL* homologs were delayed. Consistent with this, there was no clear delay in the induction of floral meristems at high temperature, in microscopic analyses. On the contrary, expression inductions of all four *AP3*/*AG*/*SEP*/*PI* homologs examined were delayed by high temperature (Fig. 12.3a). As a result, development of floral organs after generation of floral meristem is delayed in chrysanthemum. The delay of the expressions of these genes is seemingly caused by the delay in the expression induction of the *CsFTL3* gene, one of the *FT* (*Flowering Locus T*) homologs, in leaves at high temperature (Fig. 12.3b). This is consistent because *FT* is florigen, the inducer of flowering. Expression of the *CsTFL1* gene, a homolog of flowering suppressor *TFL1* (*Terminal Flower 1*), was not altered by high temperature at shoot apices, indicating that *FT* pathway is solely inhibited by high temperature. They also confirmed this phenomenon by grafting between high-temperature sensitive cultivar 'Mona Lisa' and high-temperature tolerant cultivar ‘Kurarisu’, where high-temperature retardation of flowering occurred depending on root-stock cultivars.

In summary, cultivation of chrysanthemums is the best around 18–20 °C. Symptoms are observed at higher temperatures, such as retardation of short-day induced flowering, reduction in flower area, and reduction in pigment synthesis. Physical treatments should be performed to reduce temperature in the greenhouse, or high-temperature-tolerant cultivars should be used/bred to avoid symptoms, when chrysanthemums are grown at high temperatures. Knowledge on the other short-day plants is nearly lacking, but a similar phenomenon is observed in Eustoma: elongation of inflorescence stem is inhibited at high temperatures in Eustoma seedlings, causing rosette-like structure without flowers. Thus, mechanisms of high-temperature inhibition of flowering must be also analyzed in the other plant species.

12.3 High-Temperature Effects on Petal Colors

12.3.1 Anthocyanin Synthesis

Another problematic effect of high temperature to flowers is decoloration. Anthocyanin is a flavonoid subclass which is the pigment present in flowers responsible for color variations. Temperature is a key factor reducing biosynthesis of anthocyanin (Puangkrit et al. 2018), but we have to understand the process of anthocyanin synthesis first.

Animal pollinators are generally the cause of color polymorphism in flowers (Mu et al. 2010). Seed production in plant species is correlated with the flower color, size, and visitation rates of pollinators. Conversely, recent studies provided the information that flower color diversity is related to the physical factors of the environment (Mu et al. 2010). The different color polymorphism is directly proportional to the specialized metabolite anthocyanin in many of red, purple, and blue flowers, together with yellow/orange carotenoid and yellow/pink betalain. Decoloration of flowers in high temperature may affect pollination in nature, but decoloration affects sales of ornamental flowers in the market.

Cyanidin, pelargonidin, and delphinidin are the main anthocyanidins present in higher plants (Schwinn and Davies 2004). The first step of anthocyanin synthesis is catalyzed by chalcone synthase (CHS), which synthesizes naringenin chalcone from *p*-coumaroyl-CoA and three molecules of malonyl-CoA. Then the naringenin chalcone is catalyzed to naringenin in presence of chalcone isomerase followed by further synthesis of dihydrokaempferol in presence of flavonoid 3′-hydroxlase (F3′H; Fig. 12.4). Naringenin is also catalyzed to apigenin (flavone) which is catalyzed by flavone synthase. Again, in the presence of flavonoid 3′-hydroxlase (F3′H), apigenin is catalyzed to luteolin. In addition, dihydrokaempferol produces leucopelargonidin and further catalyzed to pelargonidin in presence of

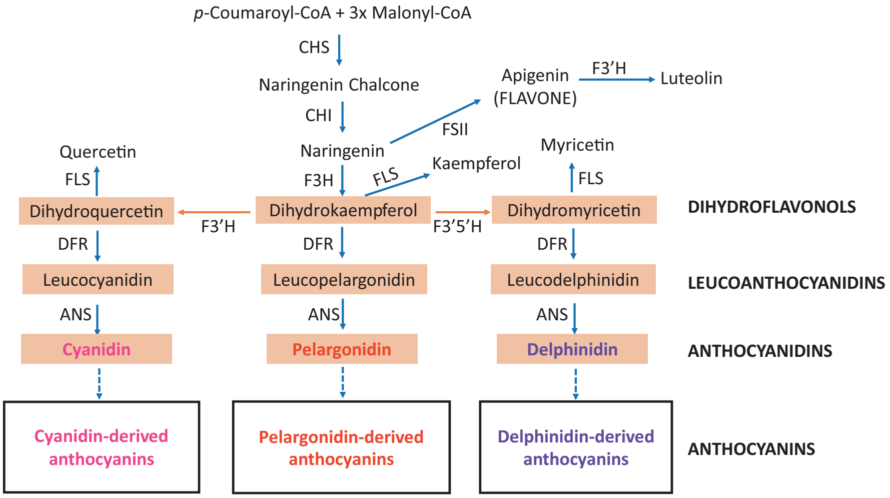

Fig. 12.4 Biosynthesis pathway of anthocyanins. *CHS* chalcone synthase, *CHI* chalcone isomerase, *F3H* flavanone 3-hydroxylase, *DFR* dihydroflavonol 4-reductase, *ANS* anthocyanidin synthase, *FLS* flavonol synthase, *F3′H* flavonoid 3′-hydroxlase, *F3′5′H* flavonoid 3′,5′-hydroxlase, *FSII* flavone synthase. This figure was generated based on the data in Berman et al. (2016)

dihydroflavonol 4-reductase (DFR) and anthocyanidin synthase, respectively. Meanwhile, dihydroquercetin synthesized by dihydrokaempferol in the presence of F3′H. Dihydroquercetin is catalyzed to both quercetin and leucocyanidin by flavonol synthase (FLS) and dihydroflavonol 4-reductase (DFR), respectively. Cyanidin synthesis is catalyzed from leucocyanidin by anthocyanidin synthase. Dihydrokaempferol is responsible for synthesizing dihydromyricetin and myricetin which is catalyzed by flavonoid 3′,5′-hydroxlase (F3′5′H) and FLS. Further, leucodelphinidin and delphinidinare are synthesized in the presence of DFR and ANS, respectively. Finally, anthocyanins are synthesized by glycosylation of cyanidin, pelargonidin, and delphinidin (Fig. 12.4). Anthocyanins derived from cyanidin, pelargonidin, and delphinidin are typically pink, red, and violet, but colors (hues) are variable depending on the type of glycosylation and chemical environment in plant cell (vacuole).

For the synthesis of kaempferol, quercetin, and myricetin in gentian, flavonol synthase (FLS) is essential. Pelargonidin, cyanidin, and deslphinidin (anthocyanidins) are altered by the sugars and other moieties binding to form anthocyanins in a species-specific manner. For example, different colors of the petals accumulate different anthocyanin like pink-flowered gentians (*Gentiana*) petals contains gentiocyanin, blue-flowered contains gentiodelphin and orange-flowered contains solely pelargonidin glycosides in their petals. In the case of *aurantiaca* and *lutea* types of gentian, similarities in amino acid sequences were revealed at *CHS*, *CHI*, *ANS1*, and *ANS2* loci, while *F3H* and *DFR* loci showed variation in amino acid sequences. Relatively high levels of transcripts are detected for *DFR*, *F3H*, *CHS*, *ANS*, and *UDP-glucose: flavonoid-3-O-glucosyltransferase* genes in *aurantiaca* petals in comparison with *lutea* petals (Berman et al. 2016).

However, structural genes above themselves do not always regulate the anthocyanin accumulation. For example, the study conducted by Fatihah et al. (2019) in *Nicotiana benthamiana* and *Lilium* flowers describes that *ROSEA1* (*ROS1*, a *MYB*-type transcription factor) and *DELILA* (*DEL*, a bHLH-type transcription factor) regulate the biosynthesis of anthocyanin. There are myeloblastosis protein (*MYB*) complexes, *WD40*, and helix-loop-helix (*bHLH*) transcription factor families (Quattrocchio et al. 1998; Koes et al. 2005). Out of these three transcription factors, *WD40* is required for stabilization of "*MBW* complexes," and *MYB* and *bHLH* co-expression is essential for activation of the structural genes for anthocyanin synthesis (Bovy et al. 2002; Hichri et al. 2011). In the process of regulating anthocyanin production, *MYB* plays a key role (Hichri et al. 2011). In many plant species, *MYB* alone is enough to stimulate anthocyanin production (e.g. *Anthocyanin1*(*ANT1*) of tomato (Schreiber et al. 2012) and *MYB10* of apple, strawberry, and potato (Kortstee et al. 2011)). In the case of maize *C1*, *MYB* is unable to stimulate anthocyanin without *bHLH* (Bovy et al. 2002). Therefore, biosynthesis of anthocyanin is regulated by both MYB- and bHLH-type transcription factors, whereas in some cases only one transcription factor is sufficient.

12.3.2 Decoloration of Petals

Anthocyanin content/accumulation varies from developmental stages and is induced by many factors including cold temperature (Chalker-Scott 1999). In other words, anthocyanin content in flowers is less at high temperatures. Conditioned low-temperature environments of petunia (Shvarts et al. 1997) and rose flowers (Biran and Halevy 1974) showed increased synthesis of anthocyanin content. In a study conducted on 'Jaguar' rose flowers by Dela et al. (2003) showed the long-term noticeable effect on concentration of anthocyanin when high temperature is applied. The anthocyanin synthesis enzymes (CHS and DFR) in 'Jaguar' were decreased by 50% after treatment of heat, revealing that declined anthocyanin content is because of reduced transcription rates of these genes. Therefore, even after the treatment with high temperature, the inhibition of anthocyanin accumulation continues by decreased levels of CHS and DFR (Dela et al. 2003). Similar studies on strawberries showed that inhibition of anthocyanin accumulation is caused by the decrease in the phenylalanine ammonia lyase (PAL) and CHI activities (Civello et al. 1997).

An interesting study by Nozaki et al. (2005, 2006) on *Chrysanthemum morifolium* Ramat. (pink flower genotype of *chrysanthemum*) revealed differential anthocyanin content under different temperatures or seasons. At 30 °C, the poor flower coloration was observed except for one genotype 'Chatoo' out of six pink-flower genotypes in greenhouse. Especially great difference in petal color was visible for 'Sei-Monako' genotype. In 'Sei-Monako', chroma (vividness) values were low under high temperature. The overall illustration of this phenomenon is shown in Fig. 12.5. In addition, contents of cyanidin3-*O*-(6″-*O*-monomalonyl-beta-glucopyranoside) and cyanidin3-*O*-(3′,6″-*O*-dimalonyl-beta-glucopyranoside) were lower at higher temperature (Nozaki et al. 2006). This study also indicated that the mean temperature is the key factor rather than day or night temperatures, to determine the coloration of flower.

Another study conducted on pink-flower chrysanthemum by Puangkrit et al. (2018) describes the effect of high temperatures on pigmentation, petal coloration, and flavonoid biosynthesis genes during the developmental stages of inflorescence. Exposures to 20 and 30 °C revealed that anthocyanin levels (cyanidin3-*O*-(6″-*O*-monomalonyl-beta-glucopyranoside) and cyaniding3-*O*-(3″,6″-*O*-dimalonyl-beta-glucopyranoside)) at 20 °C were much higher than those at 30 °C. Observation throughout the "bud break to vertical stages" at 20 or 30 °C revealed the maximum temperature sensitivity of "petal extension to vertical stage" and its importance for pigmentation. The structural genes of anthocyanin biosynthesis (*CmplCHS1*, *CmplCHS2*, *CmplCHI*, *CmplF3H2*, *CmplC3′H*, *CmplDFR1*, *CmplDFR2*, and *CmplANS*) were heat-sensitive.

12.3.3 Color Influences Flower Temperature

Floral color (hue) is also adjusted based on the temperature of the environment (Dela et al. 2003; Stiles et al. 2007). Study was conducted on petal color changes and pigment concentrations (i.e. pelargonidin/cyanidin ratio) of Baccara rose by Biran and Halevy (1974) at different temperature ranges. The inner (reddish with major pelargonin) and outer (bluish with major cyanin) side of Baccara rose petals was examined under low (14 °C/20 °C) and high (18 °C/25–30 °C) temperatures.

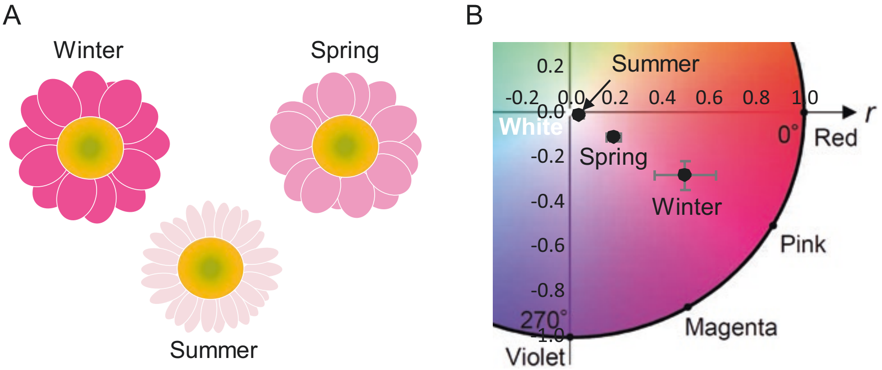

Fig. 12.5 Decoloration of chrysanthemum. (**a**) Difference in the shape and color of cultivar 'Sei Monako' depending on the seasons. (**b**) Petal colors of cultivar 'Sei Monako' grown in winter, spring, or summer. Colors were plotted on color circle (Kasajima 2016, 2019). Saturation (vividness) is higher at edges of the circle, and the center of the circle is white/gray. The pictures in (**a**) illustrate data in Nozaki et al. (2005)

The result showed that ratio among cyanin and pelargonin was high in low temperature as compared to high-temperature conditions. Lacey and Herr (2005) reported that multiple floral parts of *Plantago lanceolate* produce maroon to black (dark-colored) spots in spring and autumn when the temperature is cool. The closely clustered spikes in the inflorescence are dark in these tiny flowers. These spikes are more reflective and lighter at summer due to reduced pigmentation (Stiles et al. 2007). Dark-colored spikes produced under cool temperatures absorb solar radiation more efficiently, and thereby they produce warm condition for seed development. On the contrary, less radiation is absorbed by light-colored spikes in summer, which is effective to cool flowers (Stiles et al. 2007). Thus, flower color influences temperature conditions of the flower itself.

Petal colors influence flower interior temperature due to the variance in absorption and reflection of the light in a bit different manner as well (Seymour et al. 2009b; Mu et al. 2010). This effect can be of significance for the adaptation of plants living in stressful conditions. For example, in drought- and heat-stressed conditions, individuals with pigmented flowers usually survive better than anthocyanin-free or less ones (Steyn et al. 2002), and white-flowered individuals are frequently susceptible to the stress and therefore suffer a large loss in fitness benefit (Coberly and Rausher 2003; Mu et al. 2010). In contrast to this, in arctic or cold alpine areas, flower color may have evolved to become white to help keep interior temperatures warm and stable against fluctuating ambient temperatures (Seymour and Schultze-Motel 1998). This adaptation is essential to the development of pollen, ovules, and fertilization (Mu et al. 2010). For example, the white petals of *Crocus chrysanthus*, an arctic herb species, reflect light into flower interiors to warm. Simultaneously, at ambient temperature, white flowers are generally warmer compared to yellow or purple flowers in interior structures but not in corolla, since white petals reflect light more efficiently than dark ones (Fig. 12.6; McKee and Richards 1998; Mu et al. 2010). Studies examining the relationships between petal colors, interior temperature of flower, and pollinator visitation rates usually employ a comparative methodology like between varieties of a single species. However, the different factors involved in these studies may be confusing. For example, the three varieties of *Crocus* differ in both flower structure and petal color (McKee and Richards 1998). Hence, further studies will be necessary to obtain direct evidence as to the effects of petal colors on flower temperature, by using genetic mutants or transformants.

In summary, high temperature reduces anthocyanin synthesis in flowers. High-temperature effects on carotenoids and betalains are not clear. If syntheses of these pigments are not susceptible to high temperature, flowers synthesizing these pigments do not show decoloration symptom in high temperature, unlike the flowers accumulating anthocyanin in petal. Reports on the effect of petal color on the temperature of flower interiors are also meaningful. White petals are cooler than colored petals in accordance with our imaginations, but flower interior is oppositely cooler in flowers with colored petals. This is thought to be a consequence of lower light reflectance on the colored petal. Consistently, colored flowers seem to survive better than white flowers in heat (Steyn et al. 2002).

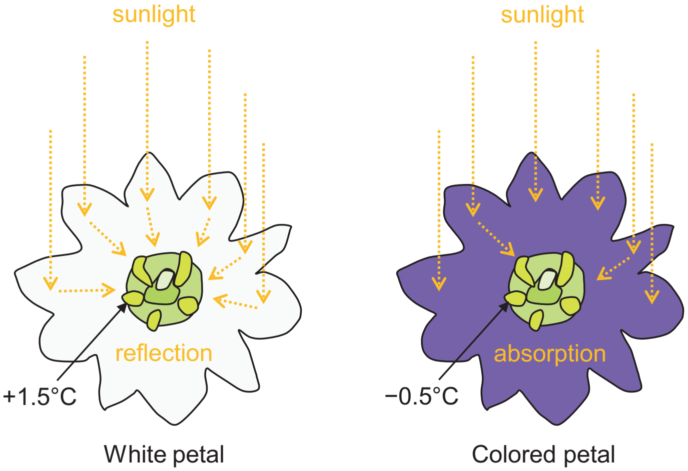

Fig. 12.6 Effect of petal color on flower temperature. Pictures illustrate reflection of sunlight on petals of *Gentiana leucomelaena*, an Alpine herb. White petals reflect more sunlight than deep-colored petals. Anthers are warmed by approximately 1.5 °C above the ambient temperature in white flowers, whereas anthers are cooled by approximately 0.5 °C in purple flowers; thus petal colors cause 2 °C difference in anther temperatures. This figure was generated based on the data in Mu et al. (2010)

12.4 Heat Production in Flowers

12.4.1 Heat-Producing Flowers

We are showing examples of heat damage to flowers, but adequate level of temperature is necessary for plants. Especially pollination seems to be dependent on relatively higher temperatures in many plant species. Some plants also heat themselves to tolerate cold temperature. In this section, we will review such examples where plants generate high temperature by themselves. Several seed plants actively elevate their body temperature above the surrounding environment. The first discovery of such plant thermogenesis was made by Jean-Baptiste de Lamarck in the eighteenth century (Lamarck 1778), who documented the thermogenesis in the inflorescence of European arum lily during blooming. To date, floral organ-specific thermogenesis (i.e. single flowers, inflorescences consisting of many florets, or cones) has been found in plants from diverse range of plant taxa, including the monocotyledon families Araceae, Arecaceae, and Cyclanthaceae; dicotyledon families Annonaceae, Aristolochiaceae, Hydnoraceae, Magnoliaceae, Nelumbonaceae, Nymphaeaceae, Rafflesiaceae, and Schisandraceae; and gymnosperm families Cycadaceae and Zamiaceae (Seymour 2010).

Heat production occurs by massive increase of cellular respiration rate in flowers (Meeuse 1975). Based on the pattern of heat production, the thermogenic plants are categorized into two groups: thermoregulatory and non-thermoregulatory (Seymour et al. 2010; Kakizaki et al. 2012).Thermoregulatory plants can regulate floral temperatures to a constant level for several days during blooming, even if ambient temperature fluctuates changes. Thermoregulation has been observed in a few species of thermogenic plants, *Philodendron*, *Symplocarpus*, and *Dracunculus* belonging to the family Araceae and *Nelumbo* belonging to the family Nelumbonaceae. In contrast, most thermogenic plants are non-thermoregulatory which cannot maintain the floral temperature, namely, thermogenesis occurs explosively and transiently.

Plant thermogenesis is closely associated with floral development (Seymour 2010; Kakizaki et al. 2012). Although the molecular mechanism for the initiation of thermogenesis has not been fully understood, some physiological experiments demonstrated that salicylic acid, which is a well-known plant hormone, is the trigger of heat production in thermogenic inflorescence of voodoo-lily (*Sauromatum guttatum*; Raskin et al. 1987; Raskin et al. 1989). Salicylic acid begins to dramatically increase in appendix of the inflorescence, the main thermogenic organ, in the late afternoon of the day before blooming, and immediately reaches 100 times higher than the basal level. In the next morning, blooming starts with the exposure of appendix by unfolding the "spathe" (a large bract that encloses the inflorescence), which is followed by the extensive thermogenesis in appendix, and the peak of its temperature reaches 10 °C above the ambient temperature. The salicylic acid-induced heat production in appendix is not observed when appendix is exposed to constant darkness, suggesting that thermogenesis is regulated by photoperiod (day/night length) as well (Raskin et al. 1989).

Other example of well-studied thermogenic plants includes sacred lotus (*Nelumbo nucifera*). About a century after observation of thermogenesis in sacred lotus by Miyake (1898), Seymour and Schultze-Motel discovered the physiological thermoregulation of its flower (Seymour and Schultze-Motel 1996, 1998). Here, it was demonstrated that the receptacle inside the petals is the main thermogenic organ. The period of thermoregulation is basically related to their pattern of "protogynous" (pistil maturating earlier than stamen) anthesis in this plant. The lotus bud initiates thermogenesis in early summer when the petals are still closed, and then thermogenesis continues when the petal opens slightly to reveal the stigmas. The thermoregulatory capacity is finally lost when flower fully opens to expose the stamens. The temperature of the thermogenic receptacle is typically around 30–36 °C within 2–4 days sequence of flowering, although the ambient temperature fluctuates between 10 and 45 °C. Moreover, the receptacle temperature is completely regulated even in constant darkness for over 3 days; thus thermoregulation of sacred lotus depends on temperature and is not influenced by photoperiod (Seymour and Schultze-Motel 1998).

Skunk cabbage, a member of Araceae family, is the only plant species demonstrating the thermogenesis at cold environment, at least at the moment (Fig. 12.7; Knutson 1974). There are species from eastern Asia (*Symplocarpus renifolius*) and eastern North America (*S. foetidus*), both of which are thermoregulatory and naturally growing on wetland (Nie et al. 2006). During blooming in early spring, they produce enough heat to melt snow (Kamata et al.

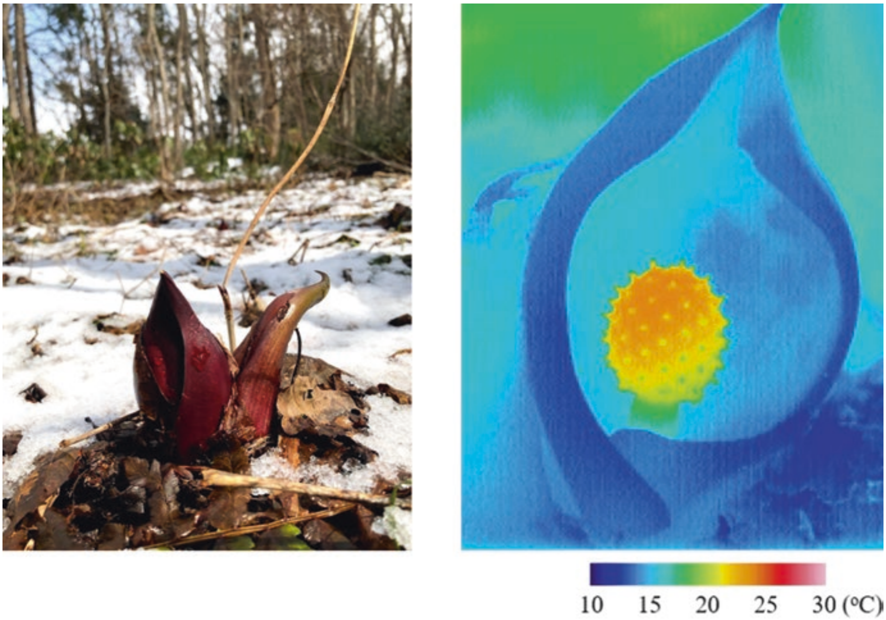

Fig. 12.7 Thermogenesis of skunk cabbage. Left: The blooming stage of skunk cabbage in the field. Right: Thermography of the skunk cabbage. One of the spathes surrounding the spadix was cut off to display the spadix

2009). The thermogenesis occurs in its inflorescence (spadix), especially in florets (Fig. 12.8; Onda et al. 2008; Sayed et al. 2016). Interestingly, skunk cabbage maintains their spadix temperature at around 23 °C even if ambient temperature drops below zero (Seymour et al. 2009a). The thermoregulation of spadix continues during the fertilizable female phase for around 1-week period, which is the longest-term thermoregulation among all currently known plant species.

12.4.2 Biochemical Basis of Thermogenesis

Biochemical mechanisms for thermogenesis of flowers are reported. Thermogenesis is associated with the metabolic heat production through the increase of respiration rate in flowers, especially with the “cyanide-resistant respiration pathway” via alternative oxidase (AOX; Moore et al. 2013). AOX is a mitochondrial enzyme in plants, fungi, and nematodes, and its expression is induced by several environmental stresses. AOX accepts electrons from the “ubiquinone pool” and uses them to reduce oxygen to water without generating ATP. Thus, the chemical energy is transformed to heat in AOX reaction. In thermogenic plants, the abundant AOX protein exists as the reduced (active) form in floral organ (Elthon et al. 1989; Umbach and Siedow 1993; Onda et al. 2007), probably due to the reduction via mitochondrial *o*-type

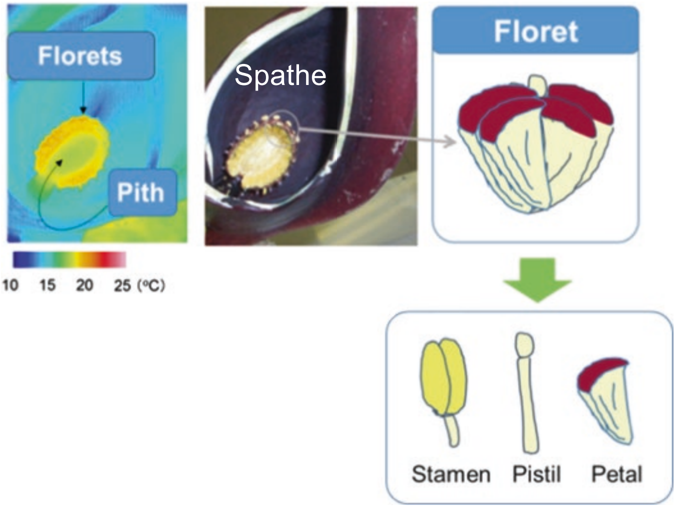

Fig. 12.8 Structure of the spadix of skunk cabbage. Spadix is composed of a pith and numerous florets. Spathes are surrounding spadix. Thermogenesis is mainly observed at the florets of spadix. Each floret contains stamens, a pistil, and petals. This figure was cited from Sayed et al. (2016) under the Creative Commons CC-BY conditions

thioredoxin "Trx *o*" (Umekawa and Ito 2018). Therefore, not only the level of respiration rate, which is comparable to most animals, but also relatively high proportion of AOX-mediated respiration within the total respiration allow the thermogenic plants (flowers) to generate heat.

In the thermoregulatory flowers, thermoregulation is achieved by the temperature-dependent control of respiration in flowers: the floral respiration rate decreases as flower temperature rises and vice versa (Seymour et al. 2010). It is noteworthy that the temperature responses of the respiration in these flowers are opposite to the general chemical reactions where the reaction rate increases as temperature rises. Recently, we performed thermodynamic analysis on the respiration in thermogenic spadices of skunk cabbage (Umekawa et al. 2016). The results indicated that the thermoregulation is achieved by temperature-dependent change of cellular biochemical equilibrium comprising "exothermic (heat producing) and endothermic (heat absorbing) reactions" in the respiratory metabolism of skunk cabbage. Namely, the cellular equilibrium is formed by an exothermic pre-equilibrium reaction which consists of a fast-reversible step (reverse reaction is endothermic) that precedes formation of unstable intermediates (k_1 and k_1), and the following rate-limiting exothermic step determines the entire reaction rate (k_2; Fig. 12.9). The occurrence of the reverse (endothermic) reaction in the pre-equilibrium reaction needs relatively high temperature due to its high activation energy (Fig. 12.9); thus the rate of the reverse (endothermic) reaction increases as temperature increases. Therefore, higher temperature increases the rate of reverse (endothermic) reactions and reduces the concentration of intermediates, and finally the entire reaction rate decreases. The

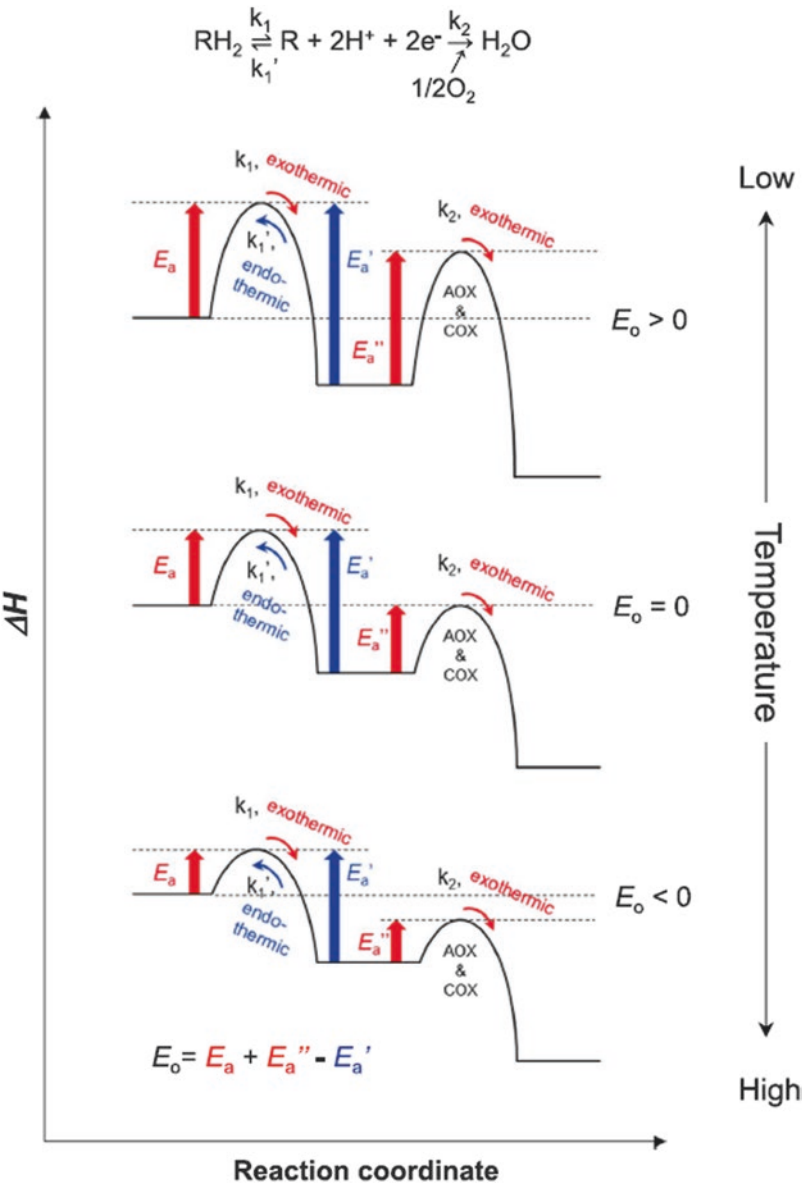

Fig. 12.9 Model of the temperature-dependent respiratory control in thermogenic spadices of skunk cabbage. The model is composed of a leading fast-reversible step that forms equilibrium (k_1 and k_1) and a final step of oxygen consumption through mitochondrial terminal oxidases (AOX and COX) (k_2). The activation energies of the exothermic reactions with reaction constants k_1 ($RH_2 \rightarrow R + 2H^+ + 2e^-$) and k_2 ($1/2O_2 + 2H^+ + 2e^- \rightarrow H_2O$) are expressed as E_a and E_a'', respectively. The endothermic reaction with reaction constant k_1' ($R + 2H^+ + 2e^- \rightarrow RH_2$) is indicated as E_a'. The overall activation energy (E_o) is expressed as: $E_o = E_a + E_a'' - E_a'$. This figure was cited from Umekawa et al. (2016) under the Creative Commons CC-BY conditions

involvement of the endothermic reaction (NADPH production catalyzed by mitochondrial isocitrate dehydrogenase) in the respiratory control was a new concept for understanding the physiological thermoregulation. Here, both AOX- and COX-mediated reactions can berate limiting steps in the pre-equilibrium reaction. To evaluate the contribution of those pathways to respiratory control, further studies on the temperature response of overall activation energy of AOX-/COX-mediated respiration were conducted (Fig. 12.10; Umekawa et al. 2016). The results indicated that AOX pathway is more sensitive to the temperature change than COX pathway. AOX-mediated respiration seems to be involved in the fast response of thermoregulation to the temperature fluctuations.

12.4.3 Significance of Self-Produced Heat

The biological significance of thermogenesis for plants has been of great concern to the researchers since its discovery. In some of the thermogenic plants, heat production initiates after flower opening; therefore thermogenesis may not be required for anthesis but is required for reproduction. Pollinator attraction is one of the most reasonable explanations so far (Meeuse and Raskin 1988). Most

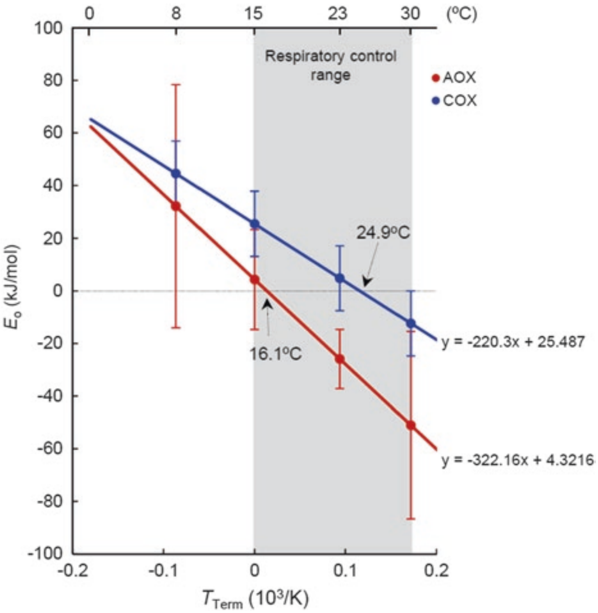

Fig. 12.10 Comparison of the temperature responses of E_o formitochondrial respiration mediated by the AOX- or COX-respiratory pathways. E_o values of NADPH-NDA/ICDH-mediated respirations thorough AOX (red) or COX (blue) pathways. This figure was cited from Umekawa et al. (2016) under the Creative Commons CC-BY conditions

non-thermoregulatory species increase the scent production by volatilization during thermogenesis that makes flowers more attractive to insects. For example, titan arum (*Amorphophallus titanum*), which possesses the largest flower in the world (a maximum height of 3 m), also transiently produces heat and the animal-like odor in its inflorescence at night (Barthlott et al. 2009). The temperature gap between the warmed large inflorescence and the cool air in its natural rain forest habitat may cause heat convection. This could enhance the transport of scent far away. Moreover, thermoregulatory flowers can offer the energy reward for insect pollinators. Flying beetles, the main pollinators of thermoregulatory plants, require high body temperatures of their flight muscles to produce sufficient power; thus the constant warm environment inside the floral chamber makes the beetles save the energy cost for their activities (Seymour et al. 2003).

Thermoregulation is more directly important for the success of fertilization in some flowers. As mentioned above, skunk cabbage begins to bloom in early spring when pollinators are not in the field and pay massive energy cost to maintain their floral temperature for about 1 week. The optimal temperature for pollen germination and pollen tube growth is 23 °C, which is the same as the temperature regulated in the spadix of the skunk cabbage (Seymour et al. 2009a). Interestingly, no pollen germination or pollen tube growth was observed at 8 °C, which is higher than the average of ambient temperature during blooming of skunk cabbage (Onda et al. 2008). This suggests that physiological temperature regulation is crucial for the fertilization of skunk cabbage in their natural habitat.

In the present section, we showed that heat is not always harmful to flowers: optimal thermogenesis has essential roles in pollination and fertilization in some occasion. Heat may also benefit floral traits in the other aspects, although they are not basically the subject of this chapter. On the contrary, plants should be cooled to attenuate the harmful effects of high temperature. Plants decrease leaf temperatures through transpiration (Cook et al. 1964; Negi et al. 2008), although there is a risk to wither by losing leaf water. Thermoregulation by chemical equilibrium may be a clue for self-cooling of plants. If plants can heat themselves by chemical reactions, they would be also able to cool themselves. It is desirable to identify such a self-cooling mechanism of plants to attenuate heat stress.

12.5 Genetic Approaches to Attenuate High-Temperature Effects

There seems to be no specific gene identified to function for flower tolerance to high temperature up to date. Nevertheless, there exists difference between cultivars as to flower tolerance to high temperature, and then some genes or genetic loci function for attenuating high-temperature effects on flowers, such as reduction of pigmentation and acceleration/delay of flowering. Such genes/loci should be identified in future studies. For example, some allele of the *MYB* gene encoding transcription factor may function for high-temperature tolerance of pigment synthesis, and some allele of the *FT* gene encoding florigen may function for high-temperature tolerance of flower induction. Genetic studies on high-temperature tolerance of flowers are quite limited, but we will overview a few related studies in the present section. These will give good hints for future breeding of high-temperature-tolerant cultivars of ornamental/floricultural plants (flowers).

As already described in a previous section, flowering of chrysanthemum is delayed by high temperature, and this is due to the reduction in the expression of the *FT* gene (Nakano et al. 2013). In this report, they also showed that there is difference in high-temperature tolerance between chrysanthemum cultivars. Cultivar ‘Mona Lisa’ was bred in the Netherlands and relatively susceptible to high temperature. The optimum growth condition of chrysanthemum is 18–20 °C. *FT* expression is half reduced at 25 °C compared with 20 °C and dramatically reduced at 30 °C in this cultivar. This results in delay of flowering even at 25 °C (Fig. 12.11). In contrast, cultivar ‘Kurarisu’ was bred for summer production in Japan and then is tolerant to high temperature to some extent. The expression of *FT* is not affected at 25 °C, but it is dramatically reduced at 30 °C. Consistent with this, flowering is not delayed in ‘Kurarisu’ at 25 °C, although it is delayed at 30 °C (Fig. 12.11).

In Eustoma (*Lisianthus*), rosette-like leaves are formed at high temperatures such as 25 or 28 °C, depending on cultivars. Thus, high temperature has deadly effect on flower production: plants do not form flowers until the next year. This will

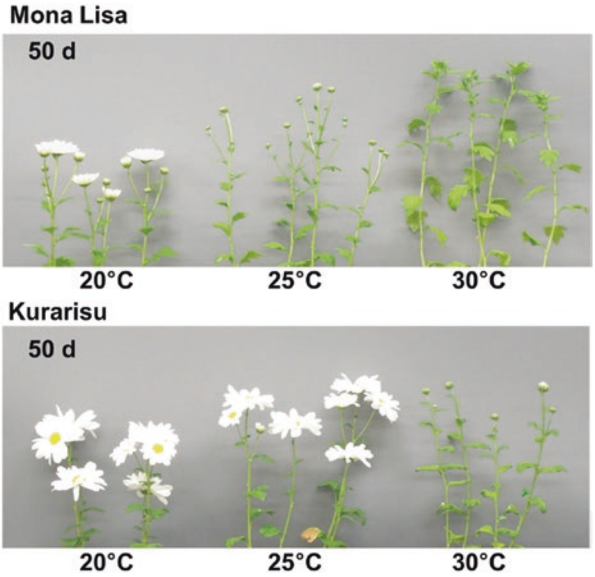

Fig. 12.11 Response of chrysanthemum to high temperature (3). Photographs of cultivars ‘Mona Lisa’ and ‘Kurarisu’, grown at 20, 25, or 30 °C. Photographs were taken 50 days after starting short-day treatment. Data were cited from Nakano et al. (2013) under the Creative Commons CC-BY conditions

be a protective mechanism of Eustoma plants against heat conditions, but agriculturally unfavorable trait. Some high-temperature-tolerant cultivars are reported such as ‘Florida Blue’ and ‘Florida Pink Frill’ (Harbaugh and Scott 2005). These cultivars can be grown at 28–31 °C without rosetting. The mechanism of their tolerance to high temperature is not clear, but *FT* pathway may be also involved in this phenomenon.

Fruits show similar symptoms as flowers in high temperature as well. Reports on genetic effects in fruits will benefit genetic approaches to attenuate the effect of high temperature in flowers. In the skin (surface) of apple fruits, synthesis of red anthocyanin pigment is inhibited by high temperature. Figure 12.12 illustrates decoloration of apple skin under high-temperature condition during fruit maturation. Anthocyanin content is reduced to approximately a quarter when this cultivar is grown in high temperature (Lin-Wang et al. 2011). In high temperature, expressions of all tested genes involved in anthocyanin synthesis, such as *chalcone synthase* (*CHS*), were suppressed. The *MYB1* gene (also called the *MYB10* gene) is responsible for the regulation of these genes and for red skin color of apple fruits (Takos et al. 2006; Kikuchi et al. 2017). Consistently, the expression of *MYB1* was reduced by high temperature, as well as the other regulatory genes. These trends were regenerated by artificial heating of fruits. Although high-temperature-tolerant apple cultivar is not identified, screening of apple cultivars may identify cultivars with strong allele of the *MYB1* gene, which can generate red fruits even in high temperature. Such trial to genetically enforce anthocyanin synthesis is performed in grape. In grape, *MYB* alleles regulate hue of skin anthocyanin (red or purple), and alleles of the *O-Methyl Transferase* (*OMT*) gene regulate anthocyanin concentration. Selection of purple *MYB* allele and strong *OMT* allele by DNA markers will generate dark-purple grape even in high temperature (Azuma et al. 2015). Identification of such “strong” alleles of the regulatory genes of anthocyanin will also improve flower tolerance as to decoloration in high temperature.

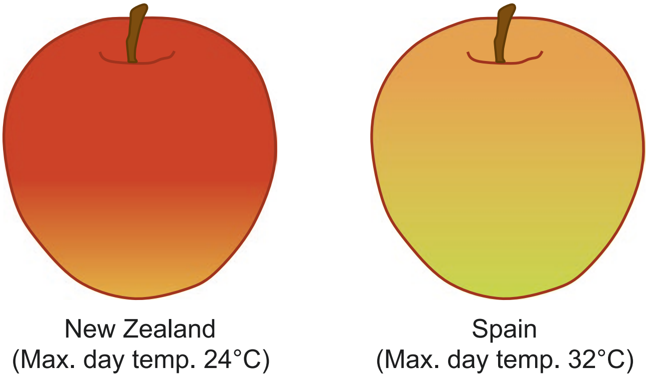

Fig. 12.12 Decoloration of apple skin. Mature fruits of cultivar ‘Mondial Gala’ grown in orchards of New Zealand and Spain. The averages of maximum day temperature during fruit maturation in the orchards are indicated in the figure. The pictures illustrate data in Lin-Wang et al. (2011)

12.6 Physiological Treatments to Attenuate High-Temperature Effects

Chemical, physical, or physiological treatments have been also tested to attenuate unfavorable effects of high temperature on flowers. Cooling the greenhouse by air circulation and water mist is a basic treatment to avoid high temperature. Other additional strategies are taken when plants are not cooled enough by these methods. An interesting effect of magnesium on flower color was observed in aster (Fig. 12.13; Shaked-Sachray et al. 2002). In the cultivar ‘Sungal’ of aster, anthocyanin concentration of petals is approximately halved when growth temperature rises from 17 to 29 °C. The authors hypothesized that magnesium ion protects anthocyanin from degradation at high temperature, and actually anthocyanin concentration was nearly recovered to the original level when they applied 0.8 mM of magnesium ion to aster. It will be important to test whether this kind of approach is also effective in other floricultural plant species.

Shading (cutting off sunlight) with shading net is a popular approach to avoid high-temperature effects. In rice, the temperature of flower was decreased by 2.4 °C (Ishimaru et al. 2016). Due to this treatment, heat sterility of rice cultivar ‘Thadokkham1’ was reduced from 23.3 to 10.0%. Zhao et al. (2012) shaded herbaceous peony cultivar ‘Dafugui’ (Fig. 12.14; Zhao and Tao 2015). By cutting off 60% of sunlight, the day temperature was reduced by 3 °C. The decreased temperature itself will merit plant growth, but reduced intensity of sunlight affected both photosynthesis and flower color: the color of petal was clearly lighter in shaded plant, due to less accumulation of anthocyanin. We can learn from this phenomenon that the deepness of flower color is increased by both lower temperature and higher light intensity, and higher light intensity is more important at least in some cases. The same phenomenon was also observed in tuberose (Huang et al. 2000). The pink flower color of tuberose cultivar ‘77A05’) is lost at 30 °C. The color remains white with 45% shading. In addition, the pink color at 25 °C is also reduced (become lighter) with 45% shading, indicating that high light intensity is necessary to

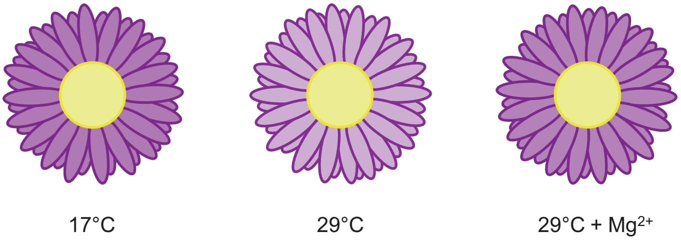

Fig. 12.13 Decoloration of aster. Colors of the petals of aster flowers are illustrated. Flowers were grown at 17 °C/9 °C or 29 °C/21 °C day/night temperatures in left or center, respectively. Flowers were grown at 29 °C/21 °C day/night temperatures, with treatment (drench for 3 times, a week apart) of 0.8 mM of $Mg(NO_3)_2$ in right. This illustration was prepared based on the data in Shaked-Sachray et al. (2002)

Fig. 12.14 Decoloration of herbaceous peony. Flowers of herbaceous peony cultivar ‘Dafugui’ grown with or without shading (‘shade’ and ‘sun’, respectively). Data were cited from Zhao and Tao (2015) under the Creative Commons CC-BY conditions

generate pink color of the flowers. The effect of shading on flower color is not clearly detected at 20 °C. Flower colors of the other plants may be also regulated by the balance between temperature and light intensity.

High temperature affects deepness of flower colors, but it may merit flower fragrance. Studies of Hirata et al. (2016) observed decoloration and decrease of rose petals in summer (Fig. 12.15), just like the other plant species. On the contrary, they noticed that the fragrance of this rose cultivar is stronger in summer. They analyzed that a different bioanalytic pathway of flower scent is active in summer. This will be because rose flowers try to compensate for the smaller size of flowers to attract pollinators.

12.7 Conclusion: Strategies to Attenuate High-Temperature Effects

Flowers change or modulate themselves in response to temperatures much more than we imagined before starting to write the present chapter together. Many parts of the changes under high temperatures are unfavorable for production of ornamental flowers, such as deformation of flowers (Fig. 12.1), but some changes may be beneficial such as increased fragrance in rose and increased number of flowers in chrysanthemum. Heat is also beneficial in heat-producing flowers, for pollinator

Fig. 12.15 Decoloration of rose. Flowers of rose cultivar ‘Yves Piaget’ grown in winter and summer. Average ambient temperatures were 6 or 26 °C in winter or summer, respectively. Data were cited from Hirata et al. (2016) under the Creative Commons CC-BY conditions

attraction and pollination reaction. Plants respond to high temperature through Phytochrome B pathway (Fig. 12.2). This pathway will be responsible for high-temperature-induced changes at least in some cases. One of the typical symptoms of high temperature is heat delay of flowering in short-day plant (chrysanthemum), although flowering is accelerated in long-day plant (thale cress). High temperatures in both day and night delay flowering of chrysanthemum (Fig. 12.3); nevertheless high-temperature-tolerant cultivars can express the *FT* gene in leaves even in moderately high temperature and can avoid heat delay of flowering (Fig. 12.11). Another typical symptom of high temperature is decoloration of anthocyanin pigment in the petal (Fig. 12.5). Magnesium treatment is potentially effective for avoiding this effect (Fig. 12.13). There are also genetic differences in tolerance to decoloration: strong alleles of *MYB* or *OMT* genes are beneficial for tolerance to decoloration. Data indicate that dark-colored petals are good at cooling interior structure of flowers (Fig. 12.6). This mechanism will function for seed production in high temperature in the field. Simple cooling of plants is certainly good to avoid high-temperature effects. For example, low-temperature treatment of Eustoma seeds and seedlings are good to avoid rosetting (Fukushima et al. 2009), although cooling needs energy and cost. Shading with shading net is an ecology way to cool plants, but decreased light intensity may cause decoloration (Figs. 12.14 and 12.15). The entire picture of the relationship between flowers and high temperatures is not still clear, but there actually exist genetic variations and physiological treatments which are effective to avoid high-temperature effects as above. Plants may be also able to cool themselves by unknown reactions, if they can heat themselves (Fig. 12.7).

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References

Azuma A, Ban Y, Sato A, Kono A, Shiraishi M, Yakushiji H, Kobayashi S (2015) MYB diplotypes at the color locus affect the ratios of tri/di-hydroxylated and methylated/non-methylated anthocyanins in grape berry skin. Tree Genet Gnomes 11:31

Barthlott W, Szarzynski J, Vlek P, Lobin W, Korotkova N (2009) A torch in the rain forest: thermogenesis of the Titan arum (*Amorphophallus titanum*). Plant Biol 11:499–505

Berkeley Earth (2019). http://berkeleyearth.lbl.gov/auto/Global/Land_and_Ocean_summary.txt

Berman J, Sheng Y, Gómez LG, Veiga T, Ni X, Farré G, Capell T, Guitián J, Guitián P, Sandmann G, Christou P (2016) Red anthocyanins and yellow carotenoids form the color of orange-flower gentian (*Gentiana lutea* L. var. aurantiaca). PLoS One 11:e0162410

Biran I, Halevy AH (1974) Effects of short-term heat and shade treatments on petal colour of 'Baccara' roses. Physiol Plant 31:180–185

Bovy A, de Vos R, Kemper M, Schijlen E, Pertejo MA, Muir S, Collins G, Robinson S, Verhoeyen M, Hughes S, Santos-Buelga C (2002) High-flavonol tomatoes resulting from the heterologous expression of the maize transcription factor genes *LC* and *C1*. Plant Cell 14:2509–2526

Carvalho SMP, Abi-Tarabay H, Heuvelink E (2005) Temperature affects *Chrysanthemum* flower characteristics differently during three phases of the cultivation period. J Hortic Sci Biotechnol 80:209–216

Chalker-Scott L (1999) Environmental significance of anthocyanins in plant stress responses. Photochem Photobiol 70:1–9

Civello PM, Martínez GA, Chaves AR, Añón MC (1997) Heat treatments delay ripening and postharvest decay of strawberry fruit. J Agric Food Chem 45:4589–4594

Cna'ani A, Mühlemann JK, Ravid J, Masci T, Klempien A, Nguyen TTH, Dudareva N, Pichersky E, Vainstein A (2015) *Petuania* × *hybrida* floral scent production is negatively affected by high-temperature growth conditions. Plant Cell Environ 38:1333–1346

Coberly LC, Rausher MD (2003) Analysis of a chalcone synthase mutant in *Ipomoea purpurea* reveals a novel function for flavonoids: amelioration of heat stress. Mol Ecol 12:1113–1124

Cook GD, Dixon JR, Leopold AC (1964) Transpiration: its effects on plant leaf temperature. Science 144:546–547

Corbesier L, Vincent C, Jang S, Fornara F, Fan Q, Searle I, Giakountis A, Farrona S, Gissot L, Turnbull C, Coupland G (2007) FT protein movement contributes to long-distance signaling in floral induction of *Arabidopsis*. Science 316:1030–1033

Dela G, Or E, Ovadia R, Nissim-Levi A, Weiss D, Oren-Shamir M (2003) Changes in anthocyanin concentration and composition in 'Jaguar' rose flowers due to transient high-temperature conditions. Plant Sci 164:333–340

Elthon TE, Nickels RL, McIntosh L (1989) Monoclonal antibodies to the alternative oxidase of higher plant mitochondria. Plant Physiol 89:1311–1317

Fatihah HN, López DM, van Arkel G, Schaart JG, Visser RG, Krens FA (2019) The *ROSEA1* and *DELILA* transcription factors control anthocyanin biosynthesis in *Nicotiana benthamiana* and *Lilium* flowers. Sci Hortic 243:327–337

Fukushima K, Katsutani N, Imamura H, Takezaki A, Minami M (2009) Night temperature for growing Eustoma seedlings after low-temperature treatment of seeds, which is effective to avoid rosetting. https://www.naro.affrc.go.jp/org/warc/research_results/h17/09_kaki/p309/index.html

Hakata M, Wada H, Masumoto-Kubo C, Tanaka R, Sato H, Morita S (2017) Development of a new heat tolerance assay system for rice spikelet sterility. Plant Methods 13:34

Harbaugh BK, Scott JW (2005) 'Florida Blue Frill' and 'Florida Pink Frill'—Semi-dwarf heat-tolerant *Lisianthus* with bicolored flowers. Hortic Sci 40:861–863

Hichri I, Barrieu F, Bogs J, Kappel C, Delrot S, Lauvergeat V (2011) Recent advances in the transcriptional regulation of the flavonoid biosynthetic pathway. J Exp Bot 62:2465–2483

Hirata H, Ohnishi T, Tomida K, Ishida H, Kanda M, Sakai M, Yoshimura J, Suzuki H, Ishikawa T, Dohra H, Watanabe N (2016) Seasonal induction of alternative principal pathway for rose flower scent. Sci Rep 6:20234

Huang KL, Miyajima I, Okubo H (2000) Effects of temperature and shade treatment on flower colors and characteristics in newly established reddish-purple tuberose (*Polianthes*). J Fac Agric Kyushu Univ 45:57–63

Ishimaru T, Hirabayashi H, Sasaki K, Ye C, Kobayashi A (2016) Breeding efforts to mitigate damage by heat stress to spikelet sterility and grain quality. Plant Prod Sci 19:12–21

Kakizaki Y, Moore Anthony L, Ito K (2012) Different molecular bases underlie the mitochondrial respiratory activity in the homoeothermic spadices of *Symplocarpus renifolius* and the transiently thermogenic appendices of *Arum maculatum*. Biochem J 445:237–246

Kamata T, Matsukawa K, Kakizaki Y, Ito K (2009) In vivo redox state of the ubiquinone pool in the spadices of the thermogenic skunk cabbage, *Symplocarpus renifolius*. J Plant Res 122:645–649

Kardailsky I, Shukla VK, Ahn JH, Dagenais N, Christensen SK, Nguyen JT, Chory J, Harrison MJ, Weigel D (1999) Activation tagging of the floral inducer FT. Science 286:1962–1965

Karlsson MG, Heins RD, Erwin JE, Berghage RD, Carlson WH, Biernbaum JA (1989) Irradiance and temperature effects on time of development and flower size in Chrysanthemum. Sci Hortic 39:257–267

Kasajima I (2016) Alexandrite-like effect in purple flowers analyzed with newly devised round RGB diagram. Sci Rep 6:29630

Kasajima I (2019) Measuring plant colors. Plant Biotechnol 36:63–75

Kikuchi T, Kasajima I, Morita M, Yoshikawa N (2017) Practical DNA markers to estimate apple *(Malus* × *domestica*Borkh.) skin color, ethylene production and pathogen resistance. J Hortic 4:1000211

Kim TS, Kim WY, Fujiwara S, Kim J, Cha JY, Park JH, Lee SY, Somers DE (2011) HSP90 functions in the circadian clock through stabilization of the client F-box protein ZEITLUPE. Proc Natl Acad Sci USA 108:16843–16,848

Knutson RM (1974) Heat production and temperature regulation in eastern skunk cabbage. Science 186:746–747

Kobayashi Y, Kaya H, Goto K, Iwabuchi M, Araki T (1999) A pair of related genes with antagonistic roles in mediating flowering signals. Science 286:1960–1962

Koes R, Verweij W, Quattrocchio F (2005) Flavonoids: a colorful model for the regulation and evolution of biochemical pathways. Trends Plant Sci 10:236–242

Kojima S, Takahashi Y, Kobayashi Y, Monna L, Sasaki T, Araki T, Yano M (2002) *Hd3a*, a rice ortholog of the *Arabidopsis FT* gene, promotes transition to flowering downstream of *Hd1* under short-day conditions. Plant Cell Physiol 43:1096–1105

Kortstee AJ, Khan SA, Helderman C, Trindade LM, Wu Y, Visser RG, Brendolise C, Allan A, Schouten HJ, Jacobsen E (2011) Anthocyanin production as a potential visual selection marker during plant transformation. Transgenic Res 20:1253–1264

Kreslavski VD, Los DA, Schmitt FJ, Zharmukhamedov SK, Kuznetsov VV, Allakhverdiev SI (2018) The impact of the phytochromes on photosynthetic processes. Biochim Biophys Acta Bioenerg 1859:400–408

Kumar SV, Lucyshyn D, Jaeger KE, Alós E, Alvey E, Harberd NP, Wigge PA (2012) Transcription factor PIF4 controls the thermosensory activation of flowering. Nature 484:242–245

Lacey EP, Herr D (2005) Phenotypic plasticity, parental effects, and parental care in plants? I. An examination of spike reflectance in *Plantagolanceolata* (Plantaginaceae). Am J Bot 92:920–930

Lamarck JB (1778) Flore Française, ou, Description succinctes de toutes les plantes qui croissentnaturellementen France, vol 3, 2nd edn. Impr. Natl, Paris

Legris M, Klose C, Burgie ES, Rojas CC, Neme M, Hiltbrunner A, Wigge PA, Schäfer E, Vierstra RD, Casal JJ (2016) Phytochrome B integrates light and temperature signals in *Arabidopsis*. Science 354:897–900

Liang S, Wu X, Byrne D (2017) Flower-size heritability and floral heat-shock tolerance in diploid roses. Hort Science 52:682–685

Lin-Wang K, Micheletti D, Palmer J, Volz R, Lozano L, Espley R, Hellens RP, Chagnè D, Rowan DD, Troggio M, Iglesias I, Allan AC (2011) High temperature reduces apple fruit colour via modulation of the anthocyanin regulatory complex. Plant Cell Environ 34:1176–1190

McKee J, Richards AJ (1998) Effect of flower structure and flower colour on intrafloral warming and pollen germination and pollen-tube growth in winter flowering *Crocus* L. (Iridaceae). Bot J Linn Soc 128:369–384

Meeuse BJD (1975) Thermogenic respiration in aroids. Annu Rev Plant Physiol 26:117–126

Meeuse BJD, Raskin I (1988) Sexual reproduction in the arum lily family, with emphasis on thermogenicity. Sex Plant Reprod 1:3–15

Miyake K (1898) Some physiological observations on *Nelumbo nucifera*, Gærtn. Bot Mag Tokyo (ShokubutugakuZasshi) 12:112–117. https://www.jstage.jst.go.jp/article/jplantres1887/12/142/12_142_112/_article/-char/ja/

Monteiro JA, Nell TA, Barrett JE (2001) High production temperature increases postproduction flower longevity and reduces bud drop of poted, miniature roses ‘Meirutral’ and ‘Meidanclar’. Hortscience 36:953–954

Moore AL, Shiba T, Young L, Harada S, Kita K, Ito K (2013) Unraveling the heater: new insights into the structure of the alternative oxidase. Annu Rev Plant Biol 64:637–663

Motozu T, Komagata T, Ichimura T, Asano A (2000) Observation on the development of forced freesia flower buds exposed to high temperature just after chilling and morphological classification of heat injury at flowering. J Jpn Soc Hortic Sci 69:109–114. (in Japanese)

Mu J, Li G, Sun S (2010) Petal color, flower temperature, and behavior in an alpine annual herb, *Gentiana leucomelaena* (Gentianaceae). Arct Antarct Alp Res 42:219–226

Nakano Y, Higuchi Y, Sumitomo K, Hisamatsu T (2013) Flowering retardation by high temperature in chrysanthemums: involvement of *FLOWERING LOCUS T-like 3* gene repression. J Exp Bot 64:909–920

Negi J, Matsuda O, Nagasawa T, Oba Y, Takahashi H, Kawai-Yamada M, Uchimiya H, Hashimoto M, Iba K (2008) CO_2 regulator SLAC1 and its homologues are essential for anion homeostasis in plant cells. Nature 452:483–486

Nie Z-L, Sun H, Li H, Wen J (2006) Intercontinental biogeography of subfamily Orontioideae (*Symplocarpus*, *Lysichiton*, and *Orontium*) of Araceae in eastern Asia and North America. Mol Phylogenet Evol 40:155–165

Nozaki K, Fukai S, Takamura T (2005) Effects of growing season on flower color and flowering in pink flower genotypes of spray chrysanthemum. Hortic Res 4:197–201. (in Japanese)

Nozaki K, Takamura T, Fukai S (2006) Effects of high temperature on flower colour and anthocyanin content in pink flower genotypes of greenhouse chrysanthemum (*Chrysanthemum morifolium* Ramat.). J Hortic Sci Biotehcnol 81:728–734

Onda Y, Kato Y, Abe Y, Ito T, Ito-Inaba Y, Morohashi M, Ito Y, Ichikawa M, Matsukawa K, Otsuka M, Koiwa H, Ito K (2007) Pyruvate-sensitive AOX exists as a non-covalently associated dimer in the homeothermic spadix of the skunk cabbage, *Symplocarpus renifolius*. FEBS Lett 581:5852–5858

Onda Y, Kato Y, Abe Y, Ito T, Morohashi M, Ito Y, Ichikawa M, Matsukawa K, Kakizaki Y, Koiwa H, Ito K (2008) Functional coexpression of the mitochondrial alternative oxidase and uncoupling protein underlies thermoregulation in the thermogenic florets of skunk cabbage. Plant Physiol 146:636–645

Prasad PV, Craufurd PQ, Summerfield RJ, Wheeler TR (2000) Effects of short episodes of heat stress on flower prodiction and fruit-set of groundnut (*Arachis hypogaea* L.). J Exp Bot 51:777–784

Puangkrit T, Narumi-kawasaki T, Takamura T, Fukai S (2018) Inflorescence developmental stage-specific high temperature effect on petal pigmentation in chrysanthemum. Environ Control Biol 56(3):99–106

Quattrocchio F, Wing JF, Va K, Mol JN, Koes R (1998) Analysis of *bHLH* and *MYB* domain proteins: species-specific regulatory differences are caused by divergent evolution of target anthocyanin genes. Plant J 13:475–488

Raskin I, Ehmann A, Melander WR, Meeuse BJ (1987) Salicylic acid: a natural inducer of heat production in arum lilies. Science 237:1601–1602

Raskin I, Turner IM, Melander WR (1989) Regulation of heat production in the inflorescences of an arum lily by endogenous salicylic acid. Proc Natl Acad Sci USA 86:2214–2218

Sangster TA, Bahrami A, Wilczek A, Watanabe E, Schellenberg K, McLellan C, Kelly A, Kong SW, Queitsch C, Lindquist S (2007) Phenotypic diversity and altered environmental plasticity in *Arabidopsis thaliana* with reduced Hsp90 levels. PLoS One 2:e648

Sangster TA, Salathia N, Lee HN, Watanabe E, Schellenberg K, Morneau K, Wang H, Undurraga S, Queitsch C, Lindquist S (2008) HSP90-buffered genetic variation is common in *Arabidopsis thaliana*. Proc Natl Acad Sci USA 105:2969–2974

Sayed MA, Umekawa Y, Ito K (2016) Metabolic interplay between cytosolic phosphoenolpyruvate carboxylase and mitochondrial alternative oxidase in thermogenic skunk cabbage, *Symplocarpus renifolius*. Plant Signal Behav 11:e1247138

Schreiber G, Reuveni M, Evenor D, Oren-Shamir M, Ovadia R, Sapir-Mir M, Bootbool-Man A, Nahon S, Shlomo H, Chen L, Levin I (2012) ANTHOCYANIN1 from *Solanum chilense* is more efficient in accumulating anthocyanin metabolites than its *Solanum lycopersicum* counterpart in association with the ANTHOCYANIN FRUIT phenotype of tomato. Theor Appl Genet 124:295–307

Schwinn KE, Davies KM (2004) Flavonoids. Annu Plant Rev. 14:92–149

Seymour RS (2010) Scaling of heat production by thermogenic flowers: limits to floral size and maximum rate of respiration. Plant Cell Environ 33:1474–1485

Seymour RS, Schultze-Motel P (1996) Thermoregulating lotus flowers. Nature 383:305–305

Seymour RS, Schultze-Motel P (1998) Physiological temperature regulation by flowers of the sacred lotus. Philos Trans R Soc Lond B Biol Sci 353:935–943

Seymour RS, White CR, Gibernau M (2003) Heat reward for insect pollinators. Nature 426:243–244

Seymour RS, Ito Y, Onda Y, Ito K (2009a) Effects of floral thermogenesis on pollen function in Asian skunk cabbage *Symplocarpus renifolius*. Biol Lett 5:568–570

Seymour RS, Maass E, Bolin JF (2009b) Floral thermogenesis of three species of *Hydnora* (Hydnoraceae) in Africa. Annal Bot 104:823–832

Seymour R, Lindshau G, Ito K (2010) Thermal clamping of temperature-regulating flowers reveals the precision and limits of the biochemical regulatory mechanism. Planta 231:1291–1300

Shaked-Sachray L, Weiss D, Reuveni M, Nissim-Levi A, Oren-Shamir M (2002) Increased anthocyanin accumulation in aster flowers at elevated temperatures due to magnesium treatment. Physiol Plant 114:559–565

Shvarts M, Borochov A, Weiss D (1997) Low temperature enhances petunia flower pigmentation and induces chalcone synthase gene expression. Physiol Plant 99:67–72

Song YH, Shim JS, Kinmonth-Schultz HA, Imaizumi T (2015) Photoperiodic flowering: time measurement mechanisms in leaves. Annu Rev Plant Biol 66:441–464

Steyn WJ, Wand SJ, Holcroft DM, Jacobs G (2002) Anthocyanins in vegetative tissues: a proposed unified function in photoprotection. New Phytol 155:349–361

Stiles EA, Cech NB, Dee SM, Lacey EP (2007) Temperature-sensitive anthocyanin production in flowers of *Plantagolanceolata*. Physiol Plant 129:756–765

Suraweera DD, Nicolas ME, Groom T (2016) Effect of short periods of heat stress during early flowering period on flower development and pyrethrin accumulation in pyrethrum. Acta Hortic 1125:121–128. https://doi.org/10.17660/ActaHortic.2016.1125.15

Takeno K (2016) Stress-induced flowering: the third category of flowering response. J Exp Bot 67:4925–4934

Takos AM, Jaffe FW, Jacob SR, Bogs J, Robinson SP, Walker AR (2006) Light-induced expression of a *MYB* gene regulates anthocyanin biosynthesis in red apples. Plant Physiol 142:1216–1232

Tamaki S, Matsuo S, Wong HL, Yokoi S, Shimamoto K (2007) Hd3a protein is a mobile flowering signal in rice. Science 316:1033–1036

Tsuji H (2017) Molecular function of florigen. Breed Sci 67:327–332

Umbach AL, Siedow JN (1993) Covalent and noncovalent dimers of the cyanide-resistant alternative oxidase protein in higher plant mitochondria and their relationship to enzyme activity. Plant Physiol 103:845–854

Umekawa Y, Ito K (2018) Thioredoxin *o*-mediated reduction of mitochondrial alternative oxidase in the thermogenic skunk cabbage *Symplocarpus renifolius*. J Biochem 165:57–65

Umekawa Y, Seymour RS, Ito K (2016) The biochemical basis for thermoregulation in heat-producing flowers. Sci Rep 6:24830

Yamada K, Fukao Y, Hayashi M, Fukazawa M, Suzuki I, Nishimura M (2007) Cytosolic HSP90 regulates the heat shock response that is responsible for heat acclimation in *Arabidopsis thaliana*. J Biol Chem 282:37794–37,804

Yang KZ, Xia C, Liu XL, Dou XY, Wang W, Chen LQ, Zhang XQ, Xie LF, He L, Ma X, Ye D (2009) A mutation in *THERMOSENSITIVE MALE STERILE 1*, encoding a heat shock protein with DnaJ and PDI domains, leads to thermosensitive gametophytic male sterility in Arabidopsis. Plant J 57:870–882

Zhang C, Li G, Chen T, Feng B, Fu W, Yan J, Islam MR, Jin Q, Tao L, Fu G (2018) Heat stress induces spikelet sterility in rice at anthesis through inhibition of pollen tube elongation interfering with auxin homeostasis in pollinated pistils. Rice 11:14

Zhao D, Tao J (2015) Recent advances on the development and regulation of flower color in ornamental plants. Front Plant Sci 6:261

Zhao D, Hao Z, Tao J (2012) Effects of shade on plant growth and flower quality in the herbaceous peony (*Paeonia lactiflora* Pall.). Plant Physiol Biochem 61:187–196

Chapter 13
Assessing the Effects of High Night Temperature on Rice Photosynthetic Parameters: Involvement of Cellular Membrane Damage and Ethylene Response

Abdul Razack Mohammed and Lee Tarpley

Contents

Abstract Plant ecophysiological response to environmental stresses involves sub-organismal mechanisms. For example, elevated ethylene levels can promote the

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degradation of chlorophyll (CD) and damage to the cellular membranes (MD), leading to decreased photosynthetic rate (P_N) and photosynthate transfer, as well as increased respiration (R_S) under heat stress, causing loss of yield. To determine the extent of contribution of ethylene-triggered responses in rice plants under high night temperature (HNT; 30 °C) stress, the capability of applied ethylene perception inhibitor, 1-methylcyclopropene (1-MCP), to prevent rice yield loss by minimizing HNT-induced, ethylene-promoted CD and MD, was examined. Rice was subjected to either 30 or 25 °C (ambient night temperature (ANT)); under each night temperature regime, sets of plants received 1-MCP application or not. High night temperature increased CD (7%), MD (46%), and R_S (28%) and decreased P_N (6%), pollen germination (42%) and spikelet fertility (SF; 31%), and yield (14%). In response to 1-MCP application, plants grown under HNT showed decreased CD (from 8 to 10.6 μg cm^{-1}), MD (from 42% to 35%), and R_S (from 1.3 to 0.9 μmol m^{-2} s^{-1}) and increased SF (49.5 to 70%), pollen germination (15 to 18.9%), and yield (15 to 17.7 g plant^{-1}). The 1-MCP application increased SF and brought rice yields under HNT up to levels observed under ANT as a result of increased pollen germination and decreased R_S and MD, indicating that ethylene-triggered responses are a major component of rice response to HNT.

Keywords 1-Methylcyclopropene · Heat stress · High night temperature · Rice · Respiration

Abbreviations

1-MCP	1-Methylcyclopropene
ANT	Ambient night temperature
CD	Chlorophyll degradation
DAT	Days after treatment
ETR	Electron transport rate
HNT	High night temperature
LNC	Leaf nitrogen content
MD	Membrane damage
NPQ	Non-photochemical quenching
NT	Night temperature
P_N	Photosynthesis
ROS	Reactive oxygen species
SF	Spikelet fertility

13.1 Introduction

Organismal plant response and adaptation to environmental stresses involve, to a large extent, sub-organismal mechanisms. This study examines the role of the ethylene response in rice (*Oryza sativa* L.) under night temperature stress. Rice is grown between 50°N and 35°S latitude (Grist 1986) and is one of the stable foods (Food and Agriculture Organization [FAO] 2008). Several studies have shown that high night temperature (HNT) can reduce rice production (Cheng et al. 2009, 2010; Mohammed and Tarpley 2009a, b, 2010). Peng et al. (2004) reported that rice yield will decrease by 10% for a 1 °C increase in night temperature. According to IPCC (2014) reports, average temperature by the end of the twenty-first century is projected to increase by 1.4–5.8 °C, and much of this increase is because of NT. According to Alward et al. (1999), less heat loss due to cloudiness can increase night temperatures.

Hays et al. (2007) and Djanaguiraman and Prasad (2010) reported that chlorophyll degradation (CD), senescence, abscission of plant parts, and yield loss are because of increased ethylene production under high temperature. Larrigaudiere et al. (2004) reported that ethylene plays an important role in production of reactive oxygen species (ROS), which are involved in CD, membrane damage (MD), and abscission of plant organs. Premature leaf senescence and CD along with damage to the photosystem and electron transport mechanism can decrease leaf photosynthetic rate (P_N) (Pettigrew et al. 1993; Havaux and Tardy 1996; Guo et al. 2006). Respiration (R_S) is increased to provide energy and substrates used to repair MD (Amthor and McCree 1990). Mohammed and Tarpley (2009a, b) have shown increased CD and MD under HNT. The resultant increase in respiration can contribute to a decrease in average grain weight, thus grain yield (Morita et al. 2005).

Under HNT, spikelet fertility (SF) in rice decreases due to decrease in translocation of photosynthates to the spikelets due to decreased P_N and increased R_S and MD (Cheng et al. 2009, 2010). Prasad et al. (2006) reported that decreased SF is linked to poor anther dehiscence and pollen tube elongation and low shedding and germination of pollen on the stigma. Under severe conditions, HNT can also cause spikelet abortion, thereby decreasing yield (Cheng et al. 2010). Counce et al. (2005) reported that reduced production and/or improper transfer of carbohydrates to the grains can decrease grain dimensions and weight. High night temperature decreased rice grain dimensions and increased chalkiness due to insufficient accumulation of photosynthates and depression of cell growth (Nagato and Ebata 1965; Lisle et al. 2000; Cooper et al. 2008).

Ethylene receptor inhibitor, 1-methylcyclopropene (1-MCP), can attach to ethylene receptors, thereby preventing signal transduction and translation, thus preventing ethylene-induced effects (Sisler and Serek 1997; Blankenship and Dole 2003). We hypothesized that 1-MCP would inhibit ethylene-triggered responses such as CD and MD, thereby preventing yield loss. Therefore, the purpose of this study was to determine the capability of applied 1-MCP to prevent rice yield loss by minimizing HNT-induced, ethylene-promoted CD and MD.

13.2 Materials and Methods

13.2.1 Plant Husbandry

"Cocodrie" (rice variety) was grown in pots containing a clay soil in both the experiments. Planting depth was 2.5 cm and plants were thinned from five to one plant per pot after emergence. Flooding was imposed at first tillering stage. At boot developmental stage, 50% of the plants were randomly moved to heat stress and 50% of the plants in each temperature regime were treated with 1-MCP. Fertilizer was applied according to Mohammed and Tarpley (2011).

13.2.2 Temperature Treatments

Heat treatments were randomly assigned to greenhouse location in both the experiments. The ANT was set at 25 °C and HNT as 30 °C. Heat stress was imposed using infrared heaters as described by Mohammed and Tarpley (2009c) from boot stage until harvest. The infrared heating system was designed to minimize direct heating of vegetation through a rapid feedback and control system utilizing incremental adjustments of the canopy air temperature (Mohammed and Tarpley 2009c).

Temperature and humidity were measured using standalone sensor from Onset Computer Corporation. Temperatures in both the temperature regimes were maintained at the set temperature "+" or "−" 0.5 °C. The temperature/humidity in control setup was 25.3 °C/15.6 g m^{-3} and in HNT setup was 30.4 °C/15.6 g m^{-3}.

13.2.3 1-MCP Treatments

Treated plants were provided with 1-MCP at the rate of 10 g (a.i) ha^{-1}. To eliminate possible drift contamination of untreated plants, the 1-MCP-treated plants were far away from the untreated plants.

13.2.4 Pigment Concentrations

Chlorophyll and carotenoid concentrations of penultimate leaves were determined 5 days after treatment (DAT). Three leaf discs (totaling 1.0 cm^2) were obtained from mid-blade for pigment extraction in dimethyl sulfoxide and incubated in the dark for 24 h at room temperature. The absorbances of the extracts at 480, 648, and 664 nm were used to calculate the carotenoids, chlorophyll *a*, and chlorophyll *b* concentrations according to Lichtenthaler (1987) and Chappelle et al. (1992). The pigment concentration was expressed on a leaf area basis, μg cm^{-2}.

13.2.5 Leaf Nitrogen Content (LNC)

The LNC of the second topmost leaf was measured using a LECO FP-528 Nitrogen/Protein Analyzer. The LNC was expressed in percentage.

13.2.6 Membrane Damage (MD)

The MD was determined on the second topmost leaf, five DAT according to Mohammed and Tarpley (2009b) and Ibrahim and Quick (2001). The MD was calculated as $MD = \{1 - [1 - (C_i55/C_f55)]/[1 - (C_i25/C_f25)]\} \times 100$ where $C55$ and $C25$ refer to the conductance at 55 and 25 °C, respectively, and the subscripts i and f refer to the initial and final conductance. The conductance was measured using conductivity meter.

13.2.7 *Photosynthetic Rate* (P$_N$) *and Respiration* (R$_S$)

The P_N and R_S were measured at 3 and 5 DAT using a LI-6400. While measuring P_N and R_S, the leaf cuvette temperature and CO_2 concentration were set to 25 °C and 390 ppm, respectively. The light intensity in the cuvette was set at 1500 and 0 μmol m^{-2} s^{-1}, respectively, while measuring P_N and R_S. The P_N was measured in the day and R_S in the night.

13.2.8 Chlorophyll Fluorescence

A fluorometer was used for quantifying thylakoid membrane stability (F_o/F_m), capability of reaction center (F_v/F_m), quantum yield (Y), electron transport rate (ETR), and non-photochemical quenching (NPQ), 3 and 5 days after treatment. Klughammer and Schreiber (2008)'s equations were used to calculate NPQ [$NPQ = (F_m - F_{ms})/F_{ms}$].

13.2.9 Reproductive Parameters and Yield

Staining (iodine potassium iodine) technique was used to determine pollen viability (Virmani et al. 1997 with minor modifications). Microscopy was used to observe the pollens which were classified as viable or non-viable based on degree of staining, shape, and size. The sterility of pollen was presented as percentage.

Procedure from Mohammed and Tarpley (2009a) was used to determine pollen germination (in vitro germination) on a medium. The pollen was considered as germinated if the tube length was equal to or greater than grain diameter as determined. The germinated pollen was presented as percentage.

The SF was estimated according to Kobata et al. (2009). Spikelets from threshed panicles were immersed in 70% (v/v) ethanol. The floating (sterile and empty) and sunk (filled) spikelets were separated, dried, and weighed. In this study, %SF = (filled spikelet weight ÷ total spikelet weight [filled + unfilled]) × 100.

13.2.10 Grain Dimensions, Chalkiness, and Nitrogen Concentration

Grain dimensions and chalkiness of brown rice were determined using Winseedle, which uses scanned color images (image analysis) of grain.

The LECO FP-528 Nitrogen/Protein Analyzer was used to determine grain nitrogen concentration (GNC; %, w/w) from the mainstem panicle grains (brown rice).

13.2.11 Experimental Design and Data Analysis

For each experiment, a complete randomized design was executed. From both the experiments, there were 12 plants per night temperature X chemical treatment. Analysis of variance (ANOVA; SAS) was conducted to test the significance of experiment, NT, chemical treatment, and their interactive effects on the parameters measured. Means were separated using Tukey's Honest Significant Difference (HSD; $\alpha = 0.05$).

13.3 Results

13.3.1 Pigment Concentrations, Leaf Nitrogen Content (LNC), and Membrane Damage (MD)

The chlorophyll *a* concentration (8%) and chlorophyll *a*/*b* ratio (4%) were lower under HNT than ANT (Fig. 13.1a, d). Application of 1-MCP increased carotenoids (25%) and LNC (40%), under ANT (Fig. 13.1c, f). Under HNT, application of

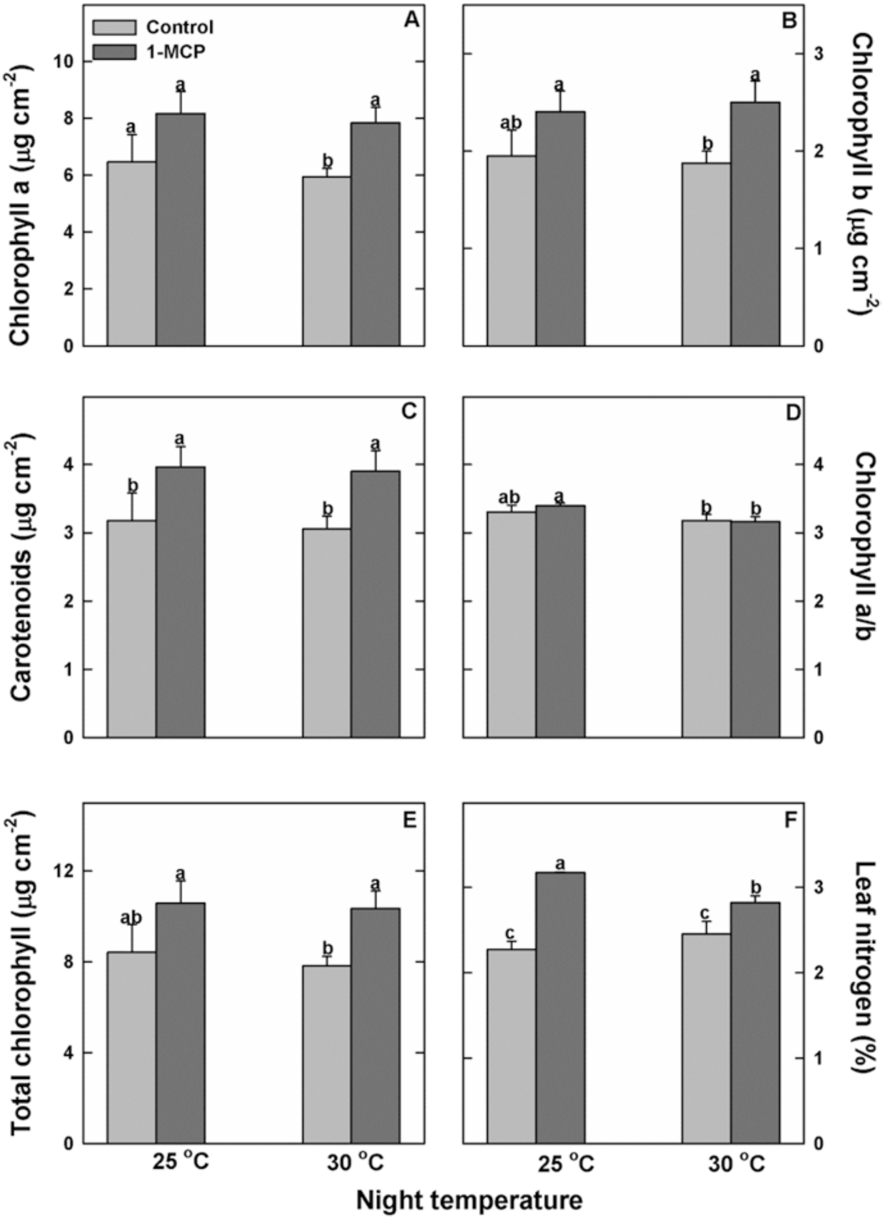

Fig. 13.1 Impact of night temperature and 1-methylcyclopropene (1-MCP) on concentrations of leaf chlorophyll *a* (**a**), chlorophyll *b* (**b**), carotenoids (**c**), chlorophyll *a/b* (**d**), total chlorophyll (**e**) and leaf nitrogen content [LNC] (**f**)

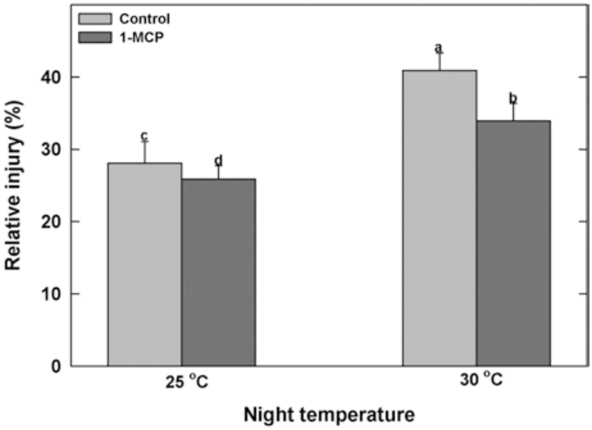

Fig. 13.2 Impact of night temperature and 1-methylcyclopropene (1-MCP) on relative injury (membrane damage [MD])

1-MCP increased chlorophyll *a* (32%), chlorophyll *b* (33%), carotenoids (27%), total chlorophyll (32%), and LNC (15%) (Fig. 13.1a–c, e, f).

Figure 13.2 shows increased MD (46%) under HNT compared to ambient for untreated plants and 1-MCP application decreased MD under ambient (8%) and HNT (17%), compared to untreated plants.

13.3.2 Photosynthetic Rate (P_N) and Chlorophyll Fluorescence

Untreated plants under HNT showed lower P_N (6%) compared to ANT, 3 DAT (Fig. 13.3a). There is no difference between the NT and chemical treatments for stomatal conductance, internal CO_2, and transpiration, 3 days after treatment (Fig. 13.3b–d). Figure 13.3a shows that 1-MCP application increased P_N (13%) compared to untreated, under ambient temperature regime, 3 days after treatment. Five DAT, no difference was observed between the NT or the chemical treatments for P_N, stomatal conductance, internal CO_2 concentration, or transpiration (Fig. 13.4a–d).

Three DAT, no difference was observed between the NT or chemical treatments for F_v/F_m, F_o/F_m or NPQ (Fig. 13.5a, b, e). For untreated plants, HNT decreased Y (15%) and ETR (15%) compared to ANT, 3 DAT (Fig. 13.5c, d). Under HNT, 1-MCP application increased Y (15%) and ETR (15%), compared to untreated, 3 DAT (Fig. 13.5c, d). For untreated plants, HNT lowered F_v/F_m (5%), Y (12%), and ETR (12%) and increased F_o/F_m (15%), compared to ANT, 5 DAT (Fig. 13.6a–d). Five DAT, no difference between 1-MCP-treated and untreated for chlorophyll fluorescence parameters was observed (Fig. 13.6a–e).

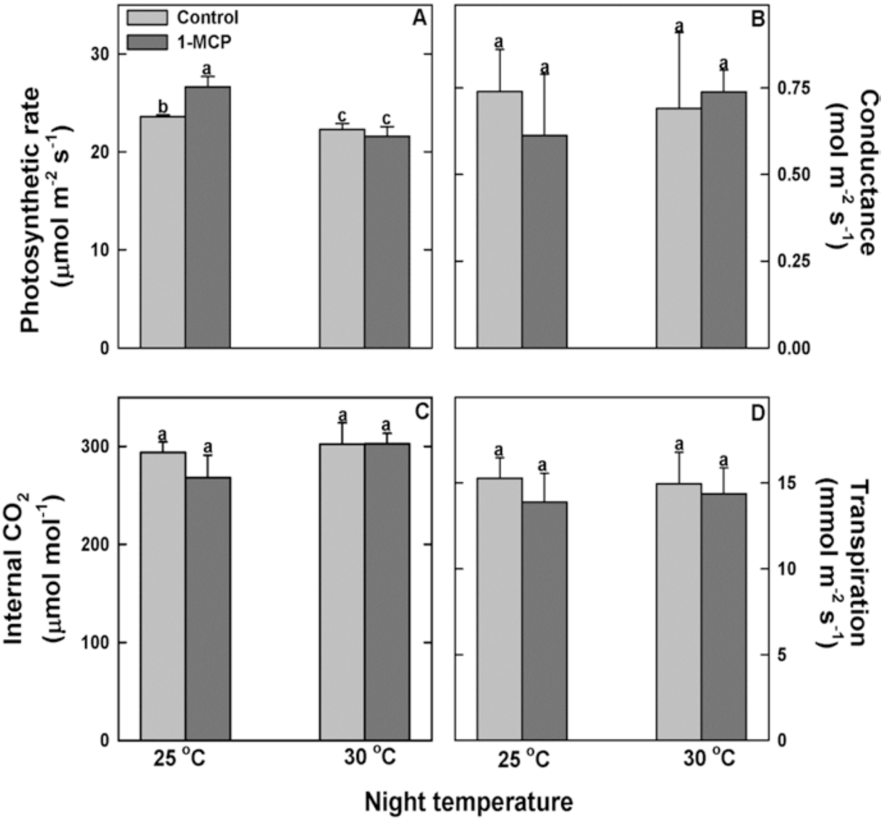

Fig. 13.3 Impact of night temperature and 1-methylcyclopropene (1-MCP) on photosynthetic rate [P_N] (**a**), stomatal conductance (**b**), internal CO_2 concentration (**c**) and transpiration (**d**) measured on the penultimate leaves, 3 days after treatment

13.3.3 Leaf Respiration Rate

High night temperature increased R_S by 28% and 45% measured at 3 DAT and 5 DAT, respectively, compared to ambient (Fig. 13.7a, b). The application of 1-MCP lowered R_S by 13% and 18% measured 3 and 5 DAT, compared to untreated (Fig. 13.7a, b). For plants grown under HNT, application of 1-MCP lowered R_S by 14% and 30% measured at 3 and 5 DAT, compared to untreated (Fig. 13.7a, b).

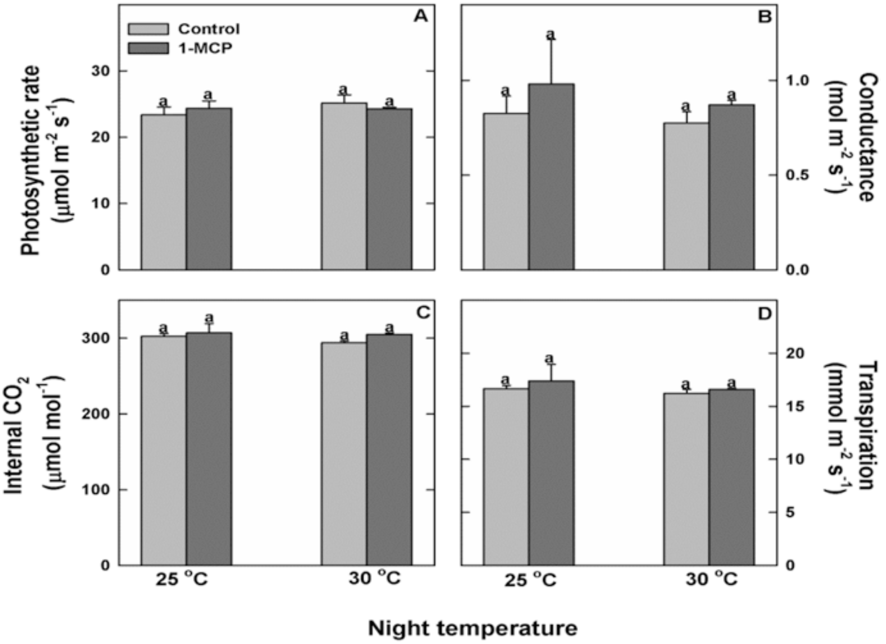

Fig. 13.4 Impact of night temperature and 1-methylcyclopropene (1-MCP) on photosynthetic rate [P_N] (**a**), stomatal conductance (**b**), internal CO_2 concentration (**c**) and transpiration (**d**) measured on the penultimate leaves, 5 days after treatment

13.3.4 Reproductive Parameters and Yield

High night temperature or 1-MCP application showed no effect on pollen viability (Fig. 13.8a). However, HNT lowered pollen germination (42%), SF (31%), and yield (14%), compared to ANT (Fig. 13.8b–d). Under ambient temperature regime, 1-MCP application increased pollen germination (15%), SF (8%), and yield (13%), compared to untreated (Fig. 13.8b–d). Under elevated NT, 1-MCP application increased yield (18%), pollen germination (27%), and SF (41%) (Fig. 13.8b–d).

13.3.5 Grain Dimensions, Chalkiness, and Nitrogen Concentration

High night temperature decreased grain length (3%), compared to ambient (Fig. 13.9a). For plants grown under HNT, application of 1-MCP increased grain length (3%), width (2%), volume (6%), and surface area (5%) compared to untreated plants (Fig. 13.9a–d). High night temperature or 1-MCP application showed no effect on GNC (Fig. 13.9f).

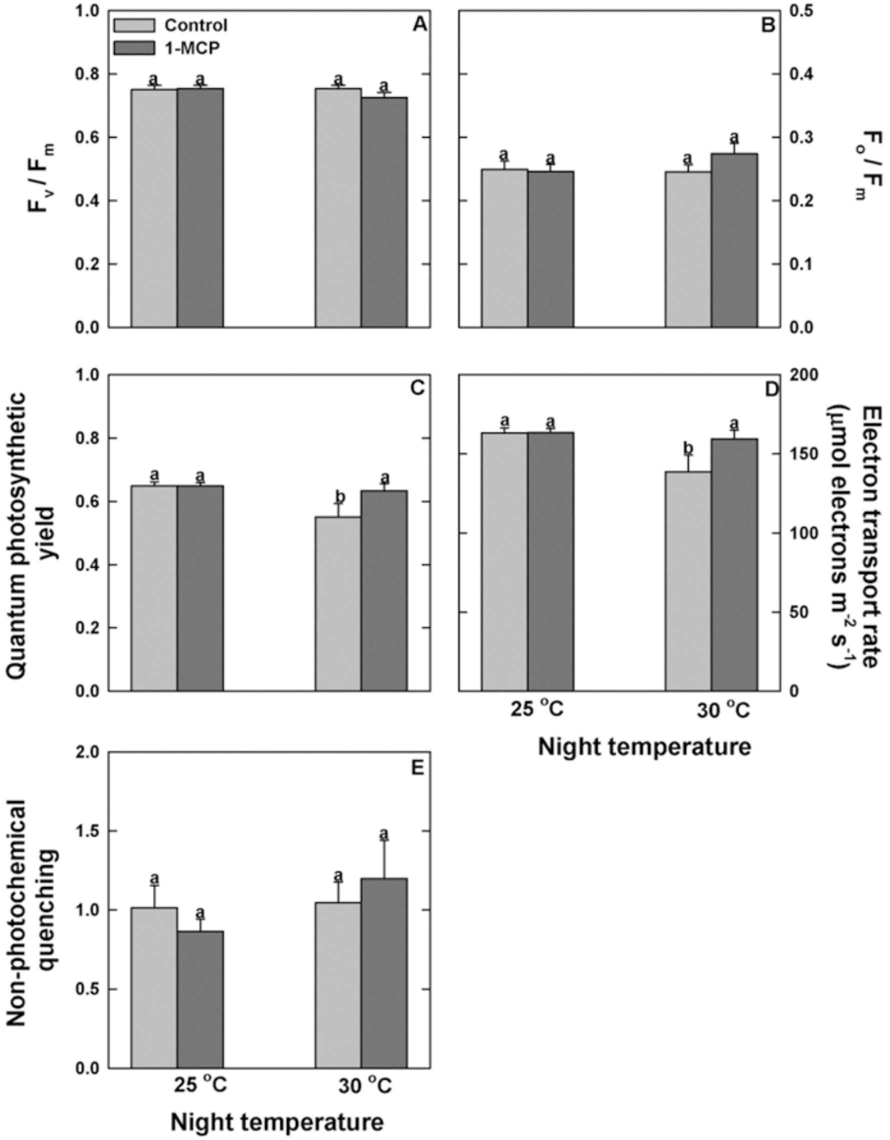

Fig. 13.5 Impact of night temperature and 1-methylcyclopropene (1-MCP) on F_v/F_m (**a**), F_o/F_m (**b**), quantum photosynthetic yield [Y] (**c**), electron transport rate [ETR] (**d**) and non-photochemical quenching [NPQ] (**e**), 3 days after treatment

13.4 Discussion

It was observed in this study that HNT increased chlorophyll degradation (CD), which might be a result of chloroplast membrane lipid peroxidation as shown by greater damage to the membrane. Ristic et al. (2007) stated that thylakoid mem-

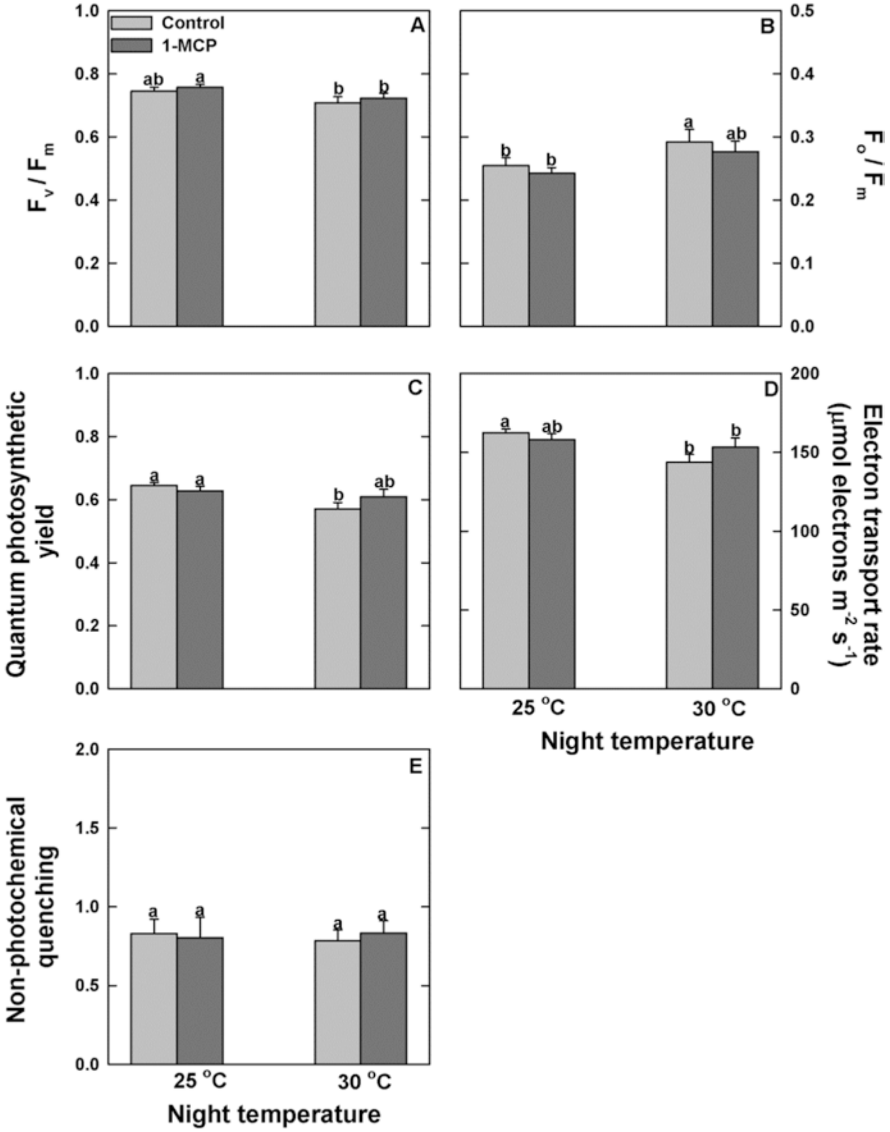

Fig. 13.6 Impact of night temperature and 1-methylcyclopropene (1-MCP) on F_v/F_m (**a**), F_o/F_m (**b**), quantum photosynthetic yield [Y] (**c**), electron transport rate [ETR] (**d**) and non-photochemical quenching [NPQ] (**e**), 5 days after treatment

brane damage usually results in CD. Guo et al. (2006) and Mohammed and Tarpley (2009a) reported increased CD, and Xu and Zhou (2006) reported decreased LNC under heat stress. Yang et al. (2006) stated that ethylene plays an important role in CD. It was observed in this study that application of ethylene perception inhibitor (1-MCP) decreased CD and increased LNC indicating the involvement of ethylene

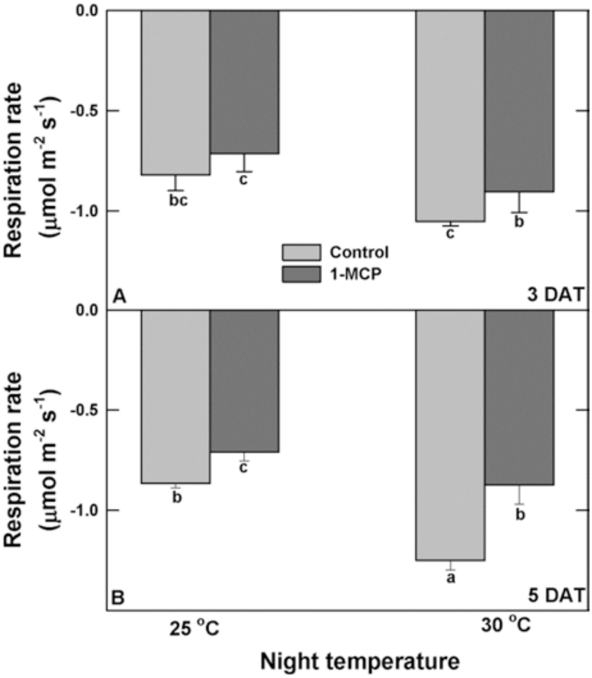

Fig. 13.7 Impact of night temperature and 1-methylcyclopropene (1-MCP) on respiration rate [R_S], 3 (**a**) and 5 (**b**) days after treatment (DAT)

in CD. Previous study has indicated that 1-MCP can prevent CD under heat stress (Djanaguiraman and Prasad 2010; Djanaguiraman et al. 2011). The P_N of the leaf is positively associated with total chlorophyll concentration and LNC (Mae 1997; Llorens et al. 2003). It was observed in this study that HNT decreased leaf chlorophyll concentration and LNC, thereby decreasing P_N. Apart from chlorophyll and LNC, HNT also affected photosystem II as indicated by decreased F_v/F_m, Y and ETR. Poor performance of photosystem II is indicated by decreases in Y and ETR (Genty et al. 1989). The 1-MCP application improved F_v/F_m, Y, and ETR, indicating that 1-MCP application can protect photosystem II, under HNT. Djanaguiraman and Prasad (2010) have reported positive effects of 1-MCP application on photosystem II efficiency under heat-stress conditions.

Björkman et al. (1980) stated that impaired functioning of key enzymes, thylakoid membrane activities, and photosystems under heat stress is due to increased membrane damage (MD). Ethylene production is upregulated under heat stress (Hays et al. 2007; Djanaguiraman and Prasad 2010), which can accelerate MD, increase ROS production and decrease antioxidant enzyme activities (Moeder et al. 2002; Kawakami et al. 2010). Damage to these membranes increases maintenance respiration for repair mechanisms; thus respiration (R_S) increases with temperature and for membrane repair mechanisms (Amthor and McCree 1990). It was observed in this study that HNT increased R_S, which might affect plant carbon status because increase in R_S increases the proportion of assimilates respired (Turnbull et al. 2002). Studies have shown that HNT increased R_S and MD (Cheng

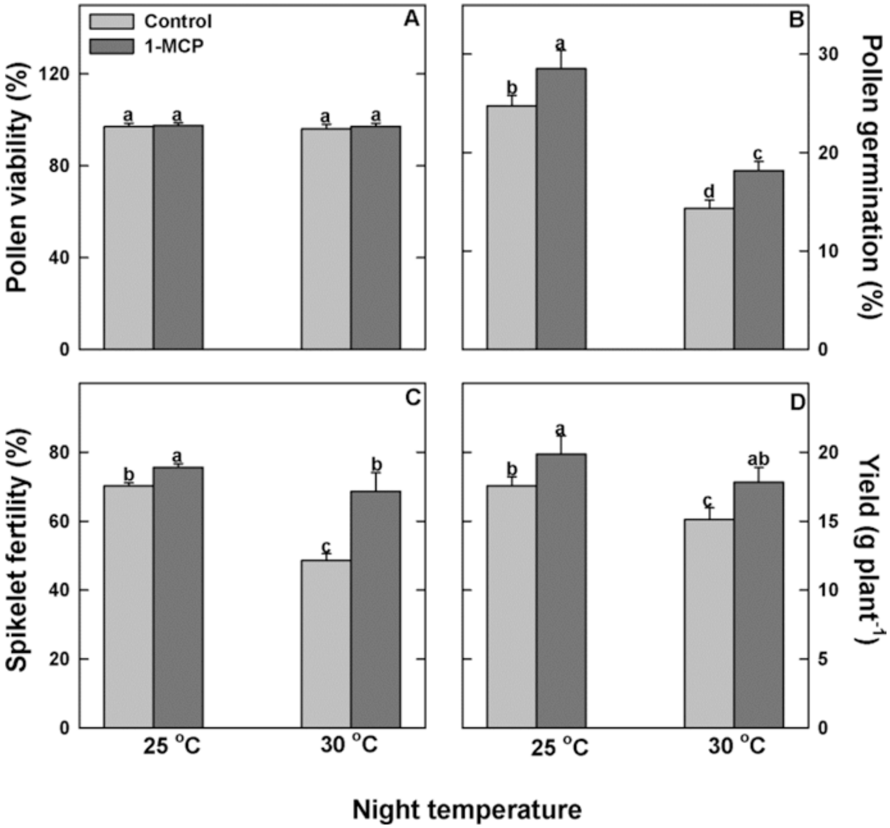

Fig. 13.8 Impact of night temperature and 1-methylcyclopropene (1-MCP) on pollen viability (**a**), pollen germination (**b**), spikelet fertility [SF] (**c**) and yield (**d**)

et al. 2009; Loka and Oosterhuis 2010). In addition, it was observed in this study that $F_o/F_{m,}$ (indicator of thylakoid membrane damage; Ristic et al. 2007) increased under HNT, thus providing more evidence that HNT can damage membranes. It was observed in this study that 1-MCP application decreased R_S, MD, and F_o/F_m. Djanaguiraman and Prasad (2010) reported decreased MD under heat stress as a result of 1-MCP application. 1-MCP decreases R_S and F_o/F_m, thereby suggesting its role in decreasing production of ethylene-triggered ROS, which is the primary cause of MD (Larrigaudiere et al. 2004; Djanaguiraman and Prasad 2010). Reid and Çelikel (2008) stated that the decrease in F_o/F_m indicates that 1-MCP prevents ethylene from binding to the receptor and thus inhibiting the ROS response cascade, hence damaging the membranes.

High night temperature decreased pollen germination, SF, and yield, but had no effect on pollen viability. Hall (1992) and Matsui et al. (2001) have shown that high temperatures can decrease pollen germination. Prasad and Djanaguiraman (2011) reported lower pollen germination as a result of pollen membrane damage due to

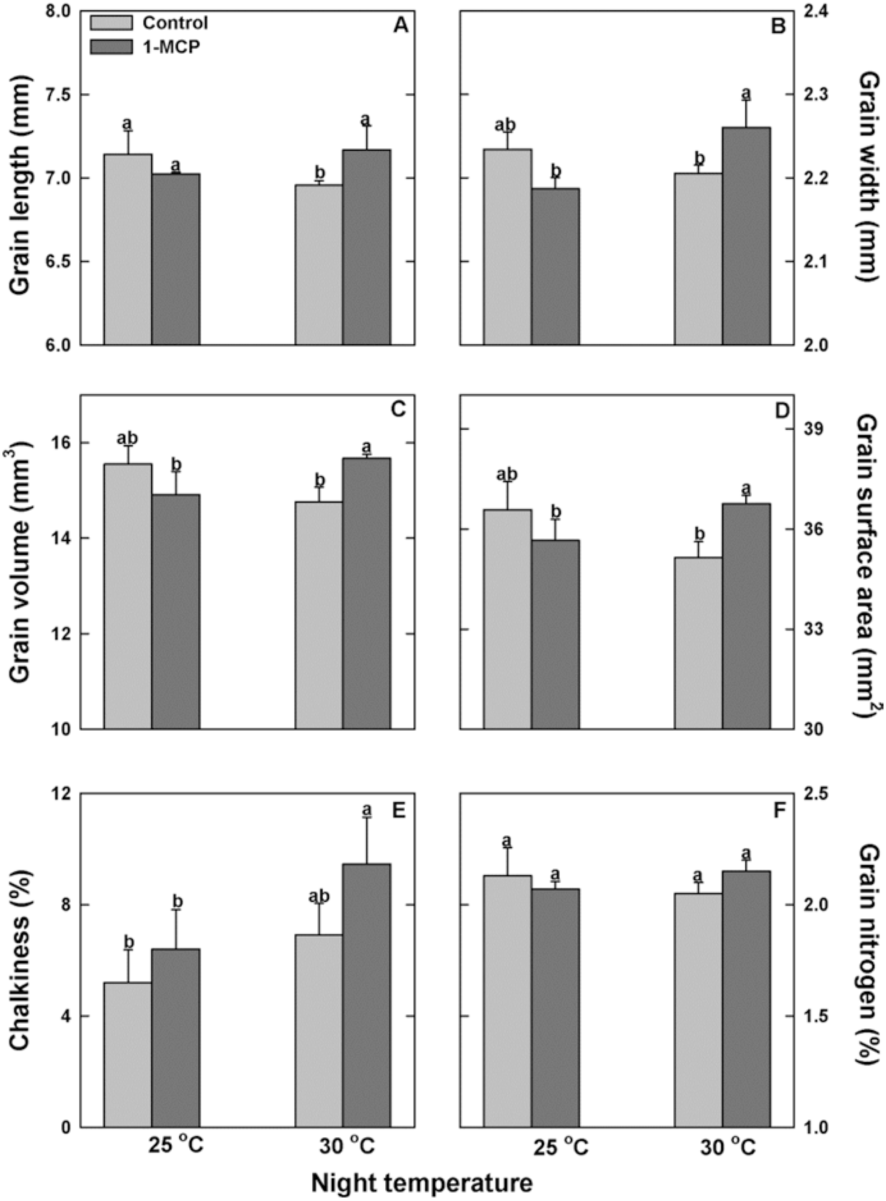

Fig. 13.9 Impact of night temperature and 1-methylcyclopropene (1-MCP) on grain length (**a**), width (**b**), volume (**c**), surface area (**d**), chalkiness (**e**) and nitrogen content (**f**)

higher ROS levels under HNT. Jain et al. (2007, 2010) stated that pollen sterility and poor germination under heat stress are due to lower sucrose utilization, reduced number of carbohydrate transporters, and lower sucrose biosynthesis by the pollen. It was observed in this study that HNT decreased SF due to decrease in P_N and pollen germination and increase in R_S. Afuakwa et al. (1984) and Dinar and Rudich (1985) reported that decrease in SF under heat stress is due to lower transport of photosynthates or inability to mobilize carbohydrates to the grain. It was observed in this study that 1-MCP application increased P_N and pollen germination and decreased R_S, thereby increasing SF, hence yield. Djanaguiraman and Prasad (2010) reported that 1-MCP application under heat stress increases yield, harvest index, and number of filled pods per plant in soybean.

It was observed in this study that HNT decreased grain length and volume and increased grain chalkiness. Several studies have reported decreased grain dimensions and increased chalkiness under HNT (Counce et al. 2005; Ambardekar et al. 2011). The increased chalkiness of the grains and decreased dimensions were due to decreased P_N and increased R_S and MD. Our previous study has shown that decreased production (P_N), increased consumption (R_S), and reduced transfer of carbohydrates to the grain due to MD can reduce grain dimensions (Mohammed and Tarpley 2010). In addition, Commuri and Jones (1999) and Morita et al. (2005) stated that HNT can reduce endosperm cell area and cell number, thereby limiting its capacity to accumulate photosynthates, thus reducing grain dimensions.

In conclusion, HNT increased ethylene-triggered reactive oxygen species-induced CD and MD. As a result of CD and MD due to HNT, there was a decrease in P_N and an increase in R_S. In addition, HNT also decreased pollen germination. High night temperature decreased rice yield as a result of reduced photosynthate production (reduced P_N), increased consumption of photosynthates (high R_S), and decreased SF. Application of ethylene perception inhibitor (1-MCP) reduced CD and MD and increased pollen germination, thereby increasing SF. Application of 1-MCP brought rice yields under HNT up to levels observed under ANT, indicating that ethylene-triggered responses are a major component of rice response to HNT stress. This study provides further evidence of the importance of considering sub-organismal mechanisms when examining plant organismal responses to environmental stresses.

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References

Afuakwa JJ, Crookston RK, Jones RJ (1984) Effect of temperature and sucrose availability on kernel black layer development in maize. Crop Sci 24:285–288

Alward RD, Detling JK, Milchunas DG (1999) Grassland vegetation changes and nocturnal global warming. Science 283:229–231

Ambardekar A, Siebenmorgen T, Counce P, Lanning S, Mauromoustakos A (2011) Impact of field-scale nighttime air temperatures during kernel development on rice milling quality. Field Crop Res 122:179–185

Amthor JS, McCree KJ (1990) Carbon balance of stress plants: a conceptual model for integrating research results. In: Alscher RG, Cumming JR (eds) Stress response in plants: adaptation and acclimation mechanism. Alan R. Liss, New York, pp 1–15

Björkman O, Badger MR, Armond PA (1980) Response and adaptation of photosynthesis to high temperature. In: Turner NC, Kramer PJ (eds) Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York, pp 233–249

Blankenship SM, Dole JM (2003) 1-Methylcyclopropene: a review. Postharvest Biol Technol 28:1–25

Chappelle EW, Kim MS, McMurtrey JE III (1992) Ratio analysis of reflectance spectra (RARS), an algorithm for the remote estimation of the concentration of chlorophyll a, chlorophyll b, and carotenoids in soybean leaves. Remote Sens Environ 39:239–247

Cheng W, Sakai H, Yagi K, Hasegawa T (2009) Interactions of elevated [CO_2] and night temperature on rice growth and yield. Agric For Meteorolo 149:51–58

Cheng W, Sakai H, Yagi K, Hasegawa T (2010) Combined effects of elevated [CO_2] and high night temperature on carbon assimilation, nitrogen absorption, and the allocations of C and N by rice (*Oryza sativa* L.). Agric For Meteorol 150:1174–1181

Commuri PD, Jones RJ (1999) Ultrastructural characterization of maize (*Zea mays* L.) kernels exposed to high temperature during endosperm cell division. Plant Cell Environ 22:375–385

Cooper NTW, Siebenmorgen TJ, Counce PA (2008) Effects of nighttime temperature during kernel development on rice physicochemical properties. Cereal Chem 85:276–282

Counce PA, Bryant RJ, Bergman CJ, Bautista RC, Wang Y-J, Siebenmorgen TJ, Moldenhauer KAK, Meullenet J-FC (2005) Rice milling quality, grain dimensions, and starch branching as affected by high night temperatures. Cereal Chem 82:645–648

Dinar M, Rudich J (1985) Effect of heat stress on assimilate partitioning in tomato. Ann Bot 56:239–249

Djanaguiraman M, Prasad PVV (2010) Ethylene production under high temperature stress causes premature leaf senescence in soybean. Funct Plant Biol 37:1071–1084

Djanaguiraman M, Prasad PVV, Al-Khatib K (2011) Ethylene perception inhibitor 1-MCP decreases oxidative damage of leaves through enhanced antioxidant defense mechanisms in soybean plants grown under high temperature stress. Environ Exp Bot 71:215–223

Food and Agriculture Organization (FAO) (2008) Rice market monitor, April 2008, vol XI, issue no. 1. ftp://ftp.fao.org/docrep/fao/010/ai760e/ai760e00.pdf. Accessed 30 Nov 2018

Genty B, Briantais J-M, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochem Biophys Acta 990:87–92

Grist DH (1986) The origin and history of rice. In: Grist DH (ed) Rice. Longman Publishers, Singapore, pp 1–9

Guo YP, Zhou HF, Zhang LC (2006) Photosynthetic characteristics and productive mechanism against photooxidation during high temperature stress in two citrus species. Sci Hortic 108:260–267

Hall AE (1992) Breeding for heat tolerance. Plant Breed Rev 10:129–168

Havaux M, Tardy F (1996) Temperature-dependent adjustment of the thermal stability of photosystem 2 in vivo: possible involvement of xanthophylls-cycle pigments. Planta 198:324–333

Hays DB, Do JH, Mason RE, Morgan G, Finlayson SA (2007) Heat stress induced ethylene production in developing wheat grains induces kernel abortion and increased maturation in a susceptible cultivar. Plant Sci 172:1113–1123

Ibrahim AMH, Quick JS (2001) Heritability of heat tolerance in winter and spring wheat. Crop Sci 41:1401–1405

IPCC (2014) Climate change 2014: synthesis, report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva

Jain M, Prasad PVV, Boote KJ, Allen LH Jr, Chourey PS (2007) Effects of season-long high temperature growth conditions on sugar-to-starch metabolism in developing microspores of grain sorghum (*Sorghum bicolor* L. Moench). Planta 227:67–79

Jain M, Chourey PS, Boote KJ, Allen LH Jr (2010) Short-term high temperature growth conditions during vegetative-to-reproductive phase transition irreversibly compromise cell wall invertase-mediated sucrose catalysis and microspore meiosis in grain sorghum (*Sorghum bicolor*). J Plant Physiol 167:578–582

Kawakami EM, Oosterhuis DM, Sinder JL (2010) Physiological effects of 1-MCP on well-watered and water-stressed cotton plants. J Plant Growth Regul 29:280–288

Kobata T, Akiyama Y, Kawaoka T (2009) Convenient identification of unfertilized grains in rice. Jpn J Crop Sci 2:4–5

Klughammer C, Schreiber U (2008) Complementary PS II quantum yields calculated from simple fluorescence parameters measured by PAM fluorometry and the Saturation Pulse method. PAM Appl. Notes 1, 27–35

Larrigaudiere C, Vilaplana R, Soria Y, Recasens I (2004) Oxidative behavior of Blanquilla pears treated with 1-methylcyclopropene during cold storage. J Sci Food Agric 84:1871–1877

Lichtenthaler HK (1987) Chlorophylls and carotenoids: pigments of photosynthesis. Methods Enzymol 148:350–352

Lisle AJ, Martin M, Fitzgerald MA (2000) Chalky and translucent rice grains differ in starch composition and structure and cooking properties. Cereal Chem 77:627–632

Llorens L, Peñuelas J, Estiarte M (2003) Ecophysiological responses of two Mediterranean shrubs, *Erica multiflora* and *Globularia alypum*, to experimentally drier and warmer conditions. Physiol Plant 119:231–243

Loka DA, Oosterhuis DM (2010) Effect of high night temperatures on cotton respiration, ATP levels, and carbohydrate content. Environ Exp Bot 68:258–263

Mae T (1997) Physiological nitrogen efficiency in rice, nitrogen utilization, photosynthesis, and yield potential. Plant Soil 196:201–210

Matsui T, Omasa K, Horie T (2001) The difference in sterility due to high temperatures during the flowering period among japonica–rice varieties. Plant Prod Sci 4:90–93

Moeder W, Barry CS, Tauriainen A, Betz C, Tuomainen J, Utriainen M, Grierson D, Sandermann H, Langebartels C, Kangasjärvi J (2002) Ethylene synthesis regulated by bi-phasic induction of ACC synthase and ACC oxidase genes is required for H_2O_2 accumulation and cell death in ozone-exposed tomato. Plant Physiol 130:1918–1926

Mohammed AR, Tarpley L (2009a) High nighttime temperature affects rice productivity through altered pollen germination and spikelet fertility. Agric For Meteorol 149:999–1008

Mohammed AR, Tarpley L (2009b) Impact of high nighttime temperature on respiration, membrane stability, antioxidant capacity and yield of rice plants. Crop Sci 49:313–322

Mohammed AR, Tarpley L (2009c) Instrumentation enabling study of plant physiological response to elevated nighttime temperature. Plant Methods 5:7

Mohammed AR, Tarpley L (2010) Effects of high night temperature and spikelet position on yield-related parameters of rice (*Oryza sativa* L.) plants. Eur J Agron 33:117–123

Mohammed AR, Tarpley L (2011) Morphological and physiological responses of nine southern U.S. rice cultivars differing in their tolerance to enhanced ultraviolet-B radiation. Environ Exp Bot 70:174–184

Morita S, Jun-Ichi Y, Jun-Ichi T (2005) Growth and endosperm cell size under high night temperatures in rice (*Oryza sativa* L.). Ann Bot 95:695–701

Nagato K, Ebata M (1965) Effect of high temperature during ripening period on the development and quality of rice kernels. Nihon Sakumotsu Gakkai 34:59–66 (In Japanese with English summary)

Peng S, Huang J, Sheehy JE, Laza RC, Visperas RM, Zhong X, Centeno GS, Khush GS, Cassman KG (2004) Rice yields decline with higher night temperature from global warming. Proc Natl Acad Sci U S A 101:9971–9975

Pettigrew WT, Heitholt JJ, Vaughn KC (1993) Gas exchange and comparative anatomy among cotton leaf-type isolines. Crop Sci 33:1295–1299

Prasad PVV, Boote KJ, Allen LH Jr, Sheehy JE, Thomas JMG (2006) Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. Field Crop Res 95:398–411

Prasad PVV, Djanaguiraman M (2011) High night temperature decreases leaf photosynthesis and pollen function in grain sorghum. Funct Plant Biol 38:993–1003

Reid MS, Çelikel FG (2008) Use of 1-methylcyclopropene in ornamentals: carnations as a model system for understanding mode of action. Hort Sci 43:95–98

Ristic Z, Bukovnik U, Prasad PVV (2007) Correlation between heat stability of thylakoid membranes and loss of chlorophyll in winter wheat under heat stress. Crop Sci 47:2067–2073

Sisler EC, Serek M (1997) Inhibitors of ethylene responses in plants at the receptor level: recent developments. Physiol Plant 100:577–582

Turnbull MH, Murthy R, Griffin KL (2002) The relative impacts of daytime and night-time warming on photosynthetic capacity in *Populus deltoides*. Plant Cell Environ 25:1729–1737

Virmani SS, Viraktamath BC, Casal CL, Toledo RS, Lopez MT, Manalo JO (1997) Hybrid rice breeding manual, international rice research notes. International Rice Research Institute, Philippines

Xu ZZ, Zhou GS (2006) Combined effects of water stress and high temperature on photosynthesis, nitrogen metabolism and lipid peroxidation of a perennial grass *Leymuschinensis*. Planta 224:1080–1090

Yang J, Zhang J, Wang Z, Liu K, Wang P (2006) Post-anthesis development of inferior and superior spikelets in rice in relation to abscisic acid and ethylene. J Exp Bot 57:149–160

Chapter 14
Ecophysiological Responses of Plants Under Metal/Metalloid Toxicity

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Abstract Heavy metal/metalloid (HM) contamination issues are becoming progressively more widespread worldwide, which are witnessed in various locations like foundries, mining industries, smelters, vehicular emissions, coal burning power plants, and agricultural sectors. Heavy metal/metalloid occurs naturally in the Earth's crust, but man-made sources and various industrial activities have led to severe environmental contamination globally. In the present era, accumulation of HMs in agricultural land is of prime concern as it possesses negative consequences on safety of food and its marketability, productivity, and health of soil organisms. Plants cultivated in HM-contaminated sites reveal reduced photosynthesis, mineral nutrients, biomass production, vegetative growth, altered metabolic activities, and higher accumulation of metal(s). Heavy metal/metalloid toxicity causes a redox imbalance and induces the enhancement in the generation of reactive oxygen species (ROS). However, when ROS reach above threshold level, an imbalance in intracellular content of it incurs, thus resulting in oxidative condition. Plants respond to such intensified concentration of HM in the natural environment by invigorating various defense responses such as sequestration of HM into vacuoles, metal chelation, control over uptake of metals ions through their carriers, and amplification of enzymatic and non-enzymatic antioxidative defense mechanisms. These responses inferred by flora are the outcomes of complex signaling cascades functioning in the plant cells so as to mediate the extracellular stimuli into an intracellular response. This section of the book reveals outlook associated with HM phytotoxicity ranging from metal uptake and its transportation, distribution, homeostasis, toxicity at cellular level, and signaling pathway. Our main intent is to highlight predominantly on the mechanisms of HM-instigated oxidative stress-related responses of plants and to unreveal signal transduction mechanism(s) under HM stress.

Keywords Environmental pollution · Metal/metalloid transporters · Phytotoxicity · Reactive oxygen species · Sequestration

14.1 Introduction

Plants, during their vegetative life cycle, encounter various biotic and abiotic stresses. Abiotic stresses include drought, temperature (both low and high), salinity, lack of essential nutrients, air pollution, heavy metals (HMs), etc. Heavy metals are recognized as most dangerous pollutants as it possess high toxicity to both flora and fauna and due to its considerable buildup into the environments as a consequence of natural and man-made processes (Yadav 2010; Wang et al. 2014). Among 90 naturally occurring elements, 53 of them are designated as HMs, based on their specific density. Thus, metals having density less than 5 g cm^{-3} and those having density exceeding 5 g cm^{-3} are termed as light metals and HMs, respectively (Xalxo and Keshavkant 2018). On the basis of HM solubility, 17 of them are probably available to all living beings under physiological conditions and are vital for living cells/organisms and different ecosystems (Schutzendubel and Polle 2002). Various metals, like cobalt-Co, copper-Cu, iron-Fe, molybdenum-Mo, manganese-Mn, nickel-Ni, and zinc-Zn are essential micronutrients, hence are mandatory for the plant's normal growth and development. These elements which act as essential micronutrients participate in redox response, electron transport, and other vital functions of plants. However, other elements, for instance, arsenic-As, cadmium-Cd, chromium-Cr, lead-Pb, mercury-Hg, etc., are potentially lethal for plants, hence reducing their growth and development (Nazar et al. 2012). The accumulation of various HMs and metalloids in soils and waters leads to severe problem globally, as these HMs and metalloids cannot be wrecked down readily either chemically or biologically into nontoxic forms, therefore persisting in various ecosystems for several years (Xalxo and Keshavkant 2018). Environmental contamination with HMs has exceeded beyond the acceptable limit these days and is injurious to all living organisms (Tak et al. 2013). As declared by the Comprehensive Environmental Response Compensation and Liability Act (CERCLA), USA, the highest permissible concentrations of some of the HMs in water are 0.002, 0.015, 0.01, 0.01, 0.05, and 0.05 mg L^{-1} for Hg, Pb, Ar, Cr, Cd, and Ag respectively (Chaturvedi et al. 2015). The soil standards, as customized by the Indian standards for HMs, are Cd = 3–6, Cu = 135–270, Ni = 75–150, Pb = 250–500, and Zn = 300–600 mg kg^{-1} (Nagajyoti et al. 2010). It is acknowledged that metals at a low concentration might have advantageous consequences that are referred as hormesis (Zengin and Munzuroglu 2006). However, all HMs have the capability to display detrimental consequences at higher level and are proficient to enter into the food web (Chandrakar et al. 2017). The toxic effect of each metal depends on various factors such as its availability to flora and fauna, type of metal, its oxidation state, pH, concentration of metal, the path and the time of exposure, and so on (Mani and Kumar 2014). United States Environmental Protection Agency (UEPA) has listed all these HMs as chief contaminants. The ramifications due to HMs in soil are very complex, and consequences caused by these rely upon various chemical processes. Among various processes, adsorption-desorption and complexation-dissociation reactions normally influence metal activity in soil, while oxidation-reduction process alters the valencies of metal (Swartjes et al. 2007). Excessive concentrations of HMs in plants cause alterations at physiological, biochemical, and molecular levels (Chandrakar et al. 2017; Xalxo and Keshavkant 2018). Heavy metal-induced alterations include decline in the rate of photosynthesis, transpiration, respiration, nitrogen metabolism, and mineral nutrition along with alterations in redox status, concentration of signal molecules, enzymatic and non-enzymatic antioxidants activity, membrane permeability, phytochelatin (PC) content, protein, phenolics content, etc., consequently leading to plant death (Tripathi et al. 2007; Hayat et al. 2012; Qadir et al. 2014; Kumar et al. 2015; Chandrakar et al. 2017; Xalxo et al. 2017). Phytotoxic consequences of HMs on various plant species were revealed in depth by various researchers (Malecka et al. 2001, 2008, 2009; Rucinska and Gwozdz 2005; Krzelowska et al. 2010; Pawlak-Sprada et al. 2011; Chandrakar et al. 2016; Rucinska-Sobkowiak 2016; Drzewiecka et al. 2018; Xalxo and

Keshavkant 2019). This chapter reviews general aspects of HM/metalloid toxicity ranging from metal uptake from soil, their transportation from ground to above aerial parts, and homeostasis to cellular stress responses. The prime objective of this section is to highlight principally on the mechanisms of HM-instigated oxidative injury-associated responses and to show the working of various signal transduction pathways under HM/metalloid toxicity. This particular subject area needs intense exploration to provide vital information to understand cellular responses against HM toxicity.

14.2 Sources of Heavy Metal Pollution in the Environments

There are various sources of HM release in the environments such as natural and anthropogenic routes. Naturally occurring HMs are available in insoluble forms like precipitated or complex forms that are not easily accessible by plants for uptake. Natural processes that cause overaccumulation of HMs in the environments include comets, erosion, volcanic eruptions, and mineral weathering. Various agricultural and horticultural sources include livestock manures, sewage sludge, inorganic fertilizers, and agricultural chemicals like fungicides, pesticides, etc. Inorganic fertilizers, fungicides, and phosphate fertilizers contain variable concentrations of HMs, like Pb, As, Cd, Cr, Ni, Zn, etc., depending on their sources. Heavy metals that are originated from man-made sources are soluble and are present in mobile reactive forms and are readily available to plants. Various anthropogenic sources comprise of battery manufacture, alloy manufacture, atmospheric deposition, manufacturing of explosive, inappropriate piling of solid wastes from industries, tanning of leather preservatives in dyes and woods, etc. (Dixit et al. 2015). The geochemical cycle of HM leads to overaccumulation of it in the environment, which may perhaps cause lethal effects to both flora and fauna, when present above permitted levels (D'amore et al. 2005). The pathways through which HMs generally enter into the natural ecosystems include crumbling of parent materials, amendments in the geochemical cycle by anthropogenic activities, shifting of excavation to different localities, and release of elevated amount of metal waste by manufacturing companies. Mining and processing of ores are chief sources of HM contamination in the ecosystems, and the revival of ecosystems from HM contamination caused by various activities may possibly take several decades.

14.3 Heavy Metal/Metalloid Transporters

In plants, the transportation of HM ions from ground to upper aerial parts is regulated by specific transporters and metal pumps; also these transporters and metal pumps maintain the metal homeostasis within the cells (Pilon et al. 2009). These transporters are the members of diverse metal transporter families and are usually made up of membrane proteins that transfer metal ions to epidermal cells from the mesophyll or transfer metal ions from the roots to aboveground parts. At subcellular level, these transporter proteins regulate the uptake and transfer of metal ions across the plasma membranes, across vacuoles through tonoplasts, and other various endomembrane organelles (Maestri et al. 2010). Overexpression of these transporter proteins increases tolerance against HM and does not show injurious effect on homeostasis at physiological condition (Curie et al. 2000; Verret et al. 2004). Few important HM transporters include HM ATPases (HMAs): CPx-type ATPases, ABC (ATP-binding casette) transporters, NRAMP (natural resistance associated macrophage proteins), CDF (cation diffusion facilitator family), and ZIP (ZRT-IRT-like protein) family. The process through which these HM transporters operate comprises of a sequence of signaling events, for instance, chain reaction that includes addition of phosphate group, hormones, mitogen-activated protein kinases (MAPK), and calcium-calmodulin systems. These signaling events finally lead to balancing of mineral nutrients within the plant cell that is vital for plant survival under unfavorable circumstances.

14.3.1 Heavy Metal ATPases (HMAs): CPx-Type ATPases

The function of HM transporters protein is to transport the metal ions across various cellular compartments, cytoplasm, and vascular tissues especially xylem. This particular HM transporter belongs to a varied class of superfamily that is found in all three kingdoms. The function of CPx-type ATPases is to propel an array of cations across the membranes. CPx-type ATPases include various ATPases, like H^+-ATPases, Na^+/K^+-ATPases, and Ca^{2+}-ATPases of fungi and plants, animals, and several other organisms, respectively (Axelsen and Palmgren 2001). Heavy metal/metalloid ATPases are made up of eight transmembrane domains, where the large-sized cytoplasmic loop is sandwiched amid transmembrane 6 and 7 (Mills et al. 2003). The P-type ATPase transporters have been divided into five chief families, i.e., type I, type II, type III, type IV, and type V. Based on their transport specificity, these major families (type I–V) are again categorized into two or more subfamilies (Axelsen and Palmgren 2001). Among various subfamilies, P_{1B} subfamily is assigned for transportation of HMs in plants. Solioz and Vulpe (1996) revealed that P_{1B} possess conserved intramembranous cysteine-prolinecysteine/histidine/serine sequences and hence are reported as the CPx-ATPases. Overexpression of AtHMA4 gene has been shown to ameliorate growth and development of roots in *Arabidopsis thaliana* even in the presence of various noxious levels of Zn, Cd, and Co (Verret et al. 2004). Mills et al. (2005) revealed that AtHMA4 deficit mutant plant leads to augmented sensitivity toward Zn and Cd toxicity, which confirmed the earlier findings. Later, Hanikenne et al. (2008) found that the AhHMA4 (homologue of AtHMA4) from the hyperaccumulating species *Arabidopsis halleri* bestowed tolerance against HMs like Zn and Cd. AhHMA4 is also engaged in translocation of Zn from root-to-shoot, its hyperaccumulation, and maintains Zn-Fe homeostasis.

Parameswaran et al. (2007) performed proteomic analysis of microsomal fractions and found another homologue of AtHMA4, generally expressed in epidermal leaf cells of *Noccaea caerulescens* (Schneider et al. 2013). In an experiment using transgenic approach, OsHMA3 gene, localized in tonoplast that principally encodes a P_{1B}-ATPase transporter, was identified in hyperaccumulating *Oryza sativa* L. that manages transport of Cd from ground part to above shoot portion (Miyadate et al. 2011). Upon Zn and Cd exposure, overexpression of HMA4 and HMA3 gene showed tolerance in *Arabidopsis thaliana* against these stresses. Moreover, overexpression of HMA5 was seen in roots and other plant parts of *Arabidopsis thaliana* upon exposure of Cu (Xu et al. 2010).

14.3.2 ATP-Binding Cassette Transporters (ABC Transporters)

The ABC transporters are exceptionally massive and varied family of membranous proteins present in organisms of all the three monarchy. ATP-binding cassette transporters are engaged in a wide array of transport functions (Theodoulou 2000; Martinoia et al. 2002). These are distinguished by the presence of couple of fundamental structural organizations in two copies, i.e., (1) an extremely hydrophobic transmembrane domain, each one of them consisting four or six transmembrane spans, and (2) a marginal (cytosolic) ATP-binding domain or nucleoside binding fold (Theodoulou 2000). Majority of these proteins serve to propel HM across the membrane and transfer a broad variety of substrates comprising of sugars, ions, lipids, pigments, peptides, antibiotics, and xenobiotics and are also engaged in vacuolar deposition of non-essential HMs within the cells. Till date, couple of subclasses of ABC transporters has been recognized in plants; these are (1) multidrug resistance-associated proteins (MRPs) and (2) the multidrug resistance proteins (MDRs). Bovet et al. (2003) revealed that gene expression of four MRPs was upregulated in roots of *Arabidopsis thaliana* upon application of Cd; however expression of AtMRP3 gene was comparatively more prominent. Furthermore, AtMRP3 was also stimulated upon Cu exposure, but under Zn toxicity, there was slight induction of AtMRP3. During transcriptome-based screening, Bovet et al. (2005) observed that ABC trasporters, like AtPDR8, AtABCG36, and PEN3, localized in plasma membranes, were highly upregulated under Cd toxicity in *Arabidopsis thaliana*. Further studies showed that similar ABC transporters were also upregulated upon Pb toxicity. The *Arabidopsis* plants overexpressing PDR8 were more resistant to Cd and Pb toxicity, while RNAi and T-DNA mutant plants were sensitive to these (Kim et al. 2007). A novel ABC transporter IDI7, which is regulated by Fe, has been recognized in the tonoplast of *Hordeum vulgare* L. roots (Yamaguchi et al. 2002). This IDI7 has characteristics similar to ABC transporter and is stimulated under Fe deficit conditions.

14.3.3 Natural Resistance-Associated Macrophage Proteins (Nramps)

The Nramps are annotated as an extremely conserved family of membrane proteins. These proteins are engaged in metal ion transport in living organisms including flora and fauna. In plants, this group of protein family was initially recognized in *Oryza sativa* L. where three Nramps, i.e., OsNramp-1, OsNramp-2, and OsNramp-3, were revealed (Belouchi et al. 1995, 1997). Alike, various genes are discovered in a variety of plants such as *Arabidopsis thaliana* in which six Nramps were distinguished (Maeser et al. 2001). The plant Nramps seems to group into two subfamilies, which include first group AtNramps 1 and 6 and second group Nramps 2 to 5 (Maeser et al. 2001). In plants, Nramps are conserved and possess 12 transmembrane domains having transport motif' sandwiched between transmembrane-8 and transmembrane-9 (Curie et al. 2000). In *Arabidopsis thaliana* roots, gene expression of AtNramps1, 3, and 4 was overexpressed under Fe deficit conditions (Thomine et al. 2000), whereas AtNramp3 was associated with uptake of Fe and Cd (Thomine et al. 2000). AtNramp3 gene was upregulated under Fe deficiency and was expressed in the xylem and phloem, localized into the vacuolar membranes, and functions in mobilizing metal pools from the vacuoles (Thomine et al. 2003). In *Solanum lycopersicum*, LeNramp1 was exclusively expressed under Fe deficit condition in roots, situated in the vascular parenchyma (Bereczky et al. 2003). Interestingly, it was noted that Nramp transcript level in *Hordeum vulgare* L. was downregulated under Cd toxicity and sufficient supply of nitrogen (N), though Nramp transcript level was notably upregulated by Cd but under N deficiency (Finkemeier et al. 2003). Consequently, above findings demonstrate that Nramp carry out various physiological functions, and few of the Nramps are concerned with Fe and Cd uptake and homeostasis.

14.3.4 Cation Diffusion Facilitator (CDF) Family

Cation diffusion facilitator transporter gene was originally differentiated in *Arabidopsis* and was named as ZAT. Upregulation of this gene in genetically modified plants results in resistance against Zn stress (van der Zaal et al. 1999). It was anticipated that ZAT gene is engaged in the vesicular/vacuolar sequestration of Zn and therefore is concerned with Zn homeostasis and tolerance. A ZAT gene, ZTP1, has been recognized in *Thlaspi caerulescens* and was seen to be upregulated principally in the leaf tissue, followed by root tissue (Assunceaao et al. 2001). Degree of expression was higher in plants grown on calamine (which are enriched in Zn, Cd, and Pb) soil as compared with non-metalliferous soil. Majority of plants expressing these genes were found to be the Zn-tolerant, signifying the role of ZTP1/ZAT-like transporters in intracellular sequestration and tolerance against Zn stress (van der Zaal et al. 1999; Assunceaao et al. 2001). Persans et al. (2001) have distinguished CDF transporter (TgMTP1) which is accountable for metal ion accumulation within the shoot vacuoles in *Thlaspi goesingense*. Another CDF transporter, ShMTP1, has also been recognized in the *Stylosanthes hamata* (tropical legume) that can be grown in acid or high Mn^{2+} containing soils (Delhaize et al. 2003). The ShMTP1 provide tolerance against Mn^{2+} toxicity by sequestrating metal ions and functions antiporter of proton/Mn^{2+} in yeast and *Arabidopsis thaliana* (Delhaize et al. 2003). An experiment conducted in *Arabidopsis thaliana* revealed the presence of eight genes showing homology with the members of CDF family (Maeser et al. 2001).

14.3.5 The ZIP Family

The ZIP proteins are basically affianced in the uptake of Fe and Zn and their accumulations (Guerinot 2000). Nevertheless, they may possibly be engaged in response against Cd toxicity (Xu et al. 2012) and Ni tolerance (Nishida et al. 2011). Approximately, 85 ZIP family members are recognized from various prokaryotes and eukaryotes organisms, out of which 15 of them belongs to *Arabidopsis* (Maeser et al. 2001). This protein contains eight transmembrane domains, where the extracellular region contains the amino- and carboxyl-terminal ends (Guerinot 2000). Regarding single member of this family, *Arabidopsis* consists of three iron-regulated transporter (IRT) genes that regulate the upward movement of metal ions in plants from soil. The upregulation of several of IRT genes like IRT1, IRT2, and IRT3 was stimulated by increased concentration of Zn, revealing their functions in regulating Zn-Fe homeostasis in *Arabidopsis thaliana*. It is interesting to note that upregultaion of IRT genes does not explicitly lead to HM tolerance. For instance, IRT1 overexpression in *Arabidopsis thaliana* led to over accumulation of Fe, Mn, Co, and Zn that caused negative effects to plant (Barberon et al. 2011). Interestingly, IRT3 overexpression in *Arabidopsis thaliana* has diverse consequences on accumulation of Fe and Zn; Zn accrual increases in the shoot, whereas Fe accretion increases in the roots of transgenic lines (Lin et al. 2009).

14.4 Potential Threats of Heavy Metals/Metalloids

14.4.1 Morphological Amendments

Presence of HM in agricultural soil and groundwater higher than the permissible level causes perturbations in the metabolism of plant cells resulting in various morphological modifications like wilting, curling, leaf necrosis, reductions in leaf number and area thus diminished photosynthesis rate and biomass accumulation, dissipation of mineral contents, reduced elongation rate, stunt growth, and reduced yield (Chandrakar et al. 2017; Xalxo and Keshavkant 2018). Mostofa and Fujita (2013) demonstrated that exposure of *Oryza sativa* L. seedlings to Cu caused severe oxidative stress which appeared in terms of chlorosis (loss of normal green coloration of leaves), necrosis (death of cell or tissues), and leaf rolling. Upon individual and combined application of Cu and/or Cd, there was a noteworthy decline in diameter of root, its breadth, and width of leaf midrib in *Sorghum bicolor* (Kasim 2006). Plants when exposed to lethal dose of Cd showed visible symptoms of injury like chlorosis, reductions in growth and development, and root tip browning which ultimately led to cell death (Guo et al. 2008). Other symptoms of Cd toxicity include noteworthy decrease in the length and diameter of the internodes, leaf area, and thickness. Heavy metals have greater affinity for sulfhydryl groups of enzymes, and binding of HM ions with these groups causes distortion of membranes; therefore loss of turgor and rigidity are accountable for plant wilting under HM stress conditions. The presence of HMs in the soil restricts the water uptake and essential minerals, thus creating dehydration inside the cells, ultimately leading to leaf curling (Panda et al. 2009). Insufficiency of vital nutrients in plants also causes additional symptoms of HM toxicity, i.e., necrosis, which predominately affects the green leaves under which leaves turn brown or black in color. Farnese et al. (2017) reported that accumulation of As results in necrosis of outer margins of leaf, indicator of cell demise in particular area, which finally leads to death of the leaf. After performing root bioassay of *Brassica napus* L. seedlings, which was exposed to As, Farooq et al. (2017) affirmed that decrease in root length resulted in lethal effect of the stresses on cell elongation. Pandey and Sharma (2002) and Rahman et al. (2005) also reported necrosis and chlorosis in *Brassica oleracea* L. and *Hordeum vulgare* L., respectively, under Ni toxicity. Steiner et al. (2012) while working on *Jatropha curcas* plants found visible symptoms of Al toxicity like presence of minute necrotic spots and chlorosis on the margins of juvenile leaves and in the margins and center of adult leaves, respectively. Recently, study conducted by Ardisana et al. (2018) revealed chlorosis and necrosis in *Solanum lycopersicum* under Pb stress, indicating altered mineral nutrient absorption and rate of photosynthesis.

14.4.2 Physiological Effects

14.4.2.1 Growth and Productivity

Root Plasmolysis

Heavy metals being a non-essential constituent and extremely fatal to flora significantly affect growth and crop production. From the soil, HMs are taken up and then transported by various transporters localized in the plasma membranes of roots (Ovecka and Takac 2014). When plants are exposed to HM toxicity, usually, roots are the foremost organ that encounters HMs, where metal ions result in discoloration and plasmolysis after entering into the cells (Shaibur and Kawai 2011). As plasmolysis is an active process and well-known characteristic feature of viable cells, it is used as a marker to observe the cell viability under various environmental stresses (Lang et al. 2014). Plants when exposed to HM toxicity show augmented lignifications in root cells and microtubule dissolution, which later results into rapid amplification in cell width, thus increasing diameter of root (Lou et al. 2015). Aluminium toxicity inhibits extension of the main axis and lateral root because of constrained cell division, and as a result root system appeared under developed and fragile, and apices were inflamed and injured (Panda et al. 2009).

Biomass

Plants when exposed to HM toxicity have popularly been reported to cause a noteworthy diminution in the biomass. This possibly may be because of the fact that root tissues are the foremost organ that comes in contact with HMs inside the soil (Chandrakar et al. 2018). As HMs have high affinity for sulfhydryl groups of numerous proteins and enzymes that are located in the radicular membranes, it causes interruption in root functions and cellular death (Shaibur and Kawai 2011). The reductions in rate of germination, root elongation, and biomass accumulation are consequences of HM contamination (Schutzendubel et al. 2001). Various researchers revealed that the prime influences of HM toxicity are the inhibition in rate of germination, biomass accumulation, root extension, and normal growth (Munzuroglu and Geckil 2002; Suzuki 2005; Chandrakar et al. 2016; Xalxo and Keshavkant 2019). In plants, reduction in germination rate and growth responses may result because of negative consequences of HMs on cellular functioning where maximum accessible energy is used for the production of stress linked vital compounds like phytochelatins (PCs), antioxidants, etc. Distinguished scientists have reported rigorous decrease in biomass production, which eventually cause decrease in crop productivity under HM toxicity (Ahmad et al. 2011; Asgher et al. 2014; Chandrakar et al. 2017; Xalxo and Keshavkant 2018). Most probable reason shown for reduction in biomass accumulation was increased permeability of cell membrane, thereby unavoidably increasing leakage of cellular constituents/fundamental nutrients which were primary components for the generation of energy and plant development (Farooq et al. 2015). Additionally, under HM stress, the water loss is increased, while water uptake is reduced by the roots which also results in diminished biomass accumulation (Gomes et al. 2013; Sidhu et al. 2018). Hence, it is obvious that when plants are exposed to HMs beyond their permissible limits, they negatively affect plant growth and development (Chandrakar et al. 2016; Xalxo and Keshavkant 2018).

Cell Division, Elongation, and Expansion

Plants when exposed to HM lead to inhibited cell division in the root meristematic zone, thus resulting in diminished growth. Reduction in mitotic activity thus decreased the rate of cellular division in the root apical meristem consequently leading to inhibited expansion and elongation of the novel cells (Suzuki 2005; Farooq et al. 2015). Heavy metal toxicity also reduces root cellular turgor leading to inhibition in cell enlargement. Exposure to HMs adversely influences the cell division machinery that is responsible for the cell cycle regulation in plants. Heavy metals also suppress the formation of proteins like cyclins and Cdk that are involved in cell cycle check points (Sharma et al. 2012). Inhibition of the enzyme activity involved in DNA repair system may be the outcome of binding of HMs to thiol groups which are accountable for DNA damage (Patra et al. 2004). Chromosomal aberrations with lower mitotic index, altered cell divisions (mitotic and meiotic), disruption of nuclear and plasma membranes, distortion in thylakoid structure, augmentation in amount of nucleoli, starch granules and plastoglobuli, severe plasmolysis, deficiency/absence of chromatin materials, and amplification in vacuoles count and size are few of the ultra-morphological alterations revealed in various plant parts under various HM toxicities (Patra et al. 2004; Aravind and Prasad 2005).

14.4.2.2 Photosynthetic System

Chlorophyll Synthesis

Among various vital biological processes, photosynthesis is one of the most studied phenomena during different biotic and abiotic stresses. Different plant species vary in patterns of metal accretion which affects biosyntheses of pigments, necessary for photosynthesis (Shakya et al. 2008; Vesely et al. 2011; Xalxo and Keshavkant 2018). Heavy metal may possibly associate with the photosynthetic machineries and may lead to a broad array of detrimental consequences together with photooxidative damage. One of the major negative effects of HM stress is inhibition of photosynthesis because HM invariably affects the function of photosynthetic system by hampering the machinery of both light and dark reactions. It is revealed that plant exposed to HM slows down the photosynthetic rate, transpiration rate, stomatal conductivity, plant growth and development, and ultimately loss in yield (Shakya et al. 2008). Babu et al. (2010) reported that the negative consequences of metal ions on growth, activities of leaf enzymes, and photosynthesis along with activities of both photosystem, i.e., PS-I and PS-II, were found to be dose dependent and were further amplified with an increase in exposure time. Heavy metal ions also influence the electron transport system and modify the energy transfer at multiple sites. Isolated chloroplasts were examined to reveal any alteration on the electron transport system due to HM ions, and it was found that PS-II was more vulnerable to HM toxicity as compared to PS-I. The activity of PS-I can be diminished on higher concentration of HM exposure (Ivanov et al. 2006). Reduction in the concentration of various enzymes like ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity and/or its biosynthetic enzymes δ-aminolevulinic acid dehydratase and protochlorophyllide reductase may be the reason for reduction in the chlorophyll content (Farooq et al. 2016). Gene expression analysis of δ-aminolevulinic acid dehydratase showed that transcript level of this gene was downregulated under various abiotic stresses (Agnihotri and Seth 2016). Heavy metals affect chlorophylls and also carotenoids in plants because phytotoxic outcome of HM appears to be linked with excess generation of ROS which stimulate the production of carotenoids (Ghnaya et al. 2009; Kumar et al. 2012). Carotenoids, a low molecular weight compound owing to their antioxidant property, function by quenching higher concentration of ROS (Gill and Tuteja 2010). Among various established mechanisms in plants, to avoid photooxidative damage, one of the fundamental photoprotective mechanisms is the liberation of excessive excitation energy (Janik et al. 2008). Various accessory pigments like zeaxanthin (Zx), antheraxanthin (Ax), and the de-epoxidized components of xanthophyll cycle are engaged in the avoidance mechanism for dissipation of energy in PS-II (Toth et al. 2007). The *Pinus sylvestris* grown in areas contaminated with heavy metals such as Al, Pb, and Cu revealed reduction in the xantophyll content (Matysiak 2001). Janik et al. (2008) reported that reduction in the second step of violaxanthin de-epoxidation leads to accumulation and augmentation in the *cis*-isomers fraction of violaxanthin in leaves of *Secale cereal* upon Cd exposure (Janik et al. 2008). On the other hand, when *Lemna minor* plants were exposed to Cd stress, amplification in the level of all the pigments of xanthophyll cycle was observed as an antioxidative response (Appenroth et al. 1996). It is well acknowledged that xanthophylls play important role in quenching of ROS-induced reactions. Xanthophylls also avoid excess production of free radicals, thus limiting the oxidative damage caused by excess ROS. Both adaptation and survival of plants under HM toxicity depend on their competence to resist the oxidative injury via antioxidant systems.

Chloroplast Membrane

Inside the cell, apart from mitochondria, peroxisomes, and other organelles, chloroplasts are one of the chief sites for the formation of free radicals and are pretty susceptible to HM-induced injury. Predominantly, this free radical modifies the function of chloroplast membrane and elements of the photosynthetic electron transport chain, thereby damaging the light reaction of photosynthesis (Ventrella et al. 2011). Li et al. (2006) and Schneider et al. (2013) revealed that *Pteris vittata* and *Leucaena leucocephala* when exposed to As toxicity resulted in structural injury to the chloroplast internal membranes. Toxic level of Cr has also shown to damage chloroplast ultrastructure, thus disturbing the photosynthetic process (Peralta et al. 2001). Plants, when exposed to Cd stress, lead to amendment in membrane function by inducing lipid peroxidation reaction and disturbances in chloroplast metabolism by reducing chlorophyll biosynthesis and decreasing the activities of enzymes involved in CO_2 fixation (Fodor et al. 1995). Degradation of chloroplasts and alteration in their internal membranes due to HMs has shown detrimental consequences on pace of photosynthesis which is responsible for decreased level of photosynthetic pigment and rate of carbon assimilation (Farnese et al. 2017). Plants when exposed to HM stress also lead to structural disorganization of chloroplast membranes and perturbations in functioning of integral photosynthetic activity, consequently leading to alterations (breakage and swelling) of thylakoid membranes and reduced synthesis of photosynthetic pigment. Reduction in pigment biosynthesis may possibly be due to the absence of appropriate regulatory mechanism for its synthesis at lethal concentrations of HMs (Sharma et al. 2012; Chandrakar et al. 2016). Heavy metal-induced over produced ROS-mediated lipid peroxidation reaction may also be accountable for destruction of chloroplast membranes (Mascher et al. 2002; Chandrakar et al. 2017; Xalxo and Keshavkant 2018).

CO_2 Fixation

The net fixation of CO_2 is a fundamental process that dictates the total amount of carbon that recycles into the biosphere. Plants on exposure to HM stress show reduction in the rate of CO_2 fixation, thus reducing photosynthetic rate (Demirevska-Kepova et al. 2004; Gusman et al. 2013). Heavy metal-induced overproduction of free radical results in distortion of chloroplasts membranes, thus interfering with CO_2 assimilation and photosynthetic activity (Stoeva and Bineva 2003; Demirevska-Kepova et al. 2004; Gusman et al. 2013). Demirevska-Kepova et al. (2004) observed reduction in biomass accumulation and inhibition in enzyme activity, thus affecting CO_2 fixation. Stoeva et al. (2005) revealed that subjection of As-stress to *Zea mays* L. decreased the rate of CO_2 fixation with a noteworthy diminution in the functioning of PS-II. Application of As also leads to significant decrease in the chlorophyll fluorescence ratio, rate of CO_2 fixation, PS-II functioning, and consequently diminished photosynthetic efficiency (Stoeva and Bineva 2003; Chandrakar et al. 2016). Plant growth reduction due to HM contamination may possibly be attributed due to inhibition of enzymes of Calvin cycle, thus diminished rate of CO_2 fixation, and also by restrictive transport of carbohydrates from source to sink regions. Because of reduced pace of CO_2 fixation, recovering of $NADP^+$ get stopped (final electron acceptor), leading to decreased photosynthetic electron transport. This overall process leads to decrease in the rate of electron transport and excess generation of excitation energy. As a result, the excess excitation energy thus produced, stimulate the alternative pathways of electron transport like, water-water cycle and photorespiration, leading to excess leakage of electrons out of electron transport chain (Gusman et al. 2013).

Stomatal Conductance

Heavy metals are well known to destroy the structures of plasma membranes. Any damage to the outer membranes results in disparity in the uptake and transportation of essential nutrients and ions in the plant cells which ultimately lead to reduction in the stomatal conductance (Paivoke and Simola 2001). Inhibition of key enzymes like δ-aminolevulinic acid dehydratase and increased activity of chlorophyllase (pigment degrading enzyme) leads to the increase/decrease in the concentration of pigment and stomatal conductance under HM stress (Sharma and Dubey 2005; Xalxo and Keshavkant 2019). Subjection of plants to HMs/metalloids leads to deposition of these in the cuticles which envelop the guard cells and its auxiliary cells that result in decreased stomatal opening (Rucinska-Sobkowiak 2016). Lead toxicity has been shown to decrease the stomatal aperture, which later leads to closing of stomata that result in slower diffusion of water vapors due to the greater diffusion gradient of it (Bondada and Oosterhuis 2000). Presence of Pb limits the compounds that are responsible for maintenance of cell wall plasticity and turgor pressure thus resulting in lowering of cellular water potential and thereby inducing stomatal closure. Closed stomata may also be an outcome of inhibited energy system or altered K^+ fluxes through membranes or Pb-induced ABA accumulation or all of these (Sharma and Dubey 2005). Furthermore, As interrupts with microtubules assembly during cell division and thus normal cell cycle regulation get hampered. Eventually, the regular pattern of cell division ceases, and there is a formation of abnormal stomata, thus leading to reduction in growth of plant (Gupta and Bhatnagar 2015). Heavy metal-induced detrimental effects include decrease in rates of photosynthesis, transpiration, and stomatal conductance which hampers the water and ion uptake (Milivojevic et al. 2006). Anjum et al. (2016) observed closing of stomata due to the Cd or As contamination which leads to deprivation of CO_2; thus it arrests photosynthetic carbon assimilation and also reduces rate of transpiration. In *Arachis hypogaea*, Shi and Cai (2008) revealed reduction in net photosynthetic rate in association with decreased stomatal conductance and photosynthetic pigment under Cd stress. Studies have reported that Ni stress inhibits rate of photosynthesis due to the decreased stomatal conductance (Seregin and Kozhevnikova 2006; Ahmed and Hader 2010). Heavy metal-induced decline in photosynthesis rate suggests that restriction in the stomatal conductance leads to decreased internal CO_2 level and as a result decrease in rate of photosynthesis (Gusman et al. 2013).

14.4.2.3 Nutrient and Water Uptake

Micro- and Macronutrients

Mineral nutrients are the major components of the plant structural component, thereby providing mechanical support to plants. These micronutrients also play a vital role in plant growth and development. However, HM toxicity may interfere with uptake and transport of essential nutrients, thus disturbing the mineral composition. Both micro- and macronutrients aid in biosyntheses of macromolecules, like proteins, carbohydrates and nucleic acids, growth substances, and chlorophylls, and most importantly help in stress tolerance (Paivoke and Simola 2001). Reactive oxygen species is accountable for oxidative damages to various biomolecules like proteins, lipids, and nucleic acids, which in turn are responsible for different physiological amendments such as diminished growth, nutrient deficiency, decreased nutrient transport, genotoxicity, and retarded photosynthesis (Nagajyoti et al. 2010). Roots are the first tissues that interact with HMs and accumulate them inside the cells and disturb the nutrient uptake (Stoeva et al. 2005). Selectivity and permeability of root cell membranes also get modified due to HM contamination, thereby resuling in reduced uptake of nutrients (Gusman et al. 2013). Adequate concentration of nutrients helps plants in accumulation of biomass. Excess accrual of HM competes with nutrient ions for their binding with transport protein and thus interferes with the uptake of nutrients (Gusman et al. 2013). Significant reduction in uptake of nutrients and transfer of ions from ground to aboveground parts were revealed in As stressed *Triticum aestivum* L., and reduced nutrient uptake was associated with decreased photosynthetic rate (Liu et al. 2008; Gusman et al. 2013). Plants obtain N from soil, in the form of nitrate or ammonium, but incidence of HM disturbs the N assimilation; thus genes that are accountable for transportation of nitrate and ammonium in plants are downregulated (Norton et al. 2008).

Water Relations

Apart from providing mechanical support to the plant and fixing it in the soil, the prime purpose of roots is the water absorption and transport of inorganic nutrients from soil. Generally, accumulation of HM is found higher in roots than other plant parts as it is the foremost organ to come in contact with HM ions (Seregin and Ivanov 2001; Chen et al. 2004; Małecka et al. 2008). Excessive availability of HM hampers the proficiency of the water flow by decreasing the rate of transpiration (Barcelo and Poschenrieder 1990). In roots, transport of water by the symplast and apoplast pathways also gets disturbed by HM exposure resulings into reduced water uptake (Steudle 2000, 2001). Heavy metal also inhibits the aquaporin activity and/or alters the expression of these proteins, thus resulting in impairment of water transport through the membranes (Przedpelska-Wasowicz and Wierzbicka 2011). Subjection of HM leads to accumulation of callose in cell walls that is accountable for the reduced movement of water. Samardakiewicz et al. (2012) revealed that subjection of Pb to *Lemna minor* roots resulted in accretion of callose within the plasmodesmata. On the other hand, deposition of metals on cell walls leads to thickening of these, which increases the apoplast resistance to water flow. It has previously revealed that Pb was responsible for thickening in the cell wall (Krzesłowska et al. 2009) and increased lignin content in *Pisum sativum* L. (Paivoke 1983) and *Glycine max* L. (Pawlak-Sprada et al. 2011), callose in *Lemna minor* roots (Samardakiewicz et al. 2012), and callose, pectins, cellulose, and sudanophilic lipid compounds in the protonemata of *Funaria hygrometrica* (Krzesłowska et al. 2009). Obstruction in leaf development due to the water deficit may be due to hampered transport of water to above parts of plants particularly to leaf. A quick reduction in osmotic potential, root vacuolization, and reorganization of tissues may be regarded as the strategy to enhance water retention in plants (Rucinska-Sobkowiak et al. 2013). It is proposed that modifications in the aquaporin permeability are linked with the alteration of aquaporin proteins by phosphorylation/dephosphorylation, the processes which may be controlled by abscisic acid (ABA). Plant exposure to HM may possibly stimulate augmentation in signaling compounds such as calcium ions, polyamines, and various plant hormones like ethylene, auxin, jasmonic acid (JA), salicylic acid (SA), and ABA.

14.4.3 Phytotoxicity of Heavy Metals/Metalloids at Cellular and Molecular Levels

14.4.3.1 Lipid Peroxidation

Lipid peroxidation is an indicator of oxidative injury, induced by various abiotic and biotic stresses including HM, and has been acknowledged in varied plant species (Cho and Park 2000; Cargnelutti et al. 2006; Ahsan et al. 2007; Wang et al. 2008; Cavusoglu et al. 2009; Pandey et al. 2009; Maheshwari and Dubey 2009; Chandrakar et al. 2017; Xalxo and Keshavkant 2018). Plants subjected to HM toxicity displayed an augmentation in lipid peroxidation reaction as a consequence of excess ROS generation (Chandrakar et al. 2017; Xalxo and Keshavkant 2018), and also acceleration in it might be done by the lipoxygenase with the formation of hydroperoxides (Huang et al. 2012). Heavy metal-induced production of free radical leads to deterioration of cellular components involving polyunsaturated fatty acid (PUFA) residues of phospholipids, which are tremendously susceptible to oxidation (Abd-Allah et al. 2015). The PUFAs like linoleic acid (18:2) and linolenic acid (18:3) are predominantly vulnerable to attack of singlet oxygen ($^1O_2$) and hydroxyl radical ($^\bullet OH$), resulting in the formation of lipid hydroperoxides (Ahmad et al. 2010). Lipid peroxidation is regarded as most detrimental process that occurs in plants during HM toxicity. Several aldehydic products such as malondialdehyde (MDA) and 4-hydroxy-2-nonenal (HNE), along with hydroxyl and keto fatty acids, are generated as consequences of PUFA peroxidation under HM stress (Chandrakar and Keshavkant 2018). Treatments of Cd, As, and Pb notably increased the accumulation of lipid peroxidized products in *Pisum sativum* L. (Metwally et al. 2005), *Glycine max* L. (Chandrakar et al. 2017), and *Trigonella foenum graecum* L. (Xalxo and Keshavkant 2018), respectively. In plant cells, some of the PUFA oxidation products function as secondary messengers either directly or after enzymatic modifications (Mittler 2002; Miller et al. 2010).

14.4.3.2 Oxidative Damage to DNA

Subjection to abiotic stress like HM can harm DNA which can affect the strong steadiness of the plant genome (Chandrakar et al. 2017). The excessively accumulated ROS are the key mediators of damage to cellular organization and significant biomolecules (Tuteja et al. 2009; Chandrakar et al. 2017). Binding of metals to the cellular nuclei results in modifications in DNA nucleotides, inter- and intramolecular cross-linking of DNA and proteins, and DNA fragmentation and reorganization, which can further induce mutation (Nagajyoti et al. 2010). For example, when ROS is produced by oxidative stress nearby DNA, it forms a mutagenic adduct 8-OxoG (7,8-dihydro-8-oxoguanine) that may possibly establish bonding with adenine. If unchecked by the repair machinery, this may lead to transverse mutation from cytosine to thiamine (Cunningham 1997). Common genotoxic effects reported due to the As toxicity involve disruption of mitotic spindle fibers. In the seeds of *Hordeum vulgare* L., the degree of anomalies found in the chromosomes was related to As aggregation (Bandyopadhyay and Maity 1995). Chromosomal behavioral analysis of Cd exposed *Pisum sativum* L. root tips revealed increased frequency of chromosomal abnormalities like fragmentation, early and late separation of chromosomes, single and double bridges, and chromosome agglutination (Siddique et al. 2009).

14.4.3.3 Oxidative Damage to Proteins

Proteins on direct reaction with excess ROS undergo oxidative modifications. Interactions with MDA and HNE (lipid peroxidation products) also result in oxidative stress (Xalxo and Keshavkant 2018). Both MDA and HNE produced as a result of lipid peroxidation undergo non-enzymatic condensation with free amino groups of proteins or nucleic acids, which leads to browning. Glycosylamine formed as a result rearranges to produce the Amadori product (1-amino-deoxyketose), which consequently degrades into intermediate products (MDA and HNE). These intermediates thus obtained mix with other amino groups which results in the formation of glycosylation end products. Oxidized protein is universally present and thus can be used as a marker to diagnose HM-imposed oxidative stress. Carbonylation is another irreversible and most frequently transpiring oxidative protein modulation under HM stress. It may result due to oxidation of amino acid side chains (leading to formation of arginine and proline to g-glutamyl semialdehyde, threonine to amino ketobutyrate, and lysine to amino adipic semialdehyde). Reaction between proteins and lipid peroxidized products, for instance, HNE and MDA, may also initiate carboxylation reaction. Scientists have revealed that the content of protein carbonylation is found more in the mitochondria in comparison to the chloroplasts and peroxisomes which signifies that the mitochondria are more vulnerable to oxidative injury (Ahmad et al. 2010; Gill and Tuteja 2010). Heavy metal-induced oxidative amendments of proteins lead to various detrimental consequences on the cellular physiology of plants. The oxidative damage caused by excess ROS can be mild to brutal on cell functions depending upon various factors such as fraction of biological molecules that are modified and for how much time the alteration persisted in the cell.

14.5 Production of Reactive Oxygen Species and Antioxidant Defense Systems: Markers in Ecophysiological Studies

Overaccumulation of ROS is considered as the first biochemical modification when plants are exposed to HM-contaminated sites (Gill and Tuteja 2010; Chandrakar et al. 2017; Yadu et al. 2017; Xalxo and Keshavkant 2018). The ROS comprises of $^1O_2$, superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), hydroperoxyl radical (HO_2), $^{\bullet}OH$, hydroperoxide (ROOH), peroxyl radical ($ROO^{\bullet}$), and alkoxyl radical ($RO^{\bullet}$). These free radicals are extremely reactive and noxious and cause injury to various biomolecules like proteins, lipids, carbohydrates, and DNA which eventually leads to death of the cells (Gill and Tuteja 2010). Excess accrual of ROS, as a consequence of diverse environmental stresses including metal toxicity, affects crop yield and food security globally (Xalxo and Keshavkant 2018). Reactive oxygen species are generally shown to damage nucleic acids, oxidize proteins, and cause lipid peroxidation, thus hampering many cellular functions (Chandrakar et al. 2017; Xalxo and Keshavkant 2018). A severe imbalance occurs between production and elimination of ROS, and this disproportion later results in remarkable physiological challenges to the plants that is cumulatively termed as "oxidative syndrome" (Kovacik et al. 2010; Morina et al. 2010; Chandrakar et al. 2017; Yadu et al. 2017; Chandra et al. 2018). Heavy metals such as As, Cu, Cd, Cr, Fe, Hg, Pb, and Zn have the capability to stimulate the excess generation of ROS inside the cells (Duquesnoy et al. 2010; Vanhoudt et al. 2010, Korpe and Aras 2011; Márquez-García et al. 2011). The mechanism of ROS generation is dissimilar for redox-active and redox-inactive metals (Pourrut et al. 2008; Opdenakker et al. 2012). Redox-active metals like Cu and Fe act as catalyst in the Haber-Weiss/Fenton reactions, wherein H_2O_2 splits into $^{\bullet}OH$ at a neutral pH (Sahi and Sharma 2005; Valko et al. 2006). On the other hand, redox-inactive metals like Cd, Pb, Hg, As, Zn, and Ni hamper enzymatic activities as they have strong affinity for –SH groups of the proteins (Pourrut et al. 2011; Chandrakar et al. 2016). As redox-inactive metals have electron-sharing affinities, they form covalent bonds with sulfhydryl groups of proteins. Heavy metals, particularly Pb, bind to functional groups (COOH) of protein molecules and inactivate enzymes (Sharma and Dubey 2005; Gupta et al. 2010). Additionally, HM induces displacement of vital cations from specific binding sites of enzymes, thus disturbing the intracellular ROS balance, resulting in excess accumulation of ROS. Heavy metals are also proficient in depleting reduced glutathione (GSH) within plant cells (Bhaduri and Fulekar 2012). Depletion of major antioxidants due to the accumulation of HMs inside the cells also disrupts the ROS balance. Heavy metals also directly bind to GSH and its derivatives whose presence is obligatory to scavenge excess ROS generated in the plants, hence leading to ROS accrual in cell

(Lee et al. 2003). In addition, plasma membrane-integrated NADPH oxidase is engaged in HM-induced oxidative injury (Pourrut et al. 2008, 2013; Potocky et al. 2012). Reactive oxygen species generation via NADPH oxidase was revealed by Rodriguez-Serrano et al. (2006), Hao et al. (2006), and Pourrut et al. (2008) in *Pisum sativum* L., *Triticum durum* L., and *Vicia faba* L. treated with Cd, Ni, and Pb, respectively.

To defend itself against these ROS, plant cells and its components (chloroplasts, mitochondria, and peroxisomes) utilize antioxidant security systems. Prior investigations have confirmed that cellular antioxidant system is significant for defense against several stresses (Tuteja 2007; Singh et al. 2008; Chandrakar et al. 2017). The antioxidant defense machinery comprises of enzymatic and non-enzymatic factors. The superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydoascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reducaste (GR) are termed as enzymatic antioxidants, while GSH, ascorbate (AsA), carotenoids, and tocopherols (lipid soluble) are placed under non-enzymatic group (Chandrakar et al. 2017; Yadu et al. 2017; Xalxo and Keshavkant 2018). These antioxidants prevent additional buildup of ROS intracellularly, thus maintaining redox homeostasis in the cell (Gill and Tuteja 2010). Many examples of amendment in the antioxidant machinery imposed by HMs in various plant species are present in the literature (Miller et al. 2010; Ahmad et al. 2011; Chandrakar et al. 2017; Xalxo and Keshavkant 2018). Antioxidative restoration to metal toxicity depends upon the metal type, quantity, and plant species. In plants, major role of ROS homeostasis maintenance is played by AsA and GSH antioxidants. Elevation in AsA and reduction in GSH amount have been studied in *Oryza sativa* L. seedlings after Ni stress (Maheshwari and Dubey 2009). Exposure of *Glycine max* L. seedlings to Ni leads to loss in AsA amount (Prasad et al. 2005). Treatment of *Phaseolus vulgaris* L. seedlings to Cd, Pb, Hg, and Cu, separately, resulted in an amplification in AsA and tocopherol levels (Zengin and Munzuroglu 2006); similarly Cd treatment also exhibited a concentration reliant increase in the GSH levels of germinating *Vicia faba* L. seeds (Szollosi et al. 2009). The level of antioxidant enzymes escalated in the leaves of *Pisum sativum* L. and *Trigonella foenum graecum* L. plants in retaliation to Cd and Pb, respectively (Dixit et al. 2001; Xalxo and Keshavkant 2018). The SOD and CAT also enhanced in the plant cells after Hg exposure (Patra et al. 2004); also, gene expression of these enzymes was upregulated by Cr and Pb in *Zea mays* L. and *Trigonella foenum graecum* L., respectively (Labra et al. 2006; Xalxo and Keshavkant 2018). The antioxidant enzyme responses to HM stress depend on the tissues, for instance, application of Cd-induced GST in *Pisum sativum* L. roots, but no induction of GST was observed in leaves (Dixit et al. 2001). Similarly, GST was upregulated by Cu in germinating *Oryza sativa* L. embryos, but downregulation was observed when whole seed was taken into consideration (Ahsan et al. 2007; Zhang et al. 2009).

14.6 Signal Transduction Under Heavy Metal/Metalloid Toxicity

To conserve the normal quantity of essential metal ions, plants have developed various methods to reduce their contact with HMs, which are non-essential for them. Few mechanisms required for homeostasis are common in all, but some of the processes target individual metal ions for their elimination from intracellular environment. When these two systems fail to overcome stress responses, plants put up a stress defense system including several proteins and signal transducing molecules like heat shock proteins, hormones, ROS, and most significantly the specific metal-responsive genes (Maksymiec 2007). However, diverse signal transduction pathways get initiated in response to HMs, most common of these includes the calcium calmodulin pathway, ROS signaling, hormones, and the MAPK phosphorylation pathway. Researchers have reported that HM toxicity in plants causes alterations in calcium (Ca) concentration, MAPK cascade, and transcriptional modifications of the genes involved in stress defense (Shao et al. 2008, 2009; Thapa et al. 2012).

14.6.1 Calcium Calmodulin System

Calcium, a vital macronutrient, enters into plants via root systems and is transferred to the other parts of the plant through xylem (Tuteja et al. 2009; Ahmad et al. 2012). Calcium ion not only acts as a major component in all signaling systems but also plays a role during normal development and several biotic and abiotic stresses including HM (Tuteja and Mahajan 2007; Himschoot et al. 2015). In plants, exposure of HM alters the concentration of cytoplasmic Ca^{2+} due to the influx of Ca^{2+} from outer environment of the cell, or due to the discharge of the stored intracellular Ca^{2+} inside the cell (Steinhorst and Kudla 2014). Plants consist of a range of Ca^{2+} sensors like calcineurin B-like proteins (CBLs), calmodulins (CaMs), calmodulin-like proteins, and Ca^{2+}-dependent protein kinases (CDPKs). These biological sensors sense and decipher alterations in the levels of cytosolic Ca^{2+} and transmit it as signal for further response (Luan et al. 2002; Sanders et al. 2002; Dodd et al. 2010; Steinhorst and Kudla 2013). The Ca^{2+}-dependent protein kinases are sensory proteins that bind to Ca^{2+} directly prior to phosphorylation of substrates which are involved in signal pathway during various stresses (Hamel et al. 2006; Schulz et al. 2013). Various experiments have been performed to explore the role of CBLs in plants vs. abiotic stresses. The identification and classification of CBLs have been done in several plant species including *Cicer arietinum* L. (Tripathi et al. 2009), *Glycine max* L. (Li et al. 2012), *Vitis vinifera* (Tripathi et al. 2009), and *Solanum lycopersicum* (de la Torre et al. 2013) to enhance their endurance toward abiotic stresses. In plants, higher intracellular accumulation of Ca^{2+} was observed under Cd stress, thus implementing adaptive techniques that help to mitigate the toxicity of

HM (Yang and Poovaiah 2003). The Ca-calmodulin system was seen to be intricated in tolerance mechanisms of *Nicotiana tabacum*, in response to Ni and Pb toxicity. High amount of toleration toward Ni and sensitivity to Pb were observed in transgenic *Nicotiana tabacum* plant expressing NtCBP4 (*Nicotiana tobacum* calmodulin-binding protein). Another Ca^{2+} sensor, i.e., CDPKs, senses and relays the downstream signaling pathway cascade (Asano et al. 2012). It aids in the regulation of *Oryza sativa* L. growth via continuous expression of CDPK gene (Manimaran et al. 2015). Reports have also proposed the possible mitigation of HM stress by the induction of exogenous Ca^{2+} which assists via influencing various vital processes of plants. Moreover, addition of Ca^{2+} also affects the action of defensive antioxidant enzymes (APX, GR, and SOD) (Ahmad et al. 2015). Thus, the study of varied expression patterns of the Ca^{2+}-binding proteins in plants against HM stress will be advantageous in further analysis of the functions and mechanisms behind Ca^{2+}-dependent signaling in plants.

14.6.2 Plant Hormones

Phytohormones are universally present and play principal roles in growth and development during plant life cycle (Divi and Krishna 2009). Auxin is known to be the best hormone for plant growth regulation; ABA positively influences bud dormancy and closing of stomata; cytokinin helps in delaying aging; gibberellin induces seed germination; and brassinosteroids regulate growth and development of plants (Sun et al. 2005; Vert et al. 2005; Jaillais and Chory 2010). Phytohormones are low molecular weight mediators between various signaling pathways, and they also influence plant retaliation to abiotic stresses (Bostock 2005). Significantly, ethylene (ET), SA, and JA are closely linked with the plant defense mechanisms vs. acting stress. The EIN2, EIN3, JAZ proteins, and AP2/ERF TF gene family are strongly influenced by ET and JA (Mauch-Mani and Mauch 2005; Fujita et al. 2006; Kazan 2015). An investigation by Singh and Shah (2014) showed that subjection to JA increases antioxidant responses, hence leading to Cd stress endurance in *Oryza sativa* L. Thus, clearly suggesting that modulation in extent of plant hormones alters the plant response to HM stress. Increase in ET biosynthesis was reported by Rodriguez-Serrano et al. (2009) in *Pisum sativum* L., Masood et al. (2012) in *Brassica oleraceae* L., and Chmielowska-Bak et al. (2013) in *Glycine max* L. under Cd stress. Experiments done by Popova et al. (2009) in Cd stressed *Pisum sativum* L. revealed augmentation in the SA level which helped to defend leaves from lipid peroxidation. The results suggested that elevated concentration of intracellular SA accumulated after Cd treatment may act directly as an antioxidant or indirectly activate other antioxidant responses. Comparative transcriptome analysis of *Oryza sativa* L. seedlings treated with As(V) and As(III) showed that As modified the signaling pathway and defense mechanism of the plant, revealing that As(III) profoundly affects hormonal signaling processes such as ABA metabolism (Chakrabarty et al. 2009). Additionally, the detailed study of signal cascade involving hormones under HM stress can help in growth of plants with increased stress bearing.

14.6.3 Role of Reactive Oxygen Species

The recognition of stress signal and initiation switching of signal transduction pathways are the adaptive reactions that decides the existence of plants under stressed environment. Production and aggregation of ROS, particularly $O_2^{\bullet -}$, H_2O_2, $^{\bullet}OH$ and $^1O_2$, is one of the stress stimuli. Due to HM stress, ROS is formed in huge amount which is termed as "oxidative burst," an alarming signal to trigger the gene expression of transcription factors (TFs) and various other protective genes (Sharma et al. 2012). The excessive formation of ROS disturbs the balance of the normal cellular functioning, resulting in oxidative harm to biomolecules (Karuppanapanadian et al. 2011; Kapoor et al. 2015). These free radicals play a dual role that is based on time, site, and their quantities. Firstly, ROS at low concentration acts as a signal messenger and helps in eliciting response against several stresses, while at elevated concentration, it poses threat to the plant cell. Reactive oxygen species receptors include histidine kinases, redox-sensitive TFs, ROS-sensitive phosphatases, and redox-regulated ion channels (Steffens 2014). Various scientists have revealed that ROS generation due to the HMs is confirmed by the accruals of lipid peroxidation products like MDA and HNE (Sharma et al. 2012; Rai et al. 2015; Chandrakar et al. 2018; Xalxo and Keshavkant 2018). Studies have confirmed that HM like Cd causes lipid peroxidation and PCD in varied plant due to the agitation in the metabolism of cell organelles like chloroplasts and mitochondria (Cho and Seo 2005; Metwally et al. 2005; Bi et al. 2009). It has been revealed that subjection to Hg toxicity induces Ca^{2+} accrual, decreases free radical generation, and activates MAPKs, which contributes to the plant resistance to Hg stress (Chen et al. 2014). As stated by various researchers, As contamination negatively affects regular growth and development of plants and instigates oxidative injury (Shri et al. 2009; Islam et al. 2015; Chandrakar et al. 2017). During stress condition, enzymatic and non-enzymatic antioxidant systems undergo several modifications (Dwivedi et al. 2010; Kanwar and Poonam 2015; Chandrakar et al. 2017). As a defense strategy, few mechanisms tackle toxicity in the plants. The primary detoxification mechanism comprises increased antioxidant activity which preserves homeostasis intracellularly by scavenging excess accumulated ROS, and secondary mechanism includes HM sequestration into the vacuoles by various peptides (Kumar et al. 2015). During stress condition, antioxidant system is triggered to lessen the negative consequences due to excess ROS (Rai et al. 2011; Chandrakar et al. 2017; Yadu et al. 2017; Xalxo and Keshavkant 2018). Shri et al. (2009), Chandrakar et al. (2017), Yadu et al. (2017), and Xalxo and Keshavkant (2018) reported amplified activities of CAT, SOD, POD, APX, and GR in *Oryza sativa* L., *Glycine max* L., *Cajanus cajan* L., and *Trigonella foenum-graecum* L. seedlings, respectively, exposed to various HMs.

14.6.4 Mitogen-Activated Protein Kinase Cascade

Mitogen-activated protein kinases are serine/threonine kinases and are signaling molecules conserved throughout evolution in the plants (Jonak et al. 2002). It is composed of MAP kinase kinase kinases, MAP kinase kinases, and MAP kinases (MAPKs/MPKs) (Nakagami et al. 2005). These molecules aid during stressed environments and are significant in the establishment of tolerance while introducing the adaptive downstream signaling. Phosphorylation occurs in signal cascade of several TFs such as DREB, bZIP, NAC, and WRKY and thus affects normal functioning like differentiation, growth, and developmental and stress responses of cells (Lin and Aarts 2012). Transcriptional initiation of these MAPKs in *Oryza sativa* L. confirms its regulatory function in plant maturation, safety, and stress signaling (Kim et al. 2003). Genomic study of different plants explained that components of this signaling pathway are determined by multigene families. Approximately, 20 MAPKs, 10 MAP kinase kinases, and 60–80 MAP kinase kinase kinases are a part of the *Arabidopsis* genome (Chen et al. 2012b), and similar quantities of these have also been reported in other species like *Oryza sativa* L. and *Zea mays* L. (Rao et al. 2010). The purpose of MAPKs has been deliberated under variety of stresses. The MAPKs under physical factors like cold, heat, drought, and salinity are differentially regulated in *Oryza sativa* L., proposing the participation of this gene family in stress signaling (Kumar et al. 2008; Chen et al. 2012a; Zhang et al. 2012). Jonak et al. (2004) reported four isoforms of MAPK in *Medicago sativa* seedlings when subjected to Cu or Cd stress. Similar results were also obtained by Yeh et al. (2007) in *Oryza sativa* L. after Cd-induced toxicity. In conclusion, all of these pathways together aid in the regulation of TFs that regulates genes necessary for plant adjustment during stress.

14.7 Assisting Plant to Survive: Future Directives and Perspectives

Accumulation of excessive HM in the environment has become a major threat due to its adverse effects in all the living organisms. Negative effects of HM toxicity on flora and fauna are a matter of serious concern globally. Even at low concentrations, HMs are very reactive and their concentrations gets build up in the food web, leading to detrimental effects to all the living organisms. Various detrimental consequences of elevated or lethal concentrations of HM ions to sensitive plants include reduced growth, crop productivity, and yields. Developing the mechanisms to help plants for the management of HM toxicity may be useful in creating new ideas for the remediation of HM. Presently, researchers are more worried in developing novel technologies of least expensive and eco-friendly land retrieval techniques. Currently, there is a couple of biotechnological approaches to limit the negative consequences of HM contaminations in the natural environments. First approach involves increasing the HM uptake capacity of plants for the amplification of their efficacy in phytoremediation of HM from contaminated sites. Another strategy includes the enhancing plant tolerance against HMs, which increases plant growth and crop yield. Genetic manipulation of transporter gene responsible for localization of HM is reassuring step as the encoded proteins can effectively regulate the entry, circulation, and accrual of metal ions in the plant tissues. On the other hand, the modifications of membrane transporters to decrease the uptake and transfer of particular HM ions may result in disparity in maintaining the redox state of essential metal ions. Therefore, molecular and cellular adaptation seems mandatory to improve their tolerance against HM toxicity, which hampers the HM entry into the food chain. It is confirmed that the overaccumulations of HMs are also responsible for imbalance in the homeostasis of antioxidants and slanting the balance that induces the ROS generation and its interference in normal functioning of cellular macromolecules (proteins, lipids, nucleic acids, etc.) and organelles. Additionally, PCs and metalothionins (MTs), responsible for metal sequestration, and their functional diversity and molecular adaptability are attracting the scientist regarding the HM detoxification and regulating the cellular ion balance. Both PCs and MTs interact with antioxidant defense system directly or indirectly and aid plants in transporting and distributing excessive HM ion between different tissues in a time- or tissue-specific manner. Glutathione also plays a major role in HM entry, passage, compartmentation, sequestration, and formation of specific metal-binding ligands such as PCs. The modification in gene expression of PCs is one of the potential mechanisms for amplifying the plant efficiency for phytoremediation. Understanding the consequences of gene expression of the GSH/PC biosynthetic pathways, probably in a tissue-specific manner, on metal tolerance and accumulation may lead to understanding of their usefulness in remediation of HM toxicity. There are evidences that used transgenic plants which overexpressed PCs and conferred HM tolerance. Presently, scientists are using microorganisms for the removal or remediation of HM stress. Strategies developed by microbes for sustained survival in HM-polluted sites include various mechanisms such as bioaccumulation, biomineralization, biosorption, and biotransformation. Signaling pathways like MAPK cascades trigger environmental and developmental signals into adaptive and programmed responses in response to HM stress. Various important physiological and developmental processes like stress and hormonal responses and innate immunity are controlled by MAPK cascade. Extensive investigations are required for finding of suitable substrates of MAPKs and their association with other signaling molecules. Importantly, for detailed understanding of the detrimental effects of HMs on seeds/seedlings, the knowledge about the signaling networks needs to be explored including the interaction of ROS, reactive nitrogen species, and seed/plant hormones with HMs.

14.8 Conclusions

It is evident from various researches that non-judicious use and excessive presence of HM have lethal consequences on flora and fauna. It is evident that there are various substitutes, by political or social actions decreasing the discharge of toxic pollutants into the natural environments, utilization of genetically modified plants or the use of naturally occurring tolerant crops, which may aid to defeat contaminated environmental conditions. Nevertheless, extensive research programs are required for enhanced understanding of deleterious impacts of HM on the living system and its related areas to control the ecological redox of our environment.

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References

Abd-Allah EF, Abeer H, Alqarawi AA, Alwathnani HA (2015) Alleviation of adverse impact of cadmium stress in sunflower (*Helianthus annuus* L.) by arbuscular mycorrhizal fungi. Pak J Bot 47:785–795

Agnihotri A, Seth CS (2016) Exogenously applied nitrate improves the photosynthetic performance and nitrogen metabolism in tomato (*Solanum lycopersicum* L. cv Pusa Rohini) under arsenic (V) toxicity. Physiol Mol Biol Plants 22:341–349

Ahmad P, Jaleel CA, Salem MA, Nabi G, Sharma S (2010) Roles of enzymatic and non enzymatic antioxidants in plants during abiotic stress. Crit Rev Biotechnol 30:161–175

Ahmad P, Nabi G, Ashraf M (2011) Cadmium-induced oxidative damage in mustard [*Brassica juncea* (L.) Czern. & Coss.] plants can be alleviated by salicylic acid. S Afr J Bot 77:36–44

Ahmad P, Ozturk M, Gucel S (2012) Oxidative damage and antioxidants induced by heavy metal stress in two cultivars of Mustard (Brassica juncea L.) Plants. Fresenius Environ Bull 21:2953–2961

Ahmad P, Sarwat M, Bhat NA, Wani MR, Kazi AG, Tran LSP (2015) Alleviation of cadmium toxicity in *Brassica juncea* L. (Czern. & Coss.) by calcium application involves various physiological and biochemical strategies. PLoS One 10:e0114571. https://doi.org/10.1371/journal.pone.0114571

Ahmed H, Hader DP (2010) Rapid ecotoxicological bioassay of nickel and cadmium using motility and photosynthetic parameters of *Euglena gracilis*. Environ Exp Bot 69:68–75

Ahsan N, Lee DG, Lee SH, Kang KY, Lee JJ, Kim PJ, Yoon HS, Kim JS, Lee BH (2007) Excess copper induced physiological and proteomic changes in germinating rice seeds. Chemosphere 67:1182–1193

Anjum SA, Tanveer M, Hussain S, Shahzad B, Ashraf U, Fahad S, Hassan W, Jan S, Khan I, Saleem MF, Bajwa AA, Wang L, Mahmood A, Samad RA, Tung SA (2016) Osmoregulation and antioxidant production in maize under combined cadmium and arsenic stress. Environ Sci Pollut Res 23:11864–11875

Appenroth KJ, Teller S, Horn M (1996) Photophysiology of turion formation and germination in *Spirodela polyrhiza*. Biol Plant 38:95–106

Aravind P, Prasad MNV (2005) Modulation of cadmium-induced oxidative stress in *Ceratophyllum demersum* by zinc involves ascorbate-glutathione cycle and glutathione metabolism. Plant Physiol Biochem 43:107–116

Ardisana EFH, Suarez M, Alvarez SP (2018) Molecular and biochemical characterization of oxidative stress in tomato plants cultivated with lead (Pb). Horti Inter J 6:399–402

Asano T, Hayashi N, Kobayashi M, Aoki N, Miyao A, Mitsuhara I, Ichikawa H, Komatsu S, Hirochika H, Kikuchi S, Ohsugi R (2012) A rice calcium-dependent protein kinase OsCPK12 oppositely modulates salt-stress tolerance and blast disease resistance. Plant J 69:26–36

Asgher M, Khan NA, Khan MIR, Fatma M, Masood A (2014) Ethylene production is associated with alleviation of cadmium-induced oxidative stress by sulfur in mustard types differing in ethylene sensitivity. Ecotoxicol Environ Saf 106:54–61

Assunceaao AGL, Costa Martins PDA, De Folter S, Vooijs R, Schat H, Aarts MGM (2001) Elevated expression of metal transporter genes in three accessions of the metal hyperaccumulator *Thlaspi caerulescens*. Plant Cell Environ 24:217–226

Axelsen KB, Palmgren MG (2001) Inventory of the superfamily of P-type ion pumps in Arabidopsis. Plant Physiol 126:696–706

Babu NG, Sarma PA, Attitalla IH, Murthy SDS (2010) Effect of selected heavy metal ions on the photosynthetic electron transport and energy transfer in the thylakoid membrane of the cyanobacterium, *Spirulina platensis*. Acad J Plant Sci 3:46–49

Bandyopadhyay B, Maity S (1995) Comparison of clastogenic effects of two arsenic salts on plant system in vivo. J Cytol Genet 30:35–39

Barberon M, Zelazny E, Robert S, Conejero G, Curie C, Friml J (2011) Monoubiquitin-dependent endocytosis of the IRON-REGULATED TRANSPORTER 1 (IRT1) transporter controls iron uptake in plants. Proc Natl Acad Sci 108:E450–E458

Barcelo J, Poschenrieder C (1990) Plant water relations as affected by heavy metal stress: a review. J Plant Nutr 13:1–37

Belouchi A, Cellier M, Kwan T, Saini HS, Leroux G, Gros P (1995) The macrophage- specific membrane protein Nramp controlling natural resistance to infections in mice has homologues expressed in the root system of plants. Plant Mol Biol 29:1181–1196

Belouchi A, Kwan T, Gros P (1997) Cloning and characterization of the OsNramp family from *Oryza sativa*, a new family of membrane proteins possibly implicated in the transport of metal ions. Plant Mol Biol 33:1085–1092

Bereczky Z, Wang HY, Schubert V, Ganal M, Bauer P (2003) Differential regulation of nramp and irt metal transporter genes in wild type and iron uptake mutants of tomato. J Biol Chem 278:24697–24704

Bhaduri AM, Fulekar MH (2012) Antioxidant enzyme responses of plants to heavy metal stress. Rev Environ Sci Biotechnol 11:55–69

Bi YH, Chen WL, Zhang WN, Zhou Q, Yun L, Xing D (2009) Production of reactive oxygen species, impairment of photosynthetic function and dynamic changes in mitochondria are early events in cadmium induced cell death in *Arabidopsis thaliana*. Biol Cell 101:629–643

Bondada BR, Oosterhuis DM (2000) Comparative epidermal ultrastructure of cotton (*Gossypium hirsutum* L) leaf, bract and capsule wall. Ann Bot 86:1143–1152

Bostock RM (2005) Signal crosstalk and induced resistance: straddling the line between cost and benefit. Annu Rev Phytopathol 43:545–580

Bovet L, Eggmann T, Meylan-Bettex M, Polier J, Kammer P, Marin E, Feller U, Martinoia E (2003) Transcript levels of AtMRPs after cadmium treatment: induction of AtMRP3. Plant Cell Environ 26:371–381

Bovet L, Feller U, Martinoia E (2005) Possible involvement of plant ABC transporters in cadmium detoxification: a cDNA sub-microarray approach. Environ Int 31:263–267

Cargnelutti D, Tabaldi LA, Spanevello RM, Jucoski GD, Battisti V, Redin M, Linares CEB, Dressler VL, Flores EMD, Nicoloso FT, Morsch VM, Schetinger MRC (2006) Mercury toxicity induces oxidative stress in growing cucumber seedlings. Chemosphere 65:999–1006

Cavusoglu K, Ergene A, Yalcin E, Tan S, Cavusoglu K, Yapar K (2009) Cytotoxic effects of lead and mercury ions on root tip cells of Cicer arietinum L. Fresenius Environ Bull 18:1654–1661

Chakrabarty D, Trivedi PK, Misra P, Tiwari M, Shri M, Shukla D, Kumar S, Rai A, Pandey A, Nigam D, Tripathi RD, Tuli R (2009) Comparative transcriptome analysis of arsenate and arsenite stresses in rice seedlings. Chemosphere 74:688–702

Chandra J, Parkhey S, Keshavkant S (2018) Ageing-regulated changes in genetic integrity of two recalcitrant seeded species having contrasting longevity. Tress 32:109–123

Chandrakar V, Keshavkant S (2018) Growth and metabolic responses of *Glycine max* L. to arsenate and arsenite: a comparative assessment. Bangladesh J Bot 47:105–113

Chandrakar V, Naithani SC, Keshavkant S (2016) Arsenic-induced metabolic disturbances and their mitigation mechanisms in crop plants: a review. Biologia 71:367–377

Chandrakar V, Parkhey S, Dubey A, Keshavkant S (2017) Modulation in arsenic-induced lipid catabolism in *Glycine max* L. using proline, 24-epibrassinolide and diphenylene iodonium. Biologia 72:292–299

Chandrakar V, Dubey A, Keshavkant S (2018) Modulation of arsenic-induced oxidative stress and protein metabolism by diphenyleneiodonium, 24-epibrassinolide and proline in *Glycine max* L. Acta Bot Croat 77:51–61

Chaturvedi AD, Pal D, Penta S, Kumar A (2015) Ecotoxic heavy metals transformation by bacteria and fungi in aquatic ecosystem. World J Microbiol Biotechnol 31:1595–1603

Chen CT, Chen TH, Lo KF, Chiu CY (2004) Effects of proline on copper transport in rice seedlings under excess copper stress. Plant Sci 166:103–111

Chen JH, Jiang HW, Hsieh EJ, Chen HY, Chein CT, Hseih HL, Lin TP (2012a) Drought and salt stress tolerance of an Arabidopsis glutathione S-transferase U17 knockout mutant are attributed to the combined effect of glutathione and abscisic acid. Plant Physiol 158:340–351

Chen L, Hu W, Tan S, Wang M, Ma Z, Zhou S, Deng X, Zhang Y, Huang C, Yang G, He G (2012b) Genome-wide identification and analysis of MAPK and MAPKK gene families in *Brachypodium distachyon*. PLoS One 7:e46774. https://doi.org/10.1371/journal.pone.0046744

Chen YA, Chi WC, Trinh NN, Huang LY, Chen YC, Cheng KT, Huang TL, Lin CY, Huang HJ (2014) Transcriptome profiling and physiological studies reveal a major role for aromatic amino acids in mercury stress tolerance in rice seedlings. PLoS One 9:e95163. https://doi.org/10.1371/journal.pone.0095163

Chmielowska-Bak J, Lefevre I, Lutts S, Deckert J (2013) Short term signaling responses in roots of young soybean seedlings exposed to cadmium stress. J Plant Physiol 170:1585–1594

Cho UH, Park JO (2000) Mercury-induced oxidative stress in tomato seedlings. Plant Sci 156:1–9

Cho UH, Seo NH (2005) Oxidative stress in Arabidopsis thaliana exposed to cadmium is due to hydrogen peroxide accumulation. Plant Sci 168:113–120

Cunningham RP (1997) DNA repair: caretakers of the genome? Curr Biol 7:576–579

Curie C, Alonso JM, Le Jean M, Ecker JR, Briat JF (2000) Involvement of NRAMP1 from *Arabidopsis thaliana* in iron transport. Biochem J 347:749–755

D'Amore JJ, Al-Abed SR, Scheckel KG, Ryan JA (2005) Methods for speciation of metals in soils: a review. J Environ Qual 34:1707–1745

de la Torre F, Gutierrez-Beltran E, Pareja-Jaime Y, Chakravarthy S, Martin GB, del Pozo O (2013) The tomato calcium sensor Cbl10 and its interacting protein kinase Cipk6 define a signaling pathway in plant immunity. Plant Cell 25:2748–2764

Delhaize E, Kataoka T, Hebb DM, White RG, Ryan PR (2003) Genes encoding proteins of the cation diffusion facilitator family that confer manganese tolerance. Plant Cell 15:1131–1142

Demirevska-Kepova K, Simova Stoilova L, Stoyanova Z, Holzer R, Feller U (2004) Biochemical changes in barley plants after excessive supply of copper and manganese. Environ Exp Bot 52:253–266

Divi UK, Krishna P (2009) Brassinosteroid: a biotechnological target for enhancing crop yield and stress tolerance. New Biotechnol 26:131–136

Dixit V, Pandey V, Shyam R (2001) Differential oxidative responses to cadmium in roots and leaves of pea (*Pisum sativum* L cv. Azad). J Exp Bot 52:1101–1109

Dixit R, Wasiullah E, Malaviya D, Pandiyan K, Singh U, Sahu A, Shukla R, Singh B, Rai J, Sharma P, Lade H, Paul D (2015) Bioremediation of heavy metals from soil and aquatic environment: an overview of principles and criteria of fundamental processes. Sustainability 7:2189–2212

Dodd I, Zinovkina N, Safronova V, Belimov A (2010) Rhizobacterial mediation of plant hormone status. Ann Appl Biol 157:361–379

Drzewiecka K, Ga secka M, Rutkowski P, Magdziak Z, Golinski P, Mleczek M (2018) Arsenic forms and their combinations induce differences in phenolic accumulation in *Ulmus laevis* Pall. J Plant Physiol 220:34–42

Duquesnoy I, Champeau GM, Evray G, Ledoigt G, Piquet-Pissaloux A (2010) Enzymatic adaptations to arsenic-induced oxidative stress in *Zea mays* and genotoxic effect of arsenic in root tips of *Vicia faba* and *Zea mays*. C R Biol 333:814–824

Dwivedi S, Tripathi RD, Tripathi P, Kumar A (2010) Arsenate exposure affects amino acids, mineral nutrient status and antioxidants in rice (*Oryza sativa* L.) genotypes. Environ Sci Technol 44:9542–9549

Farnese FS, Oliveira JA, Paiva EAS, Menezes-Silva PE, da Silva AA, Campos FV, Ribeiro C (2017) The involvement of nitric oxide in integration of plant physiological and ultrastructural adjustments in response to arsenic. Front Plant Sci 8:516. https://doi.org/10.3389/fpls.2017.00516

Farooq MA, Gill RA, Ali B, Wang J, Islam F, Ali S, Zhou W (2015) Oxidative injury and antioxidant enzymes regulation in arsenic-exposed seedlings of four *Brassica napus* L. cultivars. Environ Sci Pollut Res 22:10699–10712

Farooq MA, Islam F, Ali B, Najeeb U, Mao B, Gill RA, Yan G, Siddique KHM, Zhou W (2016) Arsenic toxicity in plants: cellular and molecular mechanisms of its transport and metabolism. Environ Exp Bot 132:42–52

Farooq MA, Islam F, Yang C, Nawaz A, Athar H, Gill RA, Ali B, Song W, Zhou W (2017) Methyl jasmonate alleviates arsenic-induced oxidative damage and modulates the ascorbate-glutathione cycle in oilseed rape roots. Plant Growth Regul 84:135–148

Finkemeier I, Kluge C, Metwally A, Georgi M, Grotjohann N, Dietz KJ (2003) Alterations in Cd-induced gene expression under nitrogen deficiency in *Hordeum vulgare*. Plant Cell Environ 26:821–833

Fodor E, Szabó-Nagy A, Erdei L (1995) The effects of cadmium on the fluidity and H^+-ATPase activity of plasma membrane from sunflower and wheat roots. J Plant Physiol 147:87–92

Fujita M, Fujita Y, Noutoshi Y, Takahashi F, Narusaka Y, Yamaguchi-Shinozaki K (2006) Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signaling networks. Curr Opin Plant Biol 9:436–442

Ghnaya AB, Charles G, Hourmant A, Hamida JB, Branchard M (2009) Physilogical behavior of four rapeseed cultivar (*Brassica napus* L.) submitted to metal stress. C R Biol 332:363–370

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 48:909–930

Gomes MP, Carneiro MMLC, Nogueira COG, Soares AM, Garcia QS (2013) The system modulating ROS content in germinating seeds of two Brazilian savanna tree species exposed to As and Zn. Acta Physiol Plant 35:1011–1022

Guerinot ML (2000) The ZIP, family of metaltransporters. Biochim Biophys Acta 1465:190–198

Guo JB, Dai X, Xu WZ, Ma M (2008) Over-expressing GSH1 and AsPCS1 simultaneously increases the tolerance and accumulation of cadmium and arsenic in *Arabidopsis thaliana*. Chemosphere 72:1020–1026

Gupta P, Bhatnagar AK (2015) Spatial distribution of arsenic in different leaf tissues and its effect on structure and development of stomata and trichomes in mung bean, *Vigna radiata* (L.) Wilczek. Environ Exp Bot 109:12–22

Gupta DK, Huang HG, Yang XE, Razafindrabe BHN, Inouhe M (2010) The detoxification of lead in *Sedum alfredii* H. is not related to phytochelatins but the glutathione. J Hazard Mater 177:437–444

Gusman GS, Oliveira JA, Farnese FS, Cambraia J (2013) Mineral nutrition and enzymatic adaptation induced by arsenate and arsenite exposure in lettuce plants. Plant Physiol Biochem 71:307–314

Hamel LP, Nicole MC, Sritubtim S, Morency MJ, Ellis M, Ehlting J, Beaudoin N, Barbazuk B, Klessig D, Lee J, Martin J, Mundy J, Ohashi Y, Scheel D, Sheen J, Xing T, Zhang S, Seguin A, Ellis BE (2006) Ancient signals: comparative genomics of plant MAPK and MAPKK gene families. Trends Plant Sci 11:192–198

Hanikenne M, Talke IN, Haydon MJ, Lanz C, Nolte A, Motte P, Kramer U (2008) Evolution of metal hyperaccumulation required cis-regulatory changes and triplication of HMA4. Nature 453:391–395

Hao F, Wang X, Chen J (2006) Involvement of plasma-membrane NADPH oxidase in nickel-induced oxidative stress in roots of wheat seedlings. Plant Sci 170:151–158

Hayat S, Khalique G, Irfan M, Wani AS, Tripathi BN, Ahmad A (2012) Physiological changes induced by chromium stress in plants: an overview. Protoplasma 249:599–611

Himschoot E, Beeckman T, Friml J, Vanneste S (2015) Calcium is an organizer of cell polarity in plants. Biochim Biophys Acta 1853(9):2168–2172

Huang H, Gupta DK, Tian S, Yang X, Li T (2012) Lead tolerance and physiological adaptation mechanism in roots of accumulating and non-accumulating ecotypes of *Sedum alfredii*. Environ Sci Pollut Res 19:1640–1651

Islam E, Khan MT, Irem S (2015) Biochemical mechanisms of signaling: perspectives in plant under arsenic stress. Ecotoxicol Environ Saf 114:126–133

Ivanov AG, Krol M, Sveshnikov D, Selstam E, Sandstrom S, Koochek M, Park YI, Vasilev S, Bruce D, Oquist G, Huner NP (2006) Iron deficiency in cyanobacteria causes monomerization of photosystem I trimers and reduces the capacity for state transitions and the effective absorption cross section of photosystem I in vivo. Plant Physiol 141:1436–1445

Jaillais Y, Chory J (2010) Unraveling the paradoxes of plant hormone signaling integration. Nat Struct Mol Biol 17:642–645

Janik E, Grudzinski W, Gruszecki WI, Krupa Z (2008) The xanthophylls cycle pigments in *Secale cereal* leaves under combined Cd and high light stress conditions. J Phytochem Photobiol B 90:47–52

Jonak C, Okresz L, Bogre L, Hirt H (2002) Complexity, cross talk and integration of plant MAP kinase signalling. Curr Opin Plant Biol 5:415–424

Jonak C, Nakagami H, Hirt H (2004) Heavy metal stress. Activation of distinct mitogen-activated protein kinase pathways by copper and cadmium. Plant Physiol 136:3276–3283

Kanwar MK, Poonam BR (2015) Arsenic induced modulation of antioxidative defense system and brassinosteroids in *Brassica juncea* L. Ecotoxicol Environ Saf 115:119–125

Kapoor D, Sharma R, Handa N, Kaur H, Rattan A, Yadav P, Gautam V, Kaur R, Bhardwaj R (2015) Redox homeostasis in plants under abiotic stress: role of electron carriers, energy metabolism mediators and proteinaceous thiols. Front Environ Sci 3:1–12

Karuppanapanadian T, Moon JC, Kim C, Manoharan K, Kim W (2011) Reactive oxygen species in plants: their generation, signal transduction, and scavenging mechanisms. Aust J Crop Sci 5:709–725

Kasim WA (2006) Changes induced by copper and cadmium stress in the anatomy and grain yield of *Sorghum bicolor* (L) Moench. Int J Agric Biol 8:123–128

Kazan K (2015) Diverse roles of jasmonates and ethylene in abiotic stress tolerance. Trends Plant Sci 20:219–229

Kim CY, Liu Y, Thorne ET, Yang H, Fukushige H, Gassmann W, Hildebrand D, Sharp RE, Zhang S (2003) Activation of a stress-responsive mitogen-activated protein kinase cascade induces the biosynthesis of ethylene in plants. Plant Cell 15:2707–2718

Kim SH, Lee HS, Song WY, Choi KS, Hur Y (2007) Chloroplast-targeted BrMT1 (Brassica rapa type-1 metallothionein) enhances resistance to cadmium and ROS in transgenic Arabidopsis plants. J Plant Biol 50:1–7

Korpe DA, Aras S (2011) Evaluation of copper-induced stress on eggplant (*Solanum melongena* L.) seedlings at the molecular and population levels by use of various biomarkers. Mutat Res 719:29–34

Kovacik J, Klejdus B, Hedbavny J, Backor M (2010) Effect of copper and salicylic acid on phenolic metabolites and free amino acids in *Scenedesmus quadricauda* (Chloro-phyceae). Plant Sci 178:307–311

Krzesłowska M, Lenartowska M, Mellerowicz EJ, Samardakiewicz S, Woźny A (2009) Pectinous cell wall thickenings formation-A response of moss protonemata cells to lead. Environ Exp Bot 65:119–131

Krzesłowska M, Lenartowska M, Samardakiewicz S, Bilski H, Woźny A (2010) Lead deposited in the cell wall of Funaria hygrometrica protonemata is not stable–a remobilization can occur. Environ Pollut 158:325–338

Kumar K, Rao KP, Sharma P, Sinha AK (2008) Differential regulation of rice mitogen activated protein kinase kinase (MKK) by abiotic stress. Plant Physiol Biochem 46:891–897

Kumar M, Bijo AJ, Baghel RS, Reddy CRK, Jha B (2012) Selenium and spermine alleviate cadmium induced toxicity in the red seaweed *Gracilaria dura* by regulating antioxidants and DNA methylation. Plant Physiol Biochem 51:129–138

Kumar S, Asif MH, Chakrabarty D, Tripathi RD, Dubey RS, Trivedi PK (2015) Comprehensive analysis of regulatory elements of the promoters of rice sulphate transporter gene family and functional characterization of OsSul1;1 promoter under different metal stress. Plant Signal Behav 10:4. https://doi.org/10.4161/15592324.2014.990843

Labra M, Gianazza E, Waitt R, Eberini I, Sozzi A, Regondi S, Grassi F, Agradi E (2006) *Zea mays* L. protein changes in response to potassium dichromate treatments. Chemosphere 62:1234–1244

Lang I, Sassmann S, Schmidt B, Komis G (2014) Plasmolysis: loss of turgor and beyond. Plan Theory 3:583–593

Lee J, Bae H, Jeong J, Lee JY, Yang YY, Hwang I, Martinoia E, Lee Y (2003) Functional expression of a bacterial heavy metal transporter in Arabidopsis enhances resistance to and decreases uptake of heavy metals. Plant Physiol 133:589–596

Li Y, Dankher OP, Carreira L, Smith AP, Meagher RB (2006) The shoot-specific expression of gamma-glutamylcysteine synthetase directs the long-distance transport of thiol-peptides to roots conferring tolerance to mercury and arsenic. Plant Physiol 141:288–298

Li ZY, Xu ZS, He GY, Yang GX, Chen M, Li LC, Ma YZ (2012) Overexpression of soybean GmCBL1 enhances abiotic stress tolerance and promotes hypocotyl elongation in Arabidopsis. Biochem Biophys Res Commun 427:731–736

Lin YF, Aarts MGM (2012) The molecular mechanism of zinc and cadmium stress response in plants. Cell Mol Life Sci 69:3187–3206

Lin CW, Lin CY, Chang CC, Lee RH, Tsai TM, Chen PY, Chi WC, Huan HJ (2009) Early signalling pathways in rice roots under vanadate stress. Plant Physiol Biochem 47:369–376

Liu D, Zou J, Wang M, Jiang W (2008) Hexavalent chromium uptake and its effects on mineral uptake, antioxidant defence system and photosynthesis in *Amaranthus viridis* L. Bioresour Technol 99:2628–2636

Lou LQ, Shi GL, Wu JH, Zhu S, Qian M, Wang HZ, Cai QS (2015) The influence of phosphorus on arsenic uptake/efflux and As toxicity to wheat roots in comparison with sulfur and silicon. J Plant Growth Regul 34:242–250

Luan S, Kudla J, Rodriguez-Concepcion M, Yalovsky S, Gruissem W (2002) Calmodulins and calcineur in B-like proteins calcium sensors for specific signal response coupling in plants. Plant Cell 14:389–400

Maeser P, Thomine S, Schroeder JI, Ward JM, Hirschi K, Sze H, Talke IN, Amtmann A, Maathuis FJM, Sanders D, Harper JF, Tchieu J, Gribskov M, Persans MW, Salt DE, Kim SA, Guerinot ML (2001) Phylogenetic relationships within cation transporter families of Arabidopsis. Plant Physiol 126:1646–1667

Maestri E, Marmiroli M, Visioli G, Marmiroli N (2010) Metal tolerance and hyperaccumulation: costs and trade-offs between traits and environment. Environ Exp Bot 68:1–13

Maheshwari R, Dubey RS (2009) Nickel-induced oxidative stress and the role of antioxidant defence in rice seedlings. Plant Growth Regul 59:37–49

Maksymiec W (2007) Signaling responses in plants to heavy metal stress. Acta Physiol Plant 29:177–187

Malecka A, Jarmuszkiewicz W, Tomaszewska B (2001) Antioxidative defense to lead stress in subcellular compartments of pea root cells. Acta Biochim Pol 48:687–698

Małecka A, Piechalak A, Morkunas I, Tomaszewska B (2008) Accumulation of lead in root cells of *Pisum sativum*. Acta Physiol Plant 30:629–637

Małecka A, Derba-Maceluch M, Kaczorowska K, Piechalak A, Tomaszewska B (2009) Reactive oxygen species production and antioxidative defense system in pea root tissues treated with lead ions: mitochondrial and peroxisomal level. Acta Physiol Plant 31:1065–1075

Mani D, Kumar C (2014) Biotechnological advances in bioremediation of heavy metals contaminated ecosystems: an overview with special reference to phytoremediation. Int J Environ Sci Technol 11:843–872

Manimaran P, Mangrauthia SK, Sundaram RM, Balachandran SM (2015) Constitutive expression and silencing of a novel seed specific calcium dependent protein kinase gene in rice reveals its role in grain filling. J Plant Physiol 174:41–48

Márquez-García B, Horemans N, Cuypers A, Guisez Y, Córdoba F (2011) Antioxidants in *Erica andevalensis*: a comparative study between wild plants and cadmium-exposed plants under controlled conditions. Plant Physiol Biochem 49:110–115

Martinoia E, Klein M, Geisler M, Bovet L, Forestier C, Kolukisaoglu U, Mueller-Roeber B, Schulz B (2002) Multifunctionality of plant ABC transporters more than just detoxifiers. Planta 214:345–355

Mascher R, Lippmann B, Holzinger S, Bergmann H (2002) Arsenate toxicity: effects on oxidative stress response molecules and enzymes in red clover plants. Plant Sci 163:961–969

Masood A, Iqbal N, Khan NA (2012) Role of ethylene in alleviation of cadmium-induced photosynthetic capacity inhibition by sulphur in mustard. Plant Cell Environ 35:524–533

Matysiak R (2001) Content of carotenoid in needles of *Pinus sylvestris* L. growing in polluted area. Dendrobiology 46:39–42

Mauch-Mani B, Mauch F (2005) The role of abscisic acid in plant–pathogen interactions. Curr Opin Plant Biol 8:409–414

Metwally A, Safronova VI, Belimov AA, Dietz KJ (2005) Genotypic variation of the response to cadmium toxicity in *Pisum sativum* L. J Exp Bot 56:167–178

Milivojevic DB, Nikolic BC, Drinic G (2006) Effects of arsenic on phosphorous content in different organs and chlorophyll fluorescence in primary leaves of soybean. Biol Plant 50:149–151

Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R (2010) Reactive oxygen species homeostasis and signaling during drought and salinity stress. Plant Cell Environ 33:453–467

Mills RF, Krijger GC, Baccarini PJ, Hall JL, Williams LE (2003) Functional expression of AtHMA4, a P1B-type ATPase in the Zn/Co/Cd/Pb subclass. Plant J 35:164–175

Mills RF, Francini A, da Rocha PSCF, Baccarini PJ, Aylett M, Krijger GC, Williams LE (2005) The plant P1B-type ATPase AtHMA4 transports Zn and Cd and plays a role in detoxification of transition metals supplied at elevated levels. FEBS Lett 597:783–791

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Miyadate H, Adachi S, Hiraizumi A, Tezuka K, Nakazawa N, Kawamoto T, Katou K, Kodama I, Sakurai K, Takahashi H, Satoh-Nagasawa N, Watanabe A, Fujimura T, Akagi H (2011) OsHMA3, a P_{1B}-type of ATPase affects root-to-shoot cadmium translocation in rice by mediating efflux into vacuoles. New Phytol 189:190–199

Morina F, Jovanovic L, Mojovic M, Vidovic M, Pankovic D, Veljovic Jovanovic S (2010) Zinc-induced oxidative stress in *Verbascum thapsus* is caused by an accumulation of reactive oxygen species and quinhydrone in the cell wall. Physiol Plant 140:209–224

Mostofa MG, Fujita M (2013) Salicylic acid alleviates copper toxicity in rice (*Oryza sativa* L.) seedlings by upregulating antioxidative and glyoxalase systems. Ecotoxicology 22:959–973

Munzuroglu O, Geckil H (2002) Effects of metals on seed germination, root elongation, and coleoptile and hypocotyls growth in *Triticum aestivum* and *Cucumis sativus*. Arch Environ Contam Toxicol 43:203–213

Nagajyoti PC, Lee KD, Sreekanth TVM (2010) Heavy metals, occurrence and toxicity for plants: a review. Environ Chem Letters 8:199–216

Nakagami H, Pitzschke A, Hirt H (2005) Emerging MAP kinase pathways in plant stress signalling. Trends Plant Sci 10:339–346

Nazar R, Iqbal N, Masood A, Khan MIR, Syeed S, Khan NA (2012) Cadmium toxicity in plants and role of mineral nutrients in its alleviation. Am J Plant Sci 3:1476–1489

Nishida S, Tsuzuki C, Kato A, Aisu A, Yoshida J, Mizuno T (2011) AtIRT1, the primary ironuptake rransporter in the root, mediates excess nickel accumulation in *Arabidopsis thaliana*. Plant Cell Physiol 52:1433–1442

Norton GJ, Lou-Hing DE, Meharg AA, Price AH (2008) Rice-arsenate interactions in hydroponics: whole genome transcriptional analysis. Exp Bot 59:2267–2276

Opdenakker K, Remans T, Vangronsveld J, Cuypers A (2012) Mitogen-Activated Protein (MAP) kinases in plant metal stress: regulation and responses in comparison to other biotic and abiotic stresses. Int J Mol Sci 13:7828–7853

Ovecka M, Takac T (2014) Managing heavy metal toxicity stress in plants: biological and biotechnological tools. Biotechnol Adv 32:73–86

Paivoke A (1983) Anatomical responses of the roots of pea seedlings to lead and arsenate ions. Ann Bot Fenn 20:307–315

Paivoke AEA, Simola LK (2001) Arsenate toxicity to *Pisum sativum*: mineral nutrients, chlorophyll content, and phytase activity. Ecotoxicol Environ Saf 49:111–121

Panda SK, Baluska F, Matsumoto H (2009) Aluminium stress signaling in plants. Plant Signal Behav 4:592–597

Pandey N, Sharma CP (2002) Effect of heavy metals Co, Ni and Cd on growth and metabolism of cabbage. Plant Sci 163:753–758

Pandey N, Pathak GC, Pandey DK, Pandey R (2009) Heavy metals, Co, Ni, Cu, Zn and Cd, produced oxidative damage and evoke differential antioxidative responses in spinach. Braz J Plant Physiol 21:103–111

Parameswaran P, Jalili R, Tao L, Shokralla S, Gharizadeh B, Ronaghi M, Fire AZ (2007) A pyrosequencing-tailored nucleotide barcode design unveils opportunities for large-scale sample multiplexing. Nucleic Acids Res 35:e130

Patra M, Bhoumik N, Bandopadhyay B, Sharma A (2004) Comparison of mercury, lead and arsenic with respect to genotoxic effects on plant systems and the development of genetic tolerance. Environ Exp Bot 52:199–223

Pawlak-Sprada S, Arasimowicz-Jelonek M, Podgórska M, Deckert J (2011) Activation of phenylpropanoid pathway in legume plants exposed to heavy metals. Part I. Effects of cadmium and lead on phenylalanine ammonia-lyase gene expression, enzyme activity and lignin content. Acta Biochim Pol 58:6

Peralta JR, Gardea Torresdey JL, Tiemann KJ, Gomez E, Arteaga S, Rascon E (2001) Uptake and effects of five heavy metals on seed germination and plant growth in alfalfa (*Medicago sativa*). Environ Contam Toxicol 66:727–734

Persans MW, Nieman K, Salt DE (2001) Functional activity and role of cation-efflux family members in Ni hyperaccumulation in *Thlaspi goesingense*. PNAS 98:9995–10000

Pilon M, Cohu CM, Ravet K, Abdel-Ghany SE, Gaymard F (2009) Essential transition metal homeostasis in plants. Curr Opin Plant Biol 12:347–357

Popova LP, Maslenkova LT, Yordanova RY, Ivanova AP, Krantev AP, Szalai G, Janda T (2009) Exogenous treatment with salicylic acid attenuates cadmium toxicity in pea seedlings. J Exp Bot 53:1351–1365

Potocky M, Pejchar P, Gutkowska M, Jiménez-Quesada MJ, Potocká A, Alché Jde D, Kost B, Zársky V (2012) NADPH oxidase activity in pollen tubes is affected by calcium ions, signaling phospholipids and Rac/Rop GTPases. J Plant Physiol 169:1654–1663

Pourrut B, Perchet G, Silvestre J, Cecchi M, Guiresse M, Pinelli E (2008) Potential role of NADPH-oxidase in early steps of lead-induced oxidative burst in *Vicia faba* roots. J Plant Physiol 165:571–579

Pourrut B, Jean S, Silvestre J, Pinelli E (2011) Lead-induced DNA damage in *Vicia faba* root cells: potential involvement of oxidative stress. Mutat Res 726:123–128

Pourrut B, Shahid M, Douay F, Dumat C, Pinelli E (2013) Molecular mechanisms involved in lead uptake, toxicity and detoxifi cation in higher plants. In: Gupta DK, Corpas FJ, Palma JM (eds) Heavy metal stress in plants. Springer, Berlin, pp 121–147

Prasad SM, Dwivedi R, Zeeshan M (2005) Growth, photosynthetic electron transport, and antioxidant responses of young soybean seedlings to simultaneous exposure of nickel and UV-B stress. Photosynthetica 43:177–185

Przedpelska-Wasowicz EM, Wierzbicka M (2011) Gating of aquaporins by heavy metals in Allium cepa L. epidermal cells. Protoplasma 248:663–671

Qadir S, Jamshieed S, Rasool S, Ashraf M, Akram NA, Ahmad P (2014) Modulation of plant growth and metabolism in cadmium-enriched environments. Rev Environ Contam Toxicol 229:51–88

Rahman H, Sabreen S, Alam S, Kawai S (2005) Effects of nickel on growth and composition of metal micronutrients in barley plants grown in nutrient solution. J Plant Nutr 28:393–404

Rai A, Tripathi P, Dwivedi S, Dubey S, Shri M, Kumar S, Tripathi PK, Dave R, Kumar A, Singh R, Adhikari B, Bag M, Tripathi RD, Trivedi PK, Chakrabarty D, Tuli R (2011) Arsenic tolerances in rice (Oryza sativa) have a predominant role in transcriptional regulation of a set of genes including sulphur assimilation pathway and antioxidant system. Chemosphere 82:986–995

Rai A, Bhardwaj A, Misra P, Bag SK, Adhikari B, Tripathi RD, Trivedi PK, Chakrabarty D (2015) Comparative transcriptional profiling of contrasting rice genotypes shows expression differences during arsenic stress. Plant Genome 8:1–14

Rao KP, Richa T, Kumar K, Raghuram B, Sinha AK (2010) In silico analysis reveals 75 members of protein kinsase kinase kinase gene family in rice. DNA Res 17:139–153

Rodriguez-Serrano M, Romero-Puertas MC, Zabalza A, Corpas FJ, Gómez M, Del Río LA, Sandalio LM (2006) Cadmium effect on oxidative metabolism of pea (*Pisum sativum* L.) roots. Imaging of reactive oxygen species and nitric oxide accumulation in vivo. Plant Cell Environ 29:1532–1544

Rodriguez-Serrano M, Romero-Puertas MC, Pazmino DM, Testillano PS, Risueno MC, del Rio LA, Sandalio LM (2009) Cellular response of pea plants to cadmium toxicity: cross talk between reactive oxygen, nitric oxide and calcium. Environ Stress Adapt Stress 150:229–243

Rucinska R, Gwozdz EA (2005) Influence of lead on membrane permeability and lipoxygenase activity in lupine roots. Biol Plant 49:617–619

Rucinska-Sobkowiak R (2016) Water relations in plants subjected to heavy metal stresses. Acta Physiol Plant 38:257. https://doi.org/10.1007/s11738-016-2277-5

Rucinska-Sobkowiak R, Nowaczyk G, Krzesłowska M, Rabeda I, Jurga S (2013) Water status and water diffusion transport in lupine roots exposed to lead. Environ Exp Bot 87:100–109

Sahi SV, Sharma NC (2005) Phytoremediation of lead. In: Shtangeeva I (ed) Trace and ultratrace elements in plants and soils, Series advances in ecological researches. Witpress, Southampton, pp 209–222

Samardakiewicz S, Krzesłowska M, Bilski H, Bartosiewicz R, Wozny A (2012) Is callose a barrier for lead ions entering Lemna minor L. root cells? Protoplasma 249:347–351

Sanders D, Pelloux J, Brownlee C, Harper JF (2002) Calcium at the crossroads of signaling. Plant Cell 14:401–417

Schneider J, Labory CR, Rangel WM, Alves E, Guilherme LR (2013) Anatomy and ultrastructure alterations of *Leucaena leucocephala* (Lam.) inoculated with mycorrhizal fungi in response to arsenic-contaminated soil. J Hazard Mater 262:1245–1258

Schulz P, Herde M, Romeis T (2013) Calcium-dependent protein kinases: hubs in plant stress signaling and development. Plant Physiol 163:523–530

Schutzendubel A, Polle A (2002) Plant responses to abiotic stresses: heavy metal-induced oxidative stress and protection by mycorrhization. J Exp Bot 53:1351–1365

Schutzendubel A, Schwanz P, Terchmann T, Grossk Langeenfeld-Heyger R, Godbold DL, Polle A (2001) Cadmium-induced changes in antioxidative systems, hydrogen peroxide content, and differentiation in Scots pine roots. Plant Physiol 75:887–898

Seregin IV, Ivanov VB (2001) Physiological aspects of cadmium and lead toxic effects on higher plants. Russ J Plant Physiol 48:523–544

Seregin IV, Kozhevnikova AD (2006) physiological role of nickel and its toxic effects on higher plants. Russ J Plant Physiol 53:257–277

Shaibur MR, Kawai S (2011) Arsenic toxicity in Akitakomachi rice in presence of Fe^{3+}-citrate. Adv Environ Biol 5:1411–1422

Shakya K, Chettri MK, Sawidis T (2008) Impact of heavy metals (copper, zinc and lead) on the chlorophyll content of some mosses. Arch Environ Contam Toxicol 54:412–421

Shao HB, Chu LY, Shao MA (2008) Calcium as a versatile plant signal transducer under soil water stress. BioEssays 30:634–641

Shao HB, Chu LY, Jaleel CA, Manivannan P, Panneerselvam R, Shao MA (2009) Understanding water deficit stress-induced changes in the basic metabolism of higher plants-biotechnologically and sustainably improving agriculture and the ecoenvironment in arid regions of the globe. Crit Rev Biotechnol 29:131–151

Sharma P, Dubey RS (2005) Lead toxicity in plants. Braz J Plant Physiol 17:35–52

Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot 2012:217037. https://doi.org/10.1155/2012/217037

Shi GR, Cai QS (2008) Photosynthetic and anatomic responses of peanut leaves to cadmium stress. Photosynthetica 46:627–630

Shri M, Kumar S, Chakrabarty D, Trivedi PK, Mallick S, Misra P, Shukla D, Mishra S, Srivastava S, Tripathi RD, Tuli R (2009) Effect of arsenic on growth, oxidative stress and antioxidant system in rice seedlings. Ecotoxicol Environ Saf 72:1102–1110

Siddique A, Mumtaz M, Zaigham NA, Mallick KA, Saied S, Zahir E (2009) Heavy metal toxicity levels in the coastal sediments of the Arabian Sea along the urban Karachi (Pakistan) region. Mar Pollut Bull 58:1406–1414

Sidhu GPS, Bali AS, Bhardwaj R, Singh HP, Batish DR, Kohli RK (2018) Bioaccumulation and physiological responses to lead (Pd) in *Chenopodium murale* L. Ecotoxicol Environ Saf 151:83–90

Singh I, Shah K (2014) Exogenous application of methyl jasmonate lowers the effect of cadmium-induced oxidative injury in rice seedlings. Phytochemistry 108:57–66

Singh HP, Batish DR, Kaur G, Arora K, Kohli RK (2008) Nitric oxide (as sodium nitroprusside) supplementation ameliorates Cd toxicity in hydroponically grown wheat roots. Environ Exp Bot 63:158–167

Solioz M, Vulpe C (1996) CPx-type ATPases: a class of P-type ATPases that pump heavy metals. Trends Biochem Sci 2:237–241

Steffens B (2014) The role of ethylene and ROS in salinity, heavy metal, and flooding responses in rice. Front Plant Sci 5:685. https://doi.org/10.3389/fpls.2014.00685

Steiner F, Zoz T, Soares Pinto Junior A, Castagnara DD, Dranski JAL (2012) Effects of aluminum on plant growth and nutrient uptake in young physic nut plants. Semina: Ciencias Agrarias (Londrina) 33:1779–1788

Steinhorst L, Kudla J (2013) Calcium and reactive oxygen species rule the waves of signaling. Plant Physiol 163:471–485

Steinhorst L, Kudla J (2014) Signaling in cells and organisms-calcium holds the line. Curr Opin Plant Biol 22:14–21

Steudle E (2000) Water uptake by plant roots: an integration of views. Plant Soil 226:45–56

Steudle E (2001) The cohesion-tension mechanism and the acquisition of water by plant roots. Annu Rev Plant Biol 52:847–875

Stoeva N, Bineva T (2003) Oxidative changes and photosynthesis in Oat plants grown in As-contaminated soil. Bulg J Plant Physiol 29:87–95

Stoeva N, Berova M, Zlatev Z (2005) Effect of arsenic on some physiological parameters in bean plants. Biol. stress in sunflower (*Helianthus annuus* L.) by arbuscular mycorrhizal fungi. Pak J Bot 47:785–795

Sun Y, Veerabomma S, Abdel-Mageed HA, Foker M, Asami T, Yoshida S, Allen RD (2005) Brassinosteroid regulates fiber development on cultured cotton ovules. Plant Cell Physiol 46:1384–1391

Suzuki N (2005) Alleviation by calcium of cadmium-induced root growth inhibition in Arabidopsis seedlings. Plant Biotech 22:19–25

Swartjes FA, Breemen EMD, Otte PF, Beelen PV, Rikken MGJ, Tuinstra J (2007) Human health risks due to consumption of vegetables from contaminated sites. RIVM report 71101040. National Institute for Public Health and the Environment, Bilthoven

Szollosi R, Varga IS, Erdei L, Mihalik E (2009) Cadmium-induced oxidative stress and antioxidative mechanisms in germinating Indian mustard (*Brassica juncea* L.) seeds. Ecotoxicol Environ Saf 72:1337–1342

Tak HI, Ahmad F, Babalola OO (2013) Advances in the application of plant growth-promoting rhizobacteria in phytoremediation of heavy metals. Rev Environ Contam Toxicol 223:33–52

Thapa SS, Paudyal I, Khanal S, Paudel N, Mansberger SL, van Rens GH (2012) Central corneal thickness toxicity in Pisum sativum L. J Exp Bot 56:167–178

Theodoulou FL (2000) Plant ABC transporters. Biochim Biophys Acta 1465:79–103

Thomine S, Wang R, Ward JM, Crawford NM, Schroeder JI (2000) Cadmium and iron transport by members of a plant metal transporter family in Arabidopsis with homology to Nramp genes. Proc Natl Acad Sci U S A 97:4991–4996

Thomine S, Lelievre F, Debarbieux E, Schroeder JI, Barbier-Brygoo H (2003) AtNRAMP3, a multispecific vacuolar metal transporter involved in plant responses to iron deficiency. Plant J 34:685–695

Toth SZ, Schansker G, Garab G, Strasser RJ (2007) Photosynthetic electron transport activity in heat-treated barley leaves: the role of internal alternative electron donors to photosystem II. Biochim Biophys Acta 1767:295–305

Tripathi RD, Srivastava S, Mishra S, Singh N, Tuli R, Gupta DK, Maathuis FJM (2007) Arsenic hazards: strategies for tolerance and remediation by plants. Trends Biotechnol 25:158–165

Tripathi V, Parasuraman B, Laxmi A, Chattopadhyay D (2009) CIPK6, a CBL-interacting protein kinase is required for development and salt tolerance in plants. Plant J 58:778–790

Tuteja N (2007) Abscisic acid and abiotic stress signaling. Plant Signal Behav 138:1559–2316

Tuteja N, Mahajan S (2007) Calcium signaling network in plants: an overview. Plant Signal Behav 2:79–85

Tuteja N, Ahmad P, Panda BB, Tuteja R (2009) Genotoxic stress in plants: shedding light on DNA damage, repair and DNA repair helicases. Mutat Res 681:134–149

Valko M, Rhodes CJ, Moncol J, Izakovic M, Mazur M (2006) Free radicals, metals and antioxidants in oxidative stress-induced cancer. Chem Biol Interact 160:1–40

Van der Zaal BJ, Neuteboom LW, Pinas JE, Chardonnens AN, Schat H, Verkleij JA (1999) Overexpression of a novel Arabidopsis gene related to putative zinc-transporter genes from animals can lead to enhanced zinc resistance and accumulation. Plant Physiol 119:1047–1055

Vanhoudt N, Vandenhove H, Horemans N, Wannijn J, Bujanic A, Vangronsveld J, Cuypers A (2010) Study of oxidative stress related responses induced in *Arabidopsis thaliana* following mixed exposure to uranium and cadmium. Plant Physiol Biochem 48:879–886

Ventrella A, Catucci L, Piletska E, Piletsky S, Agostiano A (2011) Interactions between heavy metals and photosynthetic materials studied by optical techniques. Bioelectrochemistry 77:19–25

Verret F, Gravot A, Auroy P, Leonhardt N, David P, Nussaume L (2004) Overexpression of *AtHMA4* enhances root-to-shoot translocation of zinc and cadmium and plant metal tolerance. FEBS Lett 576:306–312

Vert G, Nemhauser JL, Geldner N, Hong F, Chory J (2005) Molecular mechanisms of steroid hormone signaling in plants. Annu Rev 21:177–201

Vesely T, Neuberg M, Trakal L, Szakova J, Tlustoa P (2011) Water lettuce *Pistia stratiotes* L. response to lead toxicity. Water Air Soil Pollut 223:1847–1859

Wang Z, Zhang Y, Huang Z, Huang L (2008) Antioxidative response of metal-accumulator and non accumulator plants under cadmium stress. Plant Soil 310:137–149

Wang S, Li R, Zhang Z, Feng J, Shen F (2014) Assessment of the heavy metal pollution and potential ecological hazardous in agricultural soils and crops of Tongguan, Shaanxi Province. J Environ Sci (China) 34:2313–2320

Xalxo R, Keshavkant S (2018) Hydrolytic enzymes mediated lipid-DNA catabolism and altered gene expression of antioxidants under combined application of lead and simulated acid rain in Fenugreek (*Trigonella foenum graecum* L.) seedlings. Ecotoxicology 27(10):1404–1413.

Xalxo R, Keshavkant S (2019) Melatonin, glutathione and thiourea attenuates lead and acid rain induced deleterious responses by regulating gene expression of antioxidants in *Trigonella foenum graecum* L. Chemosphere 221:1–10

Xalxo R, Yadu B, Chakraborty P, Chandrakar V, Keshavkant S (2017) Modulation of nickel toxicity by glycinebetaine and aspirin in *Pennisetum typhoideum*. Acta Biol Szeged 61:163–171

Xu FJ, Jin CW, Liu WJ, Zhang YS, Lin XY (2010) Pretreatment with H_2O_2 alleviates aluminum-induced oxidative stress in wheat seedlings. J Integr Plant Biol 53:44–53

Xu J, Zhu Y, Ge Q, Li Y, Sun J, Zhang Y, Liu X (2012) Comparative physiological responses of *Solanum nigrum* and *Solanum torvum* to cadmium stress. New Phytol 196:125–138

Yadav SK (2010) Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. S Afr J Bot 76:167–179

Yadu B, Chandrakar V, Keshavkant S (2017) Glycinebetaine reduces oxidative injury and enhances fluoride stress tolerance via improving antioxidant enzymes, proline and genomic template stability in *Cajanus cajan* L. South Afr J Bot 111:68–75

Yamaguchi H, Nishizawa N-K, Nakanishi H, Mori S (2002) IDI7, a new iron-regulated ABC transporter from barley roots, localizes to the tonoplast. J Exp Bot 53:727–735

Yang T, Poovaiah BW (2003) Calcium/calmodulin-mediated signal network in plants. Trends Plant Sci 8:505–512

Yeh CM, Chien PS, Huang HJ (2007) Distinct signalling pathways for induction of MAP kinase activities by cadmium and copper in rice roots. J Exp Bot 58:659–671

Zengin FK, Munzuroglu O (2006) Toxic effects of cadmium (Cd^{++}) on metabolism of sunflower (*Helianthus annus*) seedlings. Acta Agric Scand B 56:224–229

Zhang F, Zhang H, Wang G, Xu L, Shen Z (2009) Cadmium-induced accumulation of hydrogen peroxide in the leaf apoplast of *Phaseolus aureus* and *Vicia sativa* and the roles of different antioxidant enzymes. J Hazard Mater 168:76–84

Zhang M, Pan J, Kong X, Zhou Y, Liu Y (2012) ZmMKK3, a novel maize group B mitogen-activated protein kinase kinase gene, mediates osmotic stress and ABA signal responses. J Plant Physiol 169:1501–1510

Chapter 15
Ecophysiology of Plants Under Cadmium Toxicity: Photosynthetic and Physiological Responses

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Contents

Abstract Cadmium (Cd) is among the elements that exhibit a pronounced toxic effect on a variety of physiological and metabolic processes. Photosynthesis is one of the main processes of autotrophic organisms. The negative effect of cadmium on the photosynthetic apparatus leads to inhibition of many metabolic pathways that ensure the vital activity of plants. Cadmium can have a direct effect on photosystem II, decreasing the electron transfer rate and inhibiting the oxygen-generating

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complex. Besides that, under the cadmium influence, there is a violation of the structure and synthesis of pigments, a quantity reduction in open reaction center (RC), as well as inhibition of enzymes in the dark phase of photosynthesis. In addition, Cd can indirectly affect photosynthesis as a result of changes in plant water metabolism, stomata closure, and reduction in CO_2 availability for assimilation centers. Under oxidative stress caused by cadmium, the integrity of thylakoid membranes is impaired, as well as the rate of photosynthesis decreases as a result of inhibition of the activity of CO_2 fixation enzymes. At the level of the whole plant, disruption of the photosynthesis process is accompanied by a decrease in the growth rate and productivity of plants. The review discusses the toxic effects of cadmium both directly on photosynthesis and on other processes associated with it.

Keywords Cadmium · Heavy metals stress · Photosynthesis · Chlorophyll fluorescence

Abbreviations

Cd	Cadmium
Chl	Chlorophyll
C_i	Intercellular CO_2 concentration
E	Transpiration rate
ETR	Electron transport rate
F_0	Minimal level of chlorophyll fluorescence
F_m	Maximum fluorescence of dark-adapted leaves
F_v	Variable fluorescence of dark-adapted state
$F_\mathrm{v}/F_\mathrm{m}$	Potential efficiency of PSII
g_s	Stomatal conductance
OEC	Oxygen evolving complex of PSII
P_N	Net photosynthetic rate
$P_\mathrm{N}/C_\mathrm{i}$	Instantaneous carboxylation efficiency
PSII	Photosystem II
$\mathrm{Q_A}$ and $\mathrm{Q_B}$	Bound plastoquinones of PSII
qN and NPQ	Nonphotochemical quenching
qP	Photochemical quenching
RC	Reaction center
ROS	Reactive oxygen species
Rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
$\varphi P_0 = \mathrm{TR_0/ABS}$	Maximum quantum yield for primary photochemistry
Φ_PSII	Effective quantum yield of PSII photochemistry

15.1 Introduction

The current rapid development of industry is accompanied by an increase in the amount of toxic heavy metals in the environment, pollution of which is gradually spreading to wider areas of our planet as a result of anthropogenic activities (Silva et al. 2014). Cadmium (Cd) is ubiquitous in the soil and is distinguished by its mutagenic and carcinogenic properties (Hasan et al. 2011). Among other heavy metals, cadmium has one of the highest emission rates in the soil (Wei and Yang 2010; Zhao et al. 2010), with agricultural areas contaminated higher than urban soils (Wang et al. 2015). The use of phosphate and organic fertilizers, soil liming, sewage sludge, industrial emissions, and the mining and metallurgy industries are anthropogenic sources of Cd (Sanità di Toppi and Gabbrielli 1999; Irfan et al. 2014). Cd consumption with food is mainly due to the use of crop products (Mo et al. 2009). Cadmium can cause serious human health problems even at low concentrations (Takahashi et al. 2011). At the same time, there are no threshold values of toxic concentrations of Cd (Clemens et al. 2013).

The negative effects of heavy metals are found in all autotrophic organisms. Cadmium is a nonnutritive heavy metal that can be very phytotoxic at low concentrations (Masood et al. 2012). The content of soluble Cd is usually about 0.01–0.7 mg kg^{-1} of soil (Kovalchuk et al. 2001), but can reach 2.2–2.5 mg kg^{-1} (Samani Majd et al. 2007). Cd is easily absorbed from the soil and transferred to the aboveground organs of plants (Gallego et al. 2012), which always leads to a significant decrease in plant growth parameters (Ci et al. 2009; Li et al. 2013), causes leaf chlorosis (Liu et al. 2011), leaf rolling, and browning of root tips (Najeeb et al. 2011), which negatively affects reproduction (Xiong and Peng 2001) and induces plant senescence (Hall 2002; Maksymiec 2007) due to significant changes in many metabolic processes (Baryla et al. 2001; Singh et al. 2006)—such as photosynthesis (Wan et al. 2011), transpiration rate (*E*; Bazzaz and Govindjee 1974), chlorophyll (chl) synthesis (Jain et al. 2007), change in the chloroplast ultrastructure (Sandalio et al. 2001), stomatal conductivity (Burzyński and Żurek 2007), sugar synthesis (Moya et al. 1993), and nutrient intake (Pinto et al. 2004; Rodríguez-Serrano et al. 2009; Zhang et al. 2014)—as well as plant death (Faller et al. 2005; He et al. 2008; Hayat et al. 2014). At the molecular level, exposure to Cd can damage many vital macromolecules, such as nucleic acids, enzymes, and membrane lipids (Watanabe et al. 2003).

15.2 Cd Uptake Into the Plant

In soil, Cd^{2+} is present in soluble form and therefore is quickly absorbed by plants through the root system (Krevešan et al. 2003), which is the first place of the negative influence of these ions (Krupa and Baszynski 1995). Uptake and accumulation of Cd causes a reduction in growth and damage to the root tips (Valentovičová et al. 2010), an imbalance in the absorption of mineral nutrients and water (Gouia et al. 2000), and enzyme inactivation (Siedlecka and Krupa 1999; Soudek et al. 2014). All this causes a significant reduction in biomass, restricting the development of plants (Riaz et al. 2014), or even plant death at high Cd concentrations. At the molecular level, Cd causes irreversible changes in protein conformation due to interactions with sulfhydryl (SH) groups (Dafré et al. 1996), changes in the permeability of cell walls and membranes due to interactions with nucleophilic groups (Ramos et al. 2002), and changes in redox cell balance.

The degree of Cd absorption by the roots depends on the availability of the metal in the root formation environment (Soudek et al. 2014; Xue et al. 2018), as well as soil characteristics and temperature. Plants do not have a system for eliminating Cd from root cells, and the movement of the absorbed metal mainly occurs in a passive manner with a transpiration flow (Gallego et al. 2012). Part of uptaken Cd is adsorbed in the cell wall of the root cortex by extracellular saccharides (Bekasova et al. 2002). On the other hand, Cd can enter the plant cell using a transport system that participates in the absorption of micronutrient, for example, using transmembrane carriers of divalent metals on the plasma membrane, most likely via Ca^{2+} channels (Song et al. 2017). Absorbed Cd either enters the vacuole of the roots, or moves to the xylem for transport to aboveground organs with a transpiration flow (Sanità di Toppi and Gabbrielli 1999). The Cd accumulation in shoots linearly depends on the transpiration rate (Liu et al. 2016).

In most higher plants, there are mechanisms that prevent the movement of Cd from roots to shoots (Baker 1981). The ratio of Cd held in the roots and translocated to the leaves varies significantly among different plant species (Ekvall and Greger 2003; Tran and Popova 2013). Among the plants studied are *Noccaea caerulescens* (Lombi et al. 2002), *Sorghum bicolor* (Xue et al. 2018), *Oryza sativa* (He et al. 2008), *Brassica napus* (Larsson et al. 1998), *Dittrichia viscosa* (Fernández et al. 2013), *Lactuca sativa*, *Hordeum vulgare* (Akhter et al. 2012), *Brassica juncea* (Mohamed et al. 2012), *Cassia alata* (Silva et al. 2018), and *Carthamus tinctorius* (Moradi and Ehsanzadeh 2015), which have a specific mechanism for the Cd accumulation in the roots that reduce the transport of Cd to the shoots (Baker 1981; Pinto et al. 2004; Degl'Innocenti et al. 2014). This strategy promotes the adaptation of plants to living in soils with a high content of heavy metals (Tran and Popova 2013; Moradi and Ehsanzadeh 2015; Liu et al. 2018). A decrease in transpiration rate is often accompanied by a decrease in the influx of Cd from the roots to the shoots through the xylem and the accumulation of Cd in the roots (Fan et al. 2011). Transporting Cd is an energy-intensive process with ATP consumption produced during photosynthesis and respiration. The negative impact of Cd on these processes may indirectly contribute to the slowing down of metal translocation to aboveground organs and its accumulation in the roots (Fernández et al. 2013), although for most plants Cd is toxic even at very low concentrations in the root medium.

Total accumulation and related Cd tolerance vary greatly between different plant species, varieties, and populations (Sorić et al. 2011; Šimić et al. 2012; Franić et al. 2017). Genotypic variations in absorption and accumulation of Cd were found in

Betula pendula, *Picea abies*, *Pinus sylvestris* (Österås et al. 2000), safflower (Pourghasemian et al. 2013), *Oryza sativa* (Liu et al. 2007), and *Triticum* (Cakmak et al. 2000; Greger and Löfstedt 2004). Resistance to stress is due to the ability of the plants to accumulate various concentrations of Cd, which vary depending on the type of tissue (Wang et al. 2008). As a result of root sequestration, a limited movement of Cd is observed both in the symplast as a result of metal localization in the vacuoles and in the apoplast due to the development of apoplastic barriers (Lux et al. 2011). From the root to the stem and leaves, Cd is transported at a very weak speed (Ernst et al. 1992) that, however, significantly exceeds the translocation of other heavy metals (Burzyński and Kłobus 2004). The effect of decreasing Cd concentration in leaves can be observed as a result of increased plant growth, that is, a dilution effect (Ekvall and Greger 2003). On the other hand, redistribution of Cd to old leaves may be one of the mechanisms of stress adaptation in shoots (Maria et al. 2013). Another mechanism for increasing tolerance to Cd toxicity in leaves may be metal isolation in vacuoles (Wu et al. 2013).

Cd accumulation in the tissues of most plants gradually decreases in the direction from the roots to the leaves (Silva et al. 2018). The critical toxic concentration of Cd in the roots is higher than that in the stem and leaves, which are less tolerant to metal accumulation. Moreover, it is these tissues that are more susceptible to oxidative stress (Silva et al. 2018).

To quantify the degree of metal transfer between plant organs, several factors can be used: for example, the bioconcentration factor (BCF)—calculated as $BCF = Cd_{pt}/Cd_{ns}$, where Cd_{pt} is the Cd concentration in plant tissue and Cd_{ns} is the Cd concentration in the soil (Yoon et al. 2006)—or the translocation factor (TF), obtained as $TF = Cd_s/Cd_r$, where Cd_s is the Cd concentration in the shoots and Cd_r is the Cd concentration in roots. For example, *Cassia alata* is considered a Cd-hyperaccumulator, since is BCF >1 in this plant (Silva et al. 2018). TF depends on the type and concentration of Cd in the solutions with which plants are treated (Sterckeman et al. 2011).

15.3 Plant Growth Inhibition

Excessive Cd can disrupt the vital processes of photosynthesis, respiration, and nitrogen metabolism, resulting in reduced plant growth (Sanità di Toppi and Gabbrielli 1999). A decrease in plant biomass is the best-known symptom of phytotoxicity of Cd (Feng et al. 2010; Akhter et al. 2012). Growth inhibition by even small amounts of Cd has been shown in various plant species, including *Medicago truncatula* (Saeidi et al. 2012), *Cucumis sativus* (Burzyński and Kłobus 2004), *Pinus sylvestris* (Ekvall and Greger 2003), *Juncus effuses* (Najeeb et al. 2011), *Helianthus annuus* (Laspina et al. 2005), *Vigna unguiculata* (Santos et al. 2018), *Ricinus communis*, *Brassica juncea* (Bauddh and Singh 2012), *Carthamus tinctorius* (Moradi and Ehsanzadeh 2015), barley, maize (Lysenko et al. 2015), *Brassica juncea* (Iqbal et al. 2010), tomatoes (Cherif et al. 2012), and *Atriplex* plants (Nedjimi and Daoud 2009).

The Cd effect on water and ionic plant relationships inhibits growth and photosynthesis. Cd treatment negatively affects water metabolism and is accompanied by a change in water potential, *E*, and relative water content (RWC), which correlate with the general state of plant metabolism (Flower and Ludlow 1986). Oxidation by cadmium of SH group of membrane transport proteins (Lösch 2004) leads to inhibition of the aquaporin activity (Przedpelska-Wasowicz and Wierzbicka 2011) and, as a result, impedes the water movement in plants (Irfan et al. 2014). Inhibition of H^+-ATPase activity on membranes leads to impaired absorption of nutrient ions and affects the cell division (Zhang et al. 2009; Janicka-Russak et al. 2012), which can lead to a reduction in leaf surface, premature senescence, and, as a result, cause a decrease in the total photosynthesis of plants (Krupa et al. 2002).

Cadmium toxicity adversely affects all aspects of plant growth, including root dry masses (Najeeb et al. 2011), shoot dry masses, net dry masses, plant growth, and total leaf area per plant (Li et al. 2013; Moradi and Ehsanzadeh 2015). A decrease in leaf area (Per et al. 2016) leads to a decrease in the efficiently used solar energy in the process of photosynthesis, which causes a decrease in the accumulation of dry matter in the plant. Cd stress inhibits cell division and root development in higher plants (Yi and Meng 2003). Excessive Cd caused a decrease in net dry masses and plant height, and also caused the formation of chlorotic or necrotic areas on old rice leaves (He et al. 2008). Wheat and rice showed a decrease in the length of shoots and roots, as well as net dry masses (Moya et al. 1993). A significant growth retardation and reduction in the total leaf area per plant was found in rape plants (Larsson et al. 1998) and in safflower genotypes (Moradi and Ehsanzadeh 2015). Cd treatment of rice seedlings caused a reduction in the length of the shoots and roots along with an increase in the dry masses/fresh masses ratio—an increase in this ratio due mainly to a decrease in fresh masses with almost constant dry masses (Moya et al. 1993). This indicates the effect of Cd on plant–water relations.

To explain stress-induced growth retardation, Potters et al. (2007, 2009) proposed the concept of stress-induced syndrome, according to which, during the implementation of the general acclimatization strategy, individual sublethal stresses can trigger a set of morphogenic reactions in order to reduce the negative impact of stress through directed growth processes. Apparently, part of this strategy is the intensive formation of reactive oxygen species (ROS) and an increase in antioxidant activity, as well as a change in the effects of plant hormones. Growth reduction can also occur as a result of the effects of Cd on plant development processes, namely photosynthesis and metabolite transport (Prasad and Zeeshan 2005; Burzyński and Żurek 2007), as well as cell division (Dalla Vecchia et al. 2005).

The degree of Cd toxicity for a plant depends on its content both in the soil and directly in the plant tissue. For example, according to Tian et al. (2015), with a low total content of Cd in the soil ($Cd \leq 5$ mg kg^{-1}), the sweet sorghum phenotype does not undergo noticeable changes. However, in pea plants, growth inhibition occurred already at 5 μM Cd^{2+}, but without changing the level of chlorophyll (Wodala et al. 2012). A high total Cd content (up to 30 mg kg^{-1}) in *Sorghum bicolor* decreased plant height and dry weight (Wang et al. 2017), length and weight of roots, shoot weight, and area and number of leaves (Xue et al. 2018). However, when growing plants in nutrient solutions, a significant decrease in sorghum biomass occurred already at 10 mg Cd L^{-1} (Pinto et al. 2004), that is, Cd exposure depends on the growing medium. According to Gill et al. (2012), in garden cress, a high total Cd content in the soil (100 mg kg^{-1}) changes photosynthesis, nitrogen metabolism, and plant growth, but with a low Cd content, sulfur metabolism and antioxidant systems are activated.

A decrease in the growth of plants treated with Cd can occur as a result of impaired CO_2 fixation, which leads to a decrease in the net photosynthetic rate (P_N) (Ahammed et al. 2012), as well as due to the effects on the photosynthetic apparatus itself and membrane permeability (Fernández et al. 2013; Fan et al. 2011; Deng et al. 2014). Under these conditions, normal root growth is impaired, which limits the ability of the plant to absorb and transport nutrients. The suppression of plant growth by cadmium strongly correlates with a decrease in the chlorophyll content (Ali et al. 2015) and, as a consequence, a decrease in the rate of photosynthesis (Li et al. 2013), which can occur as a result of a violation of the pigments' ultrastructure (Feng et al. 2010).

In addition to higher plants, Cd greatly limits growth and disrupts division (Laube et al. 1980) and ultrastructure (Fernandez-Piñas et al. 1995) of microalgae cells. Numerous studies have been conducted on different species of algae (Khoshmanesh et al. 1996; Nagel et al. 1996; Mendoza-Cozalt et al. 2002; Talarico 2002; Thapar et al. 2008; Afkar et al. 2010). For example, in *Koliella antarctica*, at a high Cd concentration, an increase and deformation of cells, a change in the structure of the cytoplasm, rupture of the chloroplast membranes, and disorganization of thylakoids were observed (La Rocca et al. 2009). With a high concentration of Cd in *Koliella antarctica* (La Rocca et al. 2009), there was an increase and deformation of cells, altered structures of the cytoplasm, chloroplast sheath breaks, and disorganization of thylakoids.

In microalgae, a significant amount of accumulated Cd was associated with cell wall components (Zhou et al. 1998), which negatively affects the absorption of nutrients into cells (La Rocca et al. 2009). Cadmium may compete with other divalent cations, mainly Ca^{2+}, for the extracellular binding sites of specific membrane transporters (Zhao et al. 2002) that can lead to changes in the cellular level of Ca^{2+}, an essential element for cell growth and development.

15.4 Stomata Activity

In plants, there is an effective translocation of metal from the root to the shoot, which leads to the accumulation of Cd in the leaves. Cadmium translocation into leaves is carried out by long-distance transport, which depends on the rate of transpiration (E) and stomatal conductance (g_s). Cadmium reduces the stomatal frequency (Barceló et al. 1988), g_s (Baryla et al. 2001), and the associated CO_2 uptake (Asgher et al. 2014). This may have an indirect effect on photosynthesis by reducing the concentration of intracellular CO_2 available for assimilation, which may lead to a decrease in P_N and E (Shi and Cai 2008; Ahammed et al. 2013; Xue et al. 2018).

The decrease in g_s level in plants is due to stomata closure as a result of exposure to guard cells by Cd (Wan et al. 2011; Moradi and Ehsanzadeh 2015). Apparently, cadmium destroys the regulation of Ca^{2+} transporters, which leads to a decrease in the absorption or use of CO_2 and, ultimately, to a decrease in photosynthesis (Pietrini et al. 2010). Thus, the likely cause of Cd's influence on stomatal movement and plant–water relations associated with them could be interference of Cd in ionic movements (K^+ and Ca^{2+}) in stomatal guard cells (Poschenrieder et al. 1989; Nedjimi and Daoud 2009). Cadmium can also inhibit stomatal opening by reducing cell wall elasticity (Barceló et al. 1986). In addition, the influence of Cd on the biosynthesis of abscisic acid is not excluded.

The effect of stomatal closure, and the associated decrease in g_s, on photosynthetic ability is due to a change in intercellular CO_2 concentration (C_i) (Seemann and Critchley 1985), which leads to a restriction of CO_2 supply for assimilation into chloroplasts. The change in C_i in plants subjected to Cd stress is shown in mung bean (Wahid et al. 2008), safflower (Moradi and Ehsanzadeh 2015), and rape (Ali et al. 2015). However, it should be noted that a decrease in the efficiency of the Rubisco enzyme, by which the carboxylation process is carried out (Hasan et al. 2011), may cause C_i to increase (Barbosa et al. 2014).

There is a correlation between a decrease in instantaneous carboxylation efficiency (P_N/C_i) and an increase in C_i, which indicates inhibition of CO_2 absorption by Cd (Nwugo and Huerta 2011; Santos et al. 2018). The fall in P_N, associated with an increase in C_i, can be directly related to the influence of stressful conditions on the activity of photosynthesis. It can often be observed that a decrease in the photosynthesis rate occurs regardless of the stomata diffusion parameters, which may be due to a change in the efficiency of the photosynthetic apparatus or its size (Seemann and Critchley 1985). According to Moradi and Ehsanzadeh (2015), a decrease in P_N under the Cd influence can only be partially associated with a decrease in g_s, and reduction in photosynthesis mainly involved nondiffusion restrictions.

Stomata closure is accompanied by a decrease in E, which limits the transport of Cd from roots to shoots and minimizes the negative effects of Cd (Gratão et al. 2015). Transpiration rate reduction by Cd has been shown in honeysuckle (Jia et al. 2015), aquatic fern (Deng et al. 2014), wheat (Hayat et al. 2014), and tomato (Degl'Innocenti et al. 2014). In addition, Januškaitienė (2010) reported a decrease in water-use efficiency (WUE) of *Pisum sativum* and *Hordeum vulgare* plants subjected to Cd stress. WUE reflects the instantaneous gas exchange state of the plant (Pinzón-Torres and Schiavinato 2008) and shows the amount of fixed carbon per unit of water lost (Boutraa et al. 2010).

The effect of Cd depends on the plant species and may be associated with their anatomical features and a decrease in pigment content. For example, in *Arachis hypogaea*, Cd initiated an increase in the number of stomata and a decrease in their length in the epidermis of the leaf (Shi and Cai 2008). However, small but numerous stomata were characterized by high productivity in the CO_2 adsorption with minimal loss of water, which is typical for xerophyte plants (Sundberg 1986; Bosabalidis and Kofidis 2002). Gas exchange of plants may also depend on the anatomical features of the leaves. It is generally accepted that a large volume of palisade parenchyma corresponds to a large surface area of CO_2 absorption (Rhizopoulou and Psaras 2003). Mesophyll compartmentalization promotes less water loss, but reduces tissue conductivity for CO_2 (Terashima 1992; Miyazawa and Terashima 2001). Treatment of Cd leads to expansion of the lamina, upper epidermis, and thickness of the palisade parenchyma (Shi and Cai 2008). These anatomical features may contribute to a decrease in g_s and E and, consequently, to a P_N decrease.

The degree of toxicity of Cd in the leaves depends on its concentration. In the leaves of barley seedlings, Cd at a high concentration (80 μM and above) had a pronounced damaging effect until necrotic spots appeared, in which the metal may be excluded (Pietrini et al. 2010). However, with small concentrations or prolonged accumulation, Cd also causes a marked decrease in leaf development, but often there are no noticeable effects at the photosynthetic level, which may be due to the inclusion of efficient metal compartmentalization and/or detoxificant–repair mechanisms. Degl'Innocenti et al. (2014) also showed no effect of Cd on g_s and E, which indicates that reduction in P_N in Cd-treated plants is not associated with stomatal limitation, which was also confirmed by unchanged C_i values. In a study by Liu et al. (2018), Cd with a total content of ≤ 4 mg kg^{-1} of soil did not significantly affect the conductivity of CO_2, as a result of adaptation to the environment already at Cd ≤ 2 mg kg^{-1}.

15.5 Chloroplast Degradation

Due to a number of defense mechanisms, only very small amounts of Cd accumulate in chloroplasts (Lysenko et al. 2015). On the path of Cd movement from soil to chloroplasts is a series of barriers in the form of selective permeability of membranes and heavy metal immobilization mechanisms (Siedlecka and Krupa 1999). In leaves, cadmium can bind to polysaccharides of the cell wall or move in vacuoles. There are plants that can accumulate Cd in trichomes or isolate on the surface of leaves (Choi et al. 2001). However, a small portion of Cd remains, which penetrates into the chloroplasts.

In some microalgae, more than half of the total amount of Cd in the cell can be concentrated in chloroplasts (Nagel et al. 1996; Mendoza-Cozalt et al. 2002). However, the degree of compartmentalization of Cd strongly depends on the cells' structure in different microalgae species. For example, *Euglena* cells do not have cell walls and vacuoles and therefore approximately 60% of Cd accumulates in chloroplasts (Mendoza-Cozalt et al. 2002). The opposite situation is observed in *Audouinella saviana*, in which Cd is absent in chloroplasts, since this alga has cell walls and vacuoles (Talarico 2002).

In higher plants, the amount of Cd in chloroplasts is species-specific and depends on the time of metal accumulation. However, data on the accumulation of Cd in plant chloroplasts vary greatly among different authors, since the accumulation of

Cd in chloroplasts depended little on the concentration of metal in the soil (Lysenko et al. 2015). For example, in *Brassica napus*, chloroplasts accumulated 0.02% of leaf Cd over a long period (Baryla et al. 2001), while in *Phragmites australis*, 10–15% (Pietrini et al. 2003).

Exposure to Cd leads to degradation of the chloroplasts' structure (Horváth et al. 1996; Maksymiec 2007), mainly as a result of the destruction of thylakoid proteins and membranes (Skórzyńska-Polit and Baszyński 1997). In addition, chlorophyll degradation can occur enzymatically due to Cd-inducible chlorophyllase (Hasan et al. 2011). The presence of Cd reduces the number of chloroplasts when calculated per cell and unit leaf area (Fagioni et al. 2009). However, there are observations when the net CO_2 assimilation ratio per unit leaf area decreases, but does not change per unit chlorophyll (Pietrini et al. 2003).

Li et al. (2016) observed a Cd-induced reduction of Ca^{2+} content in the roots, stems, and leaves of *Allium fistulosum*. A decrease in the concentration of Ca^{2+} after exposure to Cd causes damage to intracellular binding proteins, which leads to disruption of membranes integrity (Lu et al. 2010). In barley plants, Cd treatment reduced the K^+ content in both the thylakoids and stroma of the chloroplast, as well as the Mn^{2+} concentration in thylakoids. In addition, in the presence of Cd, there is a decrease in the content of Cu^{2+} in thylakoids and Ca^{2+} in the stroma, but an increase in Ca^{2+} and Fe in thylakoids and Mg^{2+} in the stroma is simultaneously observed (Lysenko et al. 2019). After Cd treatment, a decrease in Mg^{2+} was also observed in leaves, stems, and roots (Liu et al. 2015). In the roots and leaves, some researchers found a decrease also in the Fe and Mn content (Basa et al. 2014; Ali et al. 2015). Cadmium stress greatly reduces the Cu^{2+} and Zn^{2+} content in chloroplasts (Tang et al. 2013; Santos et al. 2018). The absorption of Zn^{2+} in chloroplasts may reduce due to the competition of Zn^{2+} with Cd^{2+} for space in the carrier, while the treatment of Cd does not reduce the total content of Zn^{2+} in the leaves (Gallego et al. 2012).

Lysenko et al. (2019) showed that after Cd treatment, the amount of Ca^{2+} in the stroma decreased when calculating per mg of Chl in the whole chloroplast, but increased in thylakoids, while the content of Mg^{2+} in the stroma increased with a constant content in thylakoids. Since, compared with Mg^{2+} and Ca^{2+}, the accumulation of Cd^{2+} was insignificant, competition between these metals was unlikely. This process may be a plant defense mechanism against the penetration of Cd^{2+} into the thylakoids, and Ca^{2+} may be an effective competitive inhibitor of the action of Cd^{2+} on the oxygen evolving complex (OEC; Faller et al. 2005), while Mg^{2+} does not appear to be involved in these events (Sigfridsson et al. 2004). Most likely, part of Ca^{2+} is transported from the stroma to thylakoids, while Mg^{2+} is sent to the stroma. This may serve as a mechanism for protecting thylakoids from exposure to Cd^{2+}. Moreover, the total concentration of divalent cations in chloroplasts does not change.

Under the influence of high Cd concentrations, chlorophyll (Chl) is degraded in plant leaves (Pietrini et al. 2003; Shi and Cai 2008; Wan et al. 2011; Silva et al. 2012; Liu et al. 2018; Xue et al. 2018), although a decrease in the carotenoid (Car) content was also noted (He et al. 2008; Shi and Cai 2008; Moradi and Ehsanzadeh 2015). A decrease in Chl content can partially explain the decrease in P_N observed with Cd stress (Xue et al. 2018). Cd can interfere with Chl synthesis (Burzyński and

Kłobus 2004; Laspina et al. 2005; Nedjimi and Daoud 2009; Moradi and Ehsanzadeh 2015) by inhibiting Δ-aminolevulinic acid dehydratase (EC 4.2.1.24) and protochlorophyllide reductase (EC 1.3.1.33; Ci et al. 2010), due to the interaction of Cd with sulfhydryl groups (Prasad and StrzaŁka 1999). The effect of Cd on the Chl content can also be carried out indirectly due to a nutritional deficiency (Van Assche and Clijsters 1990). Cadmium inhibits Fe uptake by roots, which can lead to leaf chlorosis (Siedlecka and Krupa 1999). Analogous results were obtained in the *Brassica juncea* leaves (Ebbs and Uchil 2008), although Pietrini et al. (2003) exclude the chlorophyll loss possibility due to low levels of Fe in the leaves. Chl and Car levels may also fall as a result of oxidative stress caused by Cd (Cherif et al. 2012).

Cd ions have a constant valence, and therefore its effect on the redox balance of the cell can be carried out indirectly, apparently by substituting divalent metals in enzymes (Maret and Moulis 2013). Cd^{2+} can replace Mg^{2+} in tetrapyrrole centers of Chl, which causes molecular degradation of the light-harvesting complex II (LHCII) (Gillet et al. 2006; Wang et al. 2014). Perhaps this process is one of the main mechanisms of the negative effect of Cd on plant photosynthesis (Küpper et al. 1998). However, the Cd^{2+}/Chl ratio in plant chloroplasts under natural conditions is very low (1/1000) (Lysenko et al. 2015). The maximum Cd^{2+}/Chl ratio reaches 1/257 (Geiken et al. 1998). However, according to Lysenko et al. (2015), Cd^{2+} affects only a very insignificant part of Chl antennas, and therefore the widespread opinion about the significant effect of ion substitution in Chl on plant photosynthetic productivity should be considered insolvent.

Many studies have reported that as Cd-induced leaf chlorosis develops, the ratio Chl *a*/*b* increases (Shi et al. 2003), although Shi and Cai (2008) in *Arachis hypogaea* observed only synchronous mixing of both Chl types. The value of Chl *a*/*b* can increase as a result of an increase in the content of Chl *a*, as well as a decrease in the content of Chl *b*. In addition, leaf chlorosis can be caused by both direct and indirect effects of Cd on the content of both types of Chl (Ebbs and Uchil 2008).

Chl *b* pool was shown to have a greater effect on chlorosis than Chl *a* pool (Angadi and Mathad 1998; Fargaová 2001). A change in the ratio of the two forms of Chl can be associated either with a decrease in the transition of Chl *a* to Chl *b*, or with an increase in the reverse reaction of Chl *b* in Chl *a*. In higher plants, the predominant form is Chl *a*. Auxiliary pigment Chl *b* is formed in a reaction with Chl oxygenase, as a result of which the methyl group of the porphyrin ring transfers to the formyl group (Porra et al. 1994). This enzyme is light-dependent and was found not only in higher plants, but also in microalgae (Masuda et al. 2003).

According to Ebbs and Uchil (2008), the preferred loss of Chl *b* during Cd stress is most likely to result from the conversion of Chl *b* into Chl *a*. A similar conversion of pigments was found in a number of plants (Ito and Tanaka 1996) and is carried out using ferredoxin-dependent Chl *b* reductase through the formation of hydroxymethyl, as occurs with the formation of Chl *b* (Scheumann et al. 1998). Similar Chl transformations can be part of the adaptive mechanism of plants under conditions of changing light intensity. Chlorophyll *b* is released from the PSII conglomerates and then transformed to form the reaction center (RC) of the Chl *a* molecule (Ohtsuka et al. 1997).

Transformation of Chl *b* into Chl *a* also occurs during catabolic processes during aging (Scheumann et al. 1998), involving enzymes that decompose Chl *a* but not Chl *b* (Dangl et al. 2000). The formation of ROS induced by Cd or nutritional deficiency (K, Mg, Zn) can also cause leaf aging with a corresponding loss of Chl *b* (Marschner 1995). For example, in *Brassica napus*, catalase gene expression increased during aging, and in *Zea mays*, expression of glutathione-S-transferase (GST; EC 2.5.1.18) increased (Dangl et al. 2000). Cd also increased expression of these two enzymes (Lang et al. 2005). An increase in Chl *a*/*b* may be due to the initiation of catalase activity during Cd stress, as shown in *Brassica juncea* (Singh and Tewari 2003). According to Ebbs and Uchil (2008), the predominant decrease in Chl *b*, aging, and Cd-induced chlorosis are associated with similar processes under oxidative stress, namely, an increase in the transformation of Chl *b* into Chl *a* and a simultaneous decrease in Chl oxygenase activity. The active reduction of Chl *b* in Chl *a* probably serves to compensate for the Cd-induced decrease in Chl synthesis and prevents the destruction of photosynthetic machinery.

15.6 Photosynthesis

The photosynthetic apparatus is one of the main objects of Cd action in phototrophic organisms (Prasad and StrzaŁka 1999; Ci et al. 2010; Cherif et al. 2012). The inhibitory effect of Cd on P_N is shown in various plant species (Krupa and Baszynski 1995; Di Cagno et al. 1999; Silva et al. 2018), including maize (Wang et al. 2009; Lysenko et al. 2015; Silva et al. 2017), legumes (Vassilev et al. 2005), rice (Moya et al. 1993; Wang et al. 2014; He et al. 2008), soybeans (Xue et al. 2013), sweet sorghum (Xue et al. 2018), *Brassica campestris*, *Brassica juncea* (Chen et al. 2011), and *Ceratopteris pteridoides* (Deng et al. 2014). Moreover, the degree of negative influence of Cd depends on the type of plant photosynthesis (C3 or C4). C3 plants are more tolerant of high Cd concentrations (Inouhe et al. 1994) and suffer less from leaf chlorosis (Siedlecka and Krupa 1999).

Cd causes negative changes at both the structural and functional levels of the organization of the photosynthetic apparatus of plants (Singh et al. 2006; Cherif et al. 2012). Under Cd stress, there may be a deterioration in chlorophyll synthesis (He et al. 2008), damage to thylakoid membranes (Maksymiec 2007), impaired electron transport (Pagliano et al. 2006), and inhibition of the effectiveness of PSII and CO_2 assimilation enzymes, and Rubisco and phosphoenolpyruvate carboxylase (PEPC; Burzyński and Kłobus 2004; Tran and Popova 2013; Masood et al. 2012; Li et al. 2015). The photosynthetic rate can also be reduced by inhibiting ferredoxin-NADP$^+$ reductase (EC 1.18.1.2; Costa et al. 2012) and ATP synthase when Cd interacts with the functional sulfhydryl groups of these enzymes (Van Assche and Clijsters 1990). Cd has been shown to negatively affect the state of PSII protein complexes (Ahmed and Tajmir-Riahi 1993).

15.6.1 Light Phase of Photosynthesis

The multiple effects of Cd toxicity can be the cause of inhibition of the photosynthetic electron transport. High Cd concentrations very quickly reduce the functional activity of photosystem II (PSII; Baszyński 1986; Burzyński and Kłobus 2004; Wodala et al. 2012; Moradi and Ehsanzadeh 2015), but not photosystem I (PSI; Bazzaz and Govindjee 1974; Küpper et al. 2007). PSII photosynthetic electron transport is already inhibited at low Cd^{2+} concentrations (5 μM), as evidenced by a decline in the effective quantum yield of PSII photochemistry (Φ_{PSII}), the maximum electron transport capacity (ETR_{max}), and the maximum quantum yield for electron transport.

It is assumed that the target sites of Cd action are located on both sides of the PSII, donor and acceptor (Pagliano et al. 2006). On the donor side, Cd^{2+} can exchange with the Ca^{2+} ions of the Ca/Mn cluster in the oxygen evolving complex (OEC) (Faller et al. 2005). Šeršeň and Kráľová (2001) observed a direct effect of Cd^{2+} on the Mn ion cluster located in the OEC. In this case, Cd caused the release of Mn^{2+}, which inactivated the electron transport from H_2O to the reaction center of photosystem II. This hypothesis is also supported by the fact that a decrease in the Mn^{2+} content was found in the thylakoids, but not in the chloroplast stroma in the Cd-stressed plants (Lysenko et al. 2019). Thus, the damaging effect of heavy metals consists in displacing Mn^{2+}, Ca^{2+}, and Cl^-, important cofactors necessary for water-splitting systems (Krupa and Baszynski 1995; Faller et al. 2005). On the other hand, under the action of Cd, a change in the OEC polypeptide composition can occur (Skórzyńska and Baszyński 1993).

On the acceptor side of PSII, Cd^{2+} most likely binds to Q_B and not to Q_A (Sigfridsson et al. 2004). According to Parmar et al. (2013), Cd is able to act on nonheme Fe in the Q_A-Fe-Q_B complex and cause a molecular reorganization of Q_B, thereby reducing the electron transport rate (ETR). On the other hand, according to Paddock et al. (2003), conformational modification of Q_B may also occur due to protonation of histidine residues. In addition, Ishikita and Knapp (2005) showed that inhibition of electron transport can occur due to the interaction of Cd with tyrosine residues in protein D1–161. In any case, inhibition of the electron transfer rate can lead to inhibition of OEC (Bazzaz and Govindjee 1974; Tripathi et al. 1981).

Inhibition of photochemical processes may also be due to inhibition of the Calvin cycle under Cd stress. In this case, there is a decrease in the consumption of ATP and NADPH, which is accompanied by a violation of the ΔpH on thylakoid membranes (Krupa et al. 1993). As a result of this, the electron transfer and quantum efficiency of PSII are reduced (Zribi et al. 2009). Exposure to Cd causes stomata to close, which leads to CO_2 limitation, the accumulation of ATP and NADPH, and, as a result, to the disturbance of photosynthetic machinery (Sayed 2003).

The degree of damage to PSII by Cd is strongly due to light conditions (Küpper et al. 2002). With minimal illumination, the suppression of PSII by Cd is mainly due to the disruption of the light-harvesting antenna functions, since Mg^{2+} in Chl II molecules is replaced by Cd^{2+}. At maximum illumination, the destruction of the PSII reaction center may be observed (Küpper et al. 2002).

Photosystem I is considered to be relatively insensitive to the action of Cd^{2+} (Pál et al. 2006). However, in the case of Cd-induced Fe deficiency in plants, some researchers observed inhibition of electron fluxes around PSI (Siedlecka and Baszynski 1993; Šeršeň and Kráľová 2001; Timperio et al. 2007). Wodala et al. (2012) also reported a reduction in the Φ_{PSI} and the number of electrons in the inter-system chain under Cd stress. Cd acts on PSI mono- and multimeric complexes, disrupting the stable binding of Chl to lipoproteins and, therefore, reducing the number of PSI complexes (Sárvári 2005; Fagioni et al. 2009). In addition, Cd can cause a decrease in the flow of electrons to the PSI from stromal donors. The potential sources of electrons from the stroma can be peripheral ferredoxin and pyridine nucleotides, primarily NADH and NADPH, which can also serve as carriers of electrons from the triozo phosphate pool in the stroma (Asada et al. 1992). Chow and Hope (2004) suggest that electrons from pyridine nucleotides can then be directed to the plastoquinone pool using NAD(P)H dehydrogenase. Ascorbate may also act as an additional potential source of electrons.

15.6.1.1 Chlorophyll Fluorescence

Under the influence of environmental changes, there is a correction of the working capacity of photosynthetic machinery. Under stressful conditions, plants require less light energy for photosynthesis. Overabundant photon energy is gently scattered in the form of heat by chlorophyll fluorescence to prevent photoinhibition and photooxidation. Changing the parameters of the fast-polyphase fluorescence of the induction transient process allows us to register a violation of the functional state of photosynthesis under stress (Strasser et al. 2004). Moreover, there is a close correlation between Chl fluorescence and the physiological state of the photosynthetic apparatus. Changes in Chl fluorescence parameters reflect the intensity of heavy metal stress (Baker and Rosenquist 2004; Żurek et al. 2014), including Cd stress (Sheoran et al. 1990; Larsson et al. 1998; Di Cagno et al. 1999; Krupa and Moniak 1998; Burzyński and Żurek 2007). Measurement of Chl fluorescence parameters allows obtaining information on the functional state of photosystems. The most important among these parameters are the F_0 (minimal level of chlorophyll fluorescence), F_{m} (maximum fluorescence of dark-adapted leaves), F_{v} ($F_{\mathrm{v}} = F_{\mathrm{m}} - F_0$; variable fluorescence of the dark-adapted state), $F_{\mathrm{v}}/F_{\mathrm{m}}$ (potential efficiency of PSII), and fluorescence curves reflecting phenomenological energy flows (Kalaji and Łoboda 2007; Tuba et al. 2010).

The negative effect of Cd is observed at different stages of the photosynthesis light phase (Maksymiec and Baszyński 1996). The effect of Cd on the electron transport rate in photosystems is determined by measuring fluorescence parameters such as $F_{\mathrm{v}}/F_{\mathrm{m}}$ and Φ_{PSII}, and qP (photochemical) and qN, NPQ (nonphotochemical quenching of the excited state of chlorophylls) (Liu et al. 2011; Ahammed et al. 2012). A decrease in these parameters with Cd stress is shown in many plant species (Filek et al. 2010; Pietrini et al. 2010), as well as in some types of hyperaccumulators (Küpper et al. 2007). However, the degree of influence of Cd is individual in each plant species and varieties, which can be explained by the different values of Cd penetration into chloroplasts. For example, prolonged exposure to Cd reduced the F_v/F_m and Φ_{PSI} in some varieties of barley and did not affect these parameters in other varieties (Wu et al. 2003). At a high Cd content (up to 600 μM) in maize seedlings, the PSII photochemical activity (F_v/F_m, Φ_{PSII}, qP, ETR) decreases only in a sensitive, but not in a tolerant line (Ekmekçi et al. 2008).

The minimum chlorophyll fluorescence (F_0) level increases under stress due to a decrease in the efficiency of electron transfer from the Chl *a* antenna to the RC of PSII or when these centers are damaged (Ralph and Burchett 1998; Pietrini et al. 2003). A decrease in F_0 can occur if inactive PSII centers function as scattering sinks (Larsson et al. 1998). Shi and Cai (2008) in peanut plants already at 10 μM Cd showed a sharp increase in F_0 as a result of a decrease in F_v/F_m and F_v/F_0. It is also interesting to note that the *Tradescantia* plants showed an increase in F_0 at 3 h, but a decrease in F_0 at 5 h Cd exposure (Judy et al. 1990).

With an increase in the Cd content, F_m also decreases (Franić et al. 2017), apparently, as a result of violation of the thylakoid membrane ultrastructure (Ekmekçi et al. 2008). This reduces the time to reach F_m (t_{max}), which indicates the stress state of the plant. Because F_m reflects PSII functionality when all Q_A are reduced, shortening t_{max} implies a decrease in the Q_A pool suitable for reduction (Mallick and Mohn 2003). After Cd treatment, the value of V_J (variable fluorescence at J step) increases, which implies a decrease in the effectiveness of Q_A^- reoxidation (accumulation of reduced Q_A^-), since V_J determines the value of part of the reduced Q_A^- (Kalaji et al. 2014). S_m indicates how many electrons move in the electron transfer chain (Stirbet and Govindjee 2011). A decrease in S_m under stress indicates that F_m can be achieved faster, because fewer electrons are used to reduce PSII acceptors. This is also observed when the parameter t_{max} decreases. Under stressful conditions, the primary incline of the relative fluorescence (M_o) increases, corresponding to the relative rate of Q_A reduction (Christen et al. 2007).

When exposed to Cd, a decrease in F_v/F_m is observed, which indicates a slowdown in electron transport in PSII (Pietrini et al. 2003; Sigfridsson et al. 2004; Küpper et al. 2007; Ahammed et al. 2013; Parmar et al. 2013; Moradi and Ehsanzadeh 2015; Liu et al. 2018) and is always used as a stress indicator (Linger et al. 2005). Shi and Cai (2008) observed a decrease in F_v/F_m and F_v/F_0 with a simultaneous change in Chl/Car, which indicates a change in the location of chlorophylls in thylakoids, leading to a decrease in photochemical potential (Gruszecki et al. 1991).

Basa et al. (2014) in *Beta vulgaris* found that Φ_{PSII} significantly decreases with Cd toxicity, which corresponds to a decrease in electron transfer in PSII apparently due to the destruction of RC (Váňová et al. 2009). A decrease in Φ_{PSII} under Cd stress may be the result of an increase in qN, which is an indicator of the dispersion of light as heat in plants (Per et al. 2016). Under Cd stress, an imbalance arises between the total amount of absorbed light and the number of photons used to generate energy in chloroplasts. Excessive light energy provokes the appearance of stable triplet forms of Chl, causing oxidative destruction of membranes (Sárvári 2005).

According to Janeczko et al. (2005), Cd reduced specific energy fluxes calculated per cross section of the sample (CS). Herewith, a slowdown in photosynthetic electron transfer was observed due to a decrease in the number of active reaction centers (RCs) of PSII capable of Q_A reduction. At the same time, Cd increased the amount of excitation energy that is dissipated as heat (DI_0/CS). This was accompanied by a decrease in the maximum quantum yield for primary photochemistry (φP_0) and efficiency, while the trapped exciton was able to travel the electron to the electron transport chain to a greater extent than Q_A^- (Ψ_0). Due to Cd-induced significant damage at some RC of PSII and a slight decrease in photon absorption by the antenna system (ABS) per CS, there is increased absorption flux per RC (ABS/RC), trapped energy flux per RC (TR_0/RC), and dissipated energy flux per RC (DI_0/RC).

At low Cd concentrations, it can often be observed that this heavy metal does not affect the photosynthetic electron transport (Wu et al. 2003; Burzyński and Żurek 2007; Tang et al. 2013). For example, in cotyledons and leaves of cucumber at 20 μM Cd (Burzyński and Żurek 2007), despite a sharp inhibition of P_N and g_s, the potential efficiency of PSII remained unchanged, and the only diminished fluorescence parameter was Φ_{PSII}. This can be explained by a decrease in the activity of carbon metabolism or insufficient use of ATP and NADP during CO_2 assimilation (Subrahmanyam and Rathore 2000). Di Cagno et al. (1999) also found changes in Φ_{PSII}, qP, and quantum efficiency of active RC of PSII (Φ_{exc}) with unchanged F_v/F_m in sunflower plants (10 or 20 μM Cd). The F_v/F_m ratio did not change in tomato leaves treated with Cd (Degl'Innocenti et al. 2014). However, other authors obtained opposite results in hyperaccumulator plants (Mobin and Khan 2007). The potential effectiveness of PSII remains unchanged if the F_v/F_m ratio exceeds 0.8 (Björkman and Demmig 1987). Degl'Innocenti et al. (2014) suggested that the short-term effect of Cd on tomato plants only moderately affects the reoxidation rate of the primary PSII acceptor. This effect caused only a slight shift in the ETR and Φ_{PSII} values due to a decrease in CO_2 assimilation. In contrast to the studies of a number of authors (Krupa et al. 1993; Castagna et al. 2013), Degl'Innocenti et al. (2014) showed that the content of Chl did not change in plants treated with Cd, which indicates the absence of inhibition of Chl biosynthesis and oxidation. At the same time, the presence of Cd inhibited plant growth without significantly affecting photosynthesis. It is possible that a decrease in growth and P_N without changes in Chl fluorescence parameters may be observed if plants partially adapted to Cd stress, as was shown in tomatoes (Degl'Innocenti et al. 2014).

After processing Cd of barley and corn seedlings, there were no essential changes in the values of such fluorescence parameters as F_v/F_m, Φ_{PSII}, and qP (Lysenko et al. 2015). The two nonphotochemical coefficients, qN and NPQ, changed independently, because, although both coefficients operate with F_m and F'_m (maximum fluorescence of light-adapted leaves), qN operates with F'_0 (fluorescence in leaves previously exposed to light) and NPQ does not. The literature describes cases where qN and NPQ have varied in different directions (Lichtenthaler et al. 2005).

The nonphotochemical quenching ratio of the Chl excited state (NPQ) tends to increase after Cd treatment (Pietrini et al. 2010). However, Liu et al. (2010) showed a decrease in NPQ under the action of Cd, associated with the fast-relaxing component of NPQ (qE), which determines the excitation of thylakoid membranes. At the same time, the slow-relaxing component of NPQ, depending mainly on photoinhibition (qI), changed insignificantly. This coefficient depends on the photoinhibition of PSII and on the dislocation of the light-harvesting complex outside the PSII. An increase in qI may be associated with an increase in the concentration of Cd in chloroplasts, while a decrease in qE depends on the external concentration of Cd and is species-specific. For example, in corn chloroplasts, NPQ remained almost unchanged, while in barley chloroplasts it decreased significantly (Lysenko et al. 2015).

According to Lysenko et al. (2015), in chloroplasts, Cd has two effects. The first effect, responsible for the decrease in ΔpH of membranes, reduces NPQ and is more responsive to the presence of Cd in the soil. The second effect causes photoinhibition or transformation of PSII antennas, increases nonphotochemical quenching, and is more responsive to the presence of Cd inside chloroplasts. In case of equal values of these changes, the final effect cannot be seen. For example, at 80–200 μM Cd, qI increases, qE decreases, and the net NPQ remains unchanged (Lysenko et al. 2015). Similarly, in pea leaves at 50 μM Cd, the second effect took precedence and qN rose, at 1 mM Cd the effects were the same and qN remained unchanged, and at 5 mM Cd the first effect dominated and qN decreased (Geiken et al. 1998).

The degree of negative influence of Cd on photosynthetic light reactions depends on the stage of leaf growth. Thus, in young leaves of *Phragmites australis*, the F_v/F_m ratio was high even at high Cd concentrations, since F_m decreased proportionally to F_0, which probably indicates poised damage or effective adaptation of the photosynthetic machinery under stressful conditions (Pietrini et al. 2003). However, in fully mature leaves, F_v/F_m was greatly reduced, with leaf chlorosis and destructive consequences for PSII. *Phragmites australis* appears to have a specific ability to protect plastids from the negative effects of Cd, and this ability has been found to be high in young leaves, but not in old leaves (Fediuc and Erdei 2002). Similar results were also obtained in different parts of the same rye leaf (Krupa and Moniak 1998).

When studying transient processes of fluorescence induction for 1 s, the key states are F_0 and F_m (Strasser et al. 2004). The intermediate points between these extremes, named K (300 μs), J (2 ms), and I (30 ms), determine the electron flux between the various components of the PSII. The state of these components is described by an informative O-J-I-P curve (Boisvert et al. 2006).

When disposing off absorbed photons in RC of PSII, some energy is needed to initiate electron transfer from Q_A to PSI. The apparent activation energy (AAE), associated with the rapid increase in fluorescence Chl *a*, is of great importance for studying the bioenergetics of various stages of electron transfer in PSII. The study of apparent activation energies in thylakoid membranes is carried out in order to analyze the transient processes of O-J-I-P fluorescence, in order to study the various stages of recovery of Q_A, Q_B, and PQ. Depending on the degree of oxidation–reduction of the pools Q_A, Q_B, and PQ, the apparent activation energies of PSII differ in the primary source (Boisvert et al. 2006). The rapid increase in Chl *a* fluorescence is used to study acceptor systems other than PSII, namely, the OEC and PSI (Schansker et al. 2005). Depending on the site of exposure, Cd may have different effects on electron transfer and cause a change in the apparent activation energies of PSII.

In chloroplasts, Cd can bind to chlorophyll–protein complexes and causes an imbalance between photon absorption and electron transport in PS (Bashir et al. 2015). To detect PSII damage, transient analysis is used according to the JIP test. In *Sorghum bicolor*, Cd induced an increase in DI_0/RC, ABS/RC, TR_0/RC, and ET_0/RC (electron transport flux per RC), and a significant decrease in φP_0, Ψ_{Eo} (probability that an electron moves further than Q_A^-), δ_{Ro} (probability that an electron is transported from the reduced intersystem electron acceptors to the final electron acceptors of PSI), PI_{abs} (performance index), and RC/CS_0 (Q_A-reducing RC per CS) (Xue et al. 2018). The decrease in Ψ_{Eo} and δ_{Ro} showed that the PSII electronic transfer was blocked due to the accumulation of Q_A^-. An increase in DI_0/RC, ABS/RC, TR_0/RC, and ET_0/RC, and a decrease in RC/CS_0 means inactivation of part of the active RC, possibly due to a decrease in the Chl concentration and also a decrease in the Chl *a*/*b* ratio when processing Cd (He et al. 2008). The functional significance of such fluorescence parameters as ABS/RC, φP_0, and Ψ_{Eo} can be combined using the performance index (PI_{abs}), the value of which is closely related to the possibility of energy conservation in photosystems and their activity. A marked reduction in PI_{abs} with an increase in Cd content in Sorghum bicolor leaves indicates a slowdown in electron transport and inhibition of photosynthesis (Xue et al. 2018).

According to Franić et al. (2017), in corn leaves, the toxic effects of Cd are manifested in a reduction in quantum yield of PSII electron transfer and in the efficiency of excitation energy capture by active RC of PSII (TR_0/ABS, ET_0/ABS, and ET_0/TR_0). The reduction in acceptor side-dependent yields (ET_0/ABS, ET_0/TR_0), which denote the efficiency of electron transfer, suggests the stimulation of photoinhibition in response to Cd action (Pagliano et al. 2006).

Cd treatment results in a decrease in TR_0/ABS (= φP_0), which is associated with the photoinhibition process (Turnau et al. 2008). An increase in ABS/RC with Cd treatment (Janeczko et al. 2005; Franić et al. 2017) indicates that part of the open RCs were closed or expanded the antenna size (Krüger et al. 1997). Simultaneously with a change in these parameters decreases the density of the RC per excited CS (RC/CS_0) and the density of the RC on Chl *a* basis (RC/ABS). Inactivation of the RC can be a downregulation protective mechanism against photoinhibition. The increase in TR_0/RC observed with Cd treatment (Franić et al. 2017) may indicate damage to the OEC (Kalaji et al. 2014). Exposure to Cd significantly increases energy dissipation (DI_0/RC), which is associated with leaf protection from oxidative stress, that is, absorbed excess light energy is dissipated instead of being used in Q_A^- reduction (Franić et al. 2017). PI_{ABS}, which is defined as the ability for the accumulation of exciton energy to restore intersystem electron acceptors, is rated as (RC/ABS)(TR_0/ABS − TR_0)(ET_0/TR_0 − ET_0). An increase in PI_{ABS} with Cd processing occurs due to an increase in all three parameters, but the component ET_0/(TR_0 − ET_0) has the most influence (Franić et al. 2017), which implies an increase in CO_2 assimilation, since a link was established between electron transfer in the photosystem and the CO_2 absorption (Krall and Edwards 1992). However, an increase in electron transfer can also be associated with other processes in the cell

(Kalaji et al. 2016). An increased PI_{ABS} value means an improvement in the overall efficiency of the photosynthetic apparatus. Some corn hybrids showed a decrease in PI_{ABS} when processing Cd, which may be due to a decline in all components of PI_{ABS}, but especially RC/ABS values (Franić et al. 2017), indicating that most of the reaction centers were inactivated (Żurek et al. 2014; Begović et al. 2016).

In some cases, after Cd treatment, an increase in Chl *a* content is observed (Aghaz and Bandehagh 2013; Franić et al. 2017), which is accompanied by a rise in F_0, F_{150}, and F_{300}. Under these conditions, stress is apparently associated with functional damage to the photosynthetic apparatus, which was accompanied by a rise in energy leakage per RC and by the reduction of TR_0/DI_0 (Strasser et al. 2000). An increased content of Chl can also be observed when plants adapt to the presence of Cd or at its low content (Chaneva et al. 2010).

15.6.2 Dark Phase of Photosynthesis

It has been shown that, in isolated chloroplasts, CO_2 assimilation slows down during Cd treatment, but no change in photochemical reactions occurs, that is, P_N deceleration by Cd occurs at the level of dark photosynthesis reactions. Weigel (1985) suggested that inhibition of Cd occurred either at the level of CO_2 fixation or as a result of a change in the activity of the Calvin cycle enzymes. Impairment of the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.39) and other enzymes of the dark stage of photosynthesis upon exposure to Cd was recorded in various plants (Prasad and StrzaŁka 1999; Burzyński and Żurek 2007; Mobin and Khan 2007).

The negative effects of Cd^{2+} observed in the carboxylation phase of photosynthesis (Weigel 1985; Di Cagno et al. 1999) can lead to inactivation of enzymes through reactions with their thiol groups (Fuhrer 1982). The main target of Cd exposure is two key enzymes of photosynthetic fixation of CO_2, Rubisco and phosphoenolpyruvate carboxylase (PEPC; EC 4.1.1.31) (Krantev et al. 2008). Cd^{2+} is able to reduce Rubisco activity by replacing Mg^{2+} in the catalytic center of the enzyme, which fixes CO_2 (Siedlecka et al. 1998). High concentrations of Cd^{2+} also lead to irrecoverable dissociation of Rubisco subunits (Lhcb1 and Lhcb2), resulting in complete enzyme inhibition (Malik et al. 1992; Hajduch et al. 2001).

It is often observed that a reduction in the maximum Rubisco activity during Cd stress is accompanied by only a slight decrease in the Rubisco protein content (Pietrini et al. 2003). A decrease in Rubisco activity may be due to Cd-induced oxidative stress or due to action of proteases activated by ROS (Prasad 1996; Romero-Puertas et al. 2002). ROSs can directly influence the dissociation of Rubisco subunits (Ishida et al. 1999). It is also possible that the decrease in Rubisco activity is associated with inhibition of Rubisco activase (EC 4.1.1.36), which has the large Cys thiol residues subunit (Portis 2003) in the carboxy terminus, with which Cd binds.

There is evidence of the effect of Cd on Calvin cycle enzymes in the stroma of chloroplasts (Prasad and StrzaŁka 1999). The phosphoglycerate kinase (EC 2.7.2.3) and glyceraldehyde-3-phosphate dehydrogenase (EC 1.2.1.12) enzymes, which are necessary during the recovery phase of the Calvin cycle, are inhibited to some extent by Cd (Sheoran et al. 1990). In addition, Cd reduces the potential activity of phosphoglycerate kinase, which indicates the effect on the synthesis of this enzyme. Decline of CO_2 reduction may affect photochemical efficiency. A decrease in Φ_{PSII} can occur as a result of a disequilibrium between the absorbed light energy and that part of it that is used in the carboxylation reaction (Burzyński and Kłobus 2004).

Cd negatively affects the dark and light stages of photosynthesis, but the site of the primary effect of Cd on photosynthesis depends on the specific conditions of the experiment, and the concentration and duration of Cd processing. For example, in maize seedlings, the degree of P_{N} decrease and the time of manifestation of the plant response to Cd treatment depended on the metal concentration (Wang et al. 2009). Prolonged Cd processing can cause significant metabolic changes, reflecting various interrelated processes in plants. According to Burzyński and Kłobus (2004), the effect of Cd on photosynthesis reactions is rather indirect, for example, due to changing numerous physiological processes. Cd reduces the rate of Fe transport into leaves, and low Fe content interferes with Chl synthesis and changes the chloroplasts' ultrastructure, which affects both stages of photosynthesis (Siedlecka and Krupa 1999). Cd also reduces the amount of OEC (Janeczko et al. 2005); disrupts water metabolism (Poschenrieder and Barceló 1999), assimilation, and distribution of nutrients (Krupa et al. 2002); induces oxidative stress (Dietz et al. 1999); and, as a result, inhibits leaf growth and reduces the total area for light absorption.

Burzyński and Kłobus (2004) noted that among other parameters of photosynthesis, Cd had the most noticeable effect on P_{N}, which suggests that Rubisco and Calvin cycle enzymes are more susceptible to Cd than light photosynthesis reactions. At the same time, a sharp decrease in P_{N} was apparently not associated with the influence of Cd on stomata activity, since, despite the low value of g_{s}, the values of C_{i} remained at a sufficiently high level. P_{N} independence from g_{s} has been proposed by Sheoran et al. (1990). Increased C_{i} values are probably associated with a decrease in P_{N} or with activation of dark respiratory processes stimulated by exposure to Cd (Romanowska et al. 2002) and usually associated with leaf aging. However, Shi and Cai (2008) showed that in *Arachis hypogaea*, Cd-induced P_{N} inhibition is mainly associated with changes in Chl and g_{s}, and an increase in C_{i} indicates inhibition of dark photosynthesis (Sas et al. 2006).

The toxicity of Cd^{2+} is manifested at varying degrees depending on the stage of plant development. So, at the early stage of vegetation of the plant pigeonpea (*Cajanus cajan* L.), 0.5 and 1.0 mM Cd^{2+} resulted in a 50% reduction in photosynthesis and activity of photosynthetic carbon reduction polymerase chain reaction (PCR)-cycle enzymes (Rubisco, phosphoglycerate kinase, NAD(P)-glyceraldehyde-3-phosphate dehydrogenase, and aldolase (EC 4.1.2.13) (Sheoran et al. 1990). At a late stage of vegetation, Cd^{2+} did not affect photosynthesis and the enzymes studied. A decrease in their activity was observed only at high concentrations of Cd^{2+} (5 mM).

Some authors argue that the main site of Cd exposure is the light phase of photosynthesis (Küpper et al. 2007). However, other researchers found that Cd primarily interferes with the functioning of the CO_2 assimilation pathway and only then affects the light reactions of photosynthesis (Burzyński and Żurek 2007). Baszyński et al. (1980) showed that the main cause of the decrease in photosynthesis after exposure to Cd is a decrease in the content of Chl, which preceded the decrease in the concentration of CO_2.

Studying the effect of Cd on photosynthesis for short periods of time has largely eliminated the indirect effects of the metal, such as Fe deficiency, a decrease in Chl, and the destruction of general cellular metabolism (Burzyński and Żurek 2007). In maize seedlings (*Zea mays* L.), Cd primarily inactivated Rubisco and PEPC and, secondly, changed the electron transfer rate of PSII, that is, Cd affected both stages of photosynthesis; however, the main goal of the toxic action of Cd was Calvin cycle reactions, not PSII (Wang et al. 2009). In sunflower plants under conditions of Cd stress, a reduction in Rubisco activity was observed at a constant F_v/F_m ratio (Di Cagno et al. 2001). This indicates that the process of photosynthesis mainly changes due to the dark phase.

According to most researchers, a decrease in P_N is most likely to occur when Cd acts on the CO_2 assimilation path. It is assumed that Cd primarily inhibits the carbon photoreduction cycle and only then affects the electron transfer in photosystems (Weigel 1985; Krupa and Moniak 1998; Burzyński and Żurek 2007).

15.6.3 Microalgae Photosynthesis

Heavy metals inhibit growth (Dudkowiak et al. 2011) and photosynthesis of algae (Nishikawa et al. 2003). In *Chlamydomonas reinhardtii*, an inhibitory effect of Cd on OEC and a decrease in ETR in both PSs were found (Perreault et al. 2011). A decrease in ETR under the influence of Cd led to a decrease in apparent activation energy (AAE) for all PSII reduction steps. The effect of Cd on OEC correlated with a variation in AAE for all the PSII reduction phases. In addition, AAE to reduce the plastoquinone pool also had an effect on PSI activity. Inhibition of these sites has shown that the OEC activity of PSII and PSI activity are dependent on AAE associated with the transfer of electrons to PSII. In *Chlamydomonas*, Cd inhibits photoactivation of PSII (i.e., the OEC assembly) by competitively binding to the Ca^{2+} main site in PSII (Faller et al. 2005).

The negative effects of Cd on photosystem II are shown in *Scenedesmus acutus* and *Chlorella vulgaris* (Ilangovan et al. 1998). In addition, the inhibitory effect of Cd on OEC activity has been found (Pagliano et al. 2006). However, La Rocca et al. (2009) at 5 ppm Cd did not show signs of a violation of the acceptor side, despite a decrease in the rate of photosynthesis. This conclusion is consistent with the assumption that Cd primarily affects the donor side of PSII.

Koliella antarctica had a rather high sensitivity to Cd. The degree of exposure to Cd depended on its concentration. After 1 ppm Cd treatment, a moderate toxic effect was shown on growth, chloroplast ultrastructure, chlorophyll content, photosynthesis efficiency (F_v/F_m), and ETR in PSII. Treatment with 5 ppm Cd led to a significant reduction in these processes and even to the death of algae cells (La Rocca et al. 2009).

15.6.3.1 Cyanobacteria Photosynthesis

Cyanobacteria rather quickly accumulate a large amount of toxic metals (Les and Walker 1984), which can lead to inhibition of photosynthesis (Dudkowiak et al. 2011). The degree of toxic accumulation of metals by cyanobacteria depends on the species, physiological conditions, and concentration of metal ions in the medium, as well as on the physicochemical properties of the medium, that is, pH and temperature (Les and Walker 1984; Koelmans et al. 1996). At the same time, it turned out that cyanobacterial thylakoid membranes are much more resistant to the effects of Cd^{2+} than in higher plants (Nováková et al. 2004). In *Synechococcus elongatus*, concentrations of 0–100 mM Cd had a rather activating effect on the thylakoid membranes. An inhibition of PSII photochemical activity was manifested only at 1000 mM Cd, while the site of action of Cd^{2+} was probably on the PSII oxidative side. Analogous data were obtained when measuring oxygen evolution. The carboxylation enzyme activity was maintained even at 1000 mM Cd (Nováková et al. 2004).

Cd^{2+} reduced the growth of cyanobacterium *Nostoc muscorum* cells (Dixit and Singh 2015). Growth inhibition occurred as a result of the destruction of cellular components or impaired absorption of nutrients, as well as due to a decrease in enzyme activity and photosynthesis (Thapar et al. 2008). Cd caused disorganization of thylakoids, a change in the proportions of the pigment antenna, and a reduction in the content of Chl, phycocyanins, and Car (Leborans and Novillo 1996; Dixit and Singh 2015), which led to a decrease in photosynthetic activity (Murthy et al. 1989).

Short-term Cd processing reduced O_2 release rate (Dixit and Singh 2015), that is most likely a result of inhibition of OEC, by replacing with cadmium of divalent cations responsible for water oxidation (Šeršeň and Kráľová 2001; Peters and Chin 2003). In addition, the inhibitory effect of Cd^{2+} is directed to the oxidative side of PSII, but before NH_2OH (Verma and Singh 1995).

At a low concentration (25 μg mL^{-1}), Cd^{2+} inhibits energy transfer on the way to the PSII center, and also causes a conformational modification in the Chl antenna in cyanobacteria (Singh et al. 1993). Higher concentrations (100 μg mL^{-1}) of Cd^{2+} can damage the photosynthetic complex (Dixit and Singh 2015).

Cd^{2+} causes the destruction of phycocyanin in the composition of phycobilisomes, which leads to a decrease in the emission intensity (Singh et al. 1993) in *Nostoc muscorum* (Dixit and Singh 2015). A decrease in the number of phycocyanin in *Nostoc muscorum* cells (Dixit and Singh 2015) and in the cyanobacterium *Spirulina platensis* (Murthy et al. 1989) is observed, which indicates a greater ease of decomposition of phycocyanin by Cd than allophycocyanin in phycobilisome.

15.7 Protection of the Photosynthetic Apparatus

15.7.1 Oxidative Stress and Antioxidant Systems

High concentrations of Cd can cause oxidative stress in plant cells, although it is not a redox metal (Cho and Seo 2005; Vassilev et al. 2005; Masood et al. 2012; Moradi and Ehsanzadeh 2015). Oxidative stress enhances lipid peroxidation (Chaoui et al. 1997), resulting in impaired membrane permeability, and inhibition of growth, photosynthesis, and normal synthesis of Chl (Mobin and Khan 2007; Masood et al. 2012). Blocking electron transfer in PSII by cadmium leads to the generation of reactive oxygen species (ROS), superoxide anion ($O_2^{\bullet -}$), hydroxyl ($OH^{\bullet}$) radicals, and H_2O_2, the accumulation of which leads to the destruction of the chloroplasts' structure and causes leaf chlorosis (Romero-Puertas et al. 2004; Hasan et al. 2011; Ahammed et al. 2012; Masood et al. 2012; Asgher et al. 2014). Cd causes the accumulation of ROS in all organs, thereby affecting the redox balance of the whole plant (Iannelli et al. 2002; Foyer and Noctor 2005).

Among all components, cell membranes are most sensitive to damage by heavy metals (Singh et al. 2006). Lipid peroxidation, determined by malondialdehyde (MDA) content, can be used as a test to determine the development degree of oxidative stress (Kumari et al. 2010; Gallego et al. 2012). The content of MDA in plant tissue increases under the action of toxic Cd concentrations (Ahammed et al. 2013; Xu et al. 2013). With prolonged exposure to Cd, there is a significant reduction in membrane stability index and in electrolyte leakage (Gonçalves et al. 2007), which indicates a serious damage to the integrity of the membranes (Moradi and Ehsanzadeh 2015).

Since Cd cannot participate in Fenton's reactions, its role in the ROS formation mechanism causing membrane damage is unclear (Rodríguez-Serrano et al. 2009). Possibly, under strong illumination of chloroplasts, Cd causes the formation of triplet forms of chlorophyll in PS antennas, and subsequently singlet O_2 and other types of ROS (Atal et al. 1991).

Under stressful conditions in plants, there is an imbalance between the production and scavenging of ROS. In order to reduce the damaging effect of Cd, various mechanisms have been developed in plants that allow both sequestering the metal and neutralizing the ROS generated by it using special absorbers (Siripornadulsil et al. 2002). Protective strategies include the formation of various antioxidants and the activation of ROS-absorbing enzymes, as well as enhancing sulfur metabolism (Fernández et al. 2013; Choppala and Bolan 2014; Ahmad et al. 2015). One mechanism may be the expression or activation of antioxidant enzymes (Ranieri et al. 2005), including superoxide dismutase (SOD; EC 1.15.1.1), which is involved in the early stages of cell defense. The activity of superoxide dismutase depends on the accumulation of Cd in the tissues, species, and stage of plant growth, as well as the time of exposure to the metal (Sandalio et al. 2001; Shah et al. 2001). Superoxide dismutase decomposes $O_2{\bullet}^-$ into H_2O_2 and O_2 (Hsu and Kao 2007; Gill and Tuteja 2010). The accumulation of hydrogen peroxide is limited to catalase localized in peroxisomes and mitochondria (CAT; EC 1.11.1.6), peroxidases (EC 1.11.1.x), and ascorbate peroxidase in chloroplast (APX; EC 1.11.1.7) (Mishra et al. 2006; Bhatt and Tripathi 2011; Sharma et al. 2012). Nonenzymatic ROS quenchers can be carotenoid pigments (Anjum et al. 2015).

Gillet et al. (2006) showed a marked increase in Mn-SOD, but a decrease in Fe-SOD in Cd-treated plants. Similar reactions to oxidative stress have also been observed in other plants (Vido et al. 2001; Sarry et al. 2006). SOD activation also occurred in *Brassica napus* (Meng et al. 2009) and tomatoes (Ahammed et al. 2013). In yeast, Mn-SOD activation and a decrease in Cu/Zn-SOD activity were observed (Vido et al. 2001). Fe-SOD transcript levels are also induced by Cd (Ahammed et al. 2013). A decrease in SOD activity probably occurs when Fe is replaced by Cd in the Fe-SOD enzyme (Yamakura and Suzuki 1980) or when the accumulation of $O_2^{\bullet-}$ exceeds the SOD's ability to eliminate, and ROS could inactivate the enzyme.

According to some authors, the formation of ROS during Cd-stress occurs as a result of a decrease in the level of glutathione and inhibition of GR, CAT, and APX (Dietz et al. 1999; Romero-Puertas et al. 2004). Indeed, in wheat plants (Ahmad et al. 2009), tomato (Ahammed et al. 2013), rice (Shah et al. 2001), and peas (Sandalio et al. 2001), there is a decrease in CAT activity, sensitive to $O_2\bullet^-$ radicals that lead to enzyme degradation (Cakmak 2000). A decrease in enzyme activity can also occur when it is destroyed by proteases or as a result of photoinactivation (Sandalio et al. 2001).

Contrary to the authors mentioned above, other studies have found an increase in APX activity (Gillet et al. 2006; Ahmad et al. 2009), which can compensate for the decrease in CAT in the presence of Cd. Increased APX activity is shown in *Brassica napus* (Meng et al. 2009), *Vigna mungo* (Singh et al. 2008), tomato (Ahammed et al. 2013), and *Brassica juncea* (Mohamed et al. 2012). Induction of the Cd level of the APX transcript is shown in tomato (Ahammed et al. 2013).

Catalase activity after Cd treatment of plants can also increase (Hasan et al. 2008). Ahammed et al. (2013) observed a Cd-induced increase in the CAT1 transcript level. Experiments with plants with different sensitivity to heavy metals revealed a pattern that catalase activity is always higher in plants resistant to Cd (Cho and Seo 2005).

Under the stress of Cd, a loss of Rubisco activity occurs, which cannot be due to the degradation of the Rubisco protein (Pietrini et al. 2003). An increase in the ROS level is accompanied by oxidation of the Rubisco SH groups, which correlates with a reduction in the photosynthesis rate (Liu et al. 2008). In plant seedlings, the main goals of the toxic effects of Cd are Calvin's cyclic reactions rather than PSII (Krupa et al. 1993). Cd stress initially inhibits the carbon photoassimilation cycle and only then affects the ETR in PSII (Burzyński and Kłobus 2004; Burzyński and Żurek 2007; Wang et al. 2009). On the other hand, the action of ROS formed by Cd leads to a decrease in the content of Chl and Car, which is accompanied by lower light absorption and adversely affects the photolysis of water and ETR (Deng et al. 2014).

15.7.2 *S-Metabolism Activation*

Cd toxicity can be reduced due to increased S-assimilation due to the involvement of S-metabolism in the formation of the antioxidant system of the cell (Bashir et al. 2015), which protects photosynthesis and supports growth under Cd stress (Asgher et al. 2014). The accumulation of Cd in the tissues of many plants stimulates the absorption of sulfates in the roots (Nocito et al. 2002), which is associated with increased expression of ATP-sulfurylase (EC. 2.7.7.4) (Gill et al. 2012), which catalyzes the activation reaction of SO_4^{2-} by interacting with ATP. In turn, plant photosynthesis also depends on S availability, which affects the efficiency of carboxylation and the stomatal movement (Iqbal et al. 2011), since sulfite reductase (EC 1.8.7.1) is a ferredoxin-dependent enzyme and, along with ferredoxin-$NADP^+$ reductase and nitrite reductase (EC 1.7.7.1), competes for the electrons of the PSI transport chain, especially since ferredoxin-$NADP^+$ reductase is inhibited by Cd (Gillet et al. 2006).

15.7.2.1 Glutathione Production

Glutathione is the main substance for maintaining the redox balance of the cell and is used to remove ROS (Noctor and Foyer 1998). Glutathione reductase (GR; EC 1.8.1.7) catalyzes the conversion of oxidized glutathione (GSSG) to reduced glutathione (GSH) (Noctor et al. 2002). The high solubility and mobility of glutathione allows it to be present in large quantities in all cellular organelles (Foyer and Rennenberg 2000). Glutathione can regulate the activity of photosynthetic enzymes associated with thioredoxin (Schürmann and Jacquot 2000). In addition to chloroplasts, glutathione is also present in mitochondria, where it supports oxidative phosphorylation and the formation of ATP (Hutchison et al. 2000).

GR activity with Cd stress is increased in leaves, but decreased in chloroplasts (Ahmad et al. 2009). High GR activity may support increased GSH/GSSG ratio. Increased GR activity is associated with transcriptional or translational modification (Romero-Puertas et al. 2002). Reduced GR expression in roots can lead to oxidative damage after Cd treatment (Mishra et al. 2006). The accumulation of Cd also leads to a reduction in GR activity in chloroplasts, which has been shown in many plants (Zhang et al. 2003; Pietrini et al. 2003; Ahmad et al. 2009).

Glutathione synthesis occurs after activation of inorganic sulfur due to the ATP-sulfurylase enzyme (ATP-S; EC EC. 2.7.7.4) followed by a cascade of enzymatic reactions (Leustek 2002; Tausz et al. 2004). Increased activity of ATP-S and other S-assimilation enzymes in leaves and chloroplasts under Cd stress (Ahmad et al. 2009) promotes plant resistance to heavy metals (Dominguez-Solis et al. 2001).

Synthesis and reduction of glutathione are highly energy-intensive processes. Sulfate reduction in chloroplasts requires eight electrons per molecule (Leustek and Saito 1999), as well as the presence of NADPH to preserve its reduced form (Noctor et al. 1998). Therefore, in order to increase the availability of GSH for the entire plant, large investments in resources are needed at the expense of other processes.

However, an increased concentration of GSH along with phytochelatins (PCs) seems to be the optimal protective strategy for saving key photosynthetic thiol enzymes from inactivating Cd (Pietrini et al. 2003). Cd-induced oxidative stress stimulates the expression of GSH synthesis genes (Schafer et al. 1998), thereby inducing a progressive increase in GSH concentration (Masood et al. 2012; Silva et al. 2018), which contributes to tolerance to oxidative stress (Pietrini et al. 2003). In addition, GSH makes it difficult to relocate Cd from roots to aboveground organs (Nakamura et al. 2013).

A key enzyme that catalyzes the conjugation of xenobiotics with GSH is glutathione S-transferase (GST; EC 2.5.1.18) (Coleman et al. 1997), whose activity (Skórzyńska-Polit et al. 2010; Gillet et al. 2006) and the transcript level GST1 is upregulated by Cd (Ahammed et al. 2013). Cd is a strong thiol scavenger that creates a sulfate deficiency (Nocito et al. 2002). However, Cd can only be captured by reduced forms of thiols (Ow 1996). In addition, GSH effectively reduces the likelihood of Cd interacting with the thiols of the enzyme catalytic centers and inhibiting their ability to carbon photoassimilate (Pietrini et al. 2003).

Thus, increasing GSH concentrations contribute to minimizing Cd stress (Xiang et al. 2001). The increased GSH content correlates with stress tolerance of plants and provides a mechanism for detoxifying heavy metals (Masood et al. 2012).

15.7.2.2 Phytochelatin Synthesis

Phytochelatins (PCs) in plants are sulfur-containing polypeptides with the structural formula $(\gamma\text{-Glu-Cys})_n\text{-Gly}$. PCs are synthesized from GSH in a sequestration reaction using phytochelatin synthase (EC 2.3.2.15) (Grill et al. 1985, 1989). PC synthesis is induced by the accumulation of Cd in plant cells (Sanità di Toppi and Gabbrielli 1999). PCs chelate Cd with SH groups of cysteine mainly in the root cell walls (Bajguz and Hayat 2009; Bajguz 2010) and thus impede the circulation of Cd in the plant (Bajguz and Hayat 2009; Bajguz 2010) and free Cd inside the cytosol (Grill et al. 1985). By the number of phytochelatins formed, one can judge the degree of development of the heavy metal's stress (Cobbett 2000).

15.7.2.3 Phytocystatin Synthesis

One of the strategies for maintaining photosynthesis in Cd stress is the synthesis of thiol compounds, for example, phytocystatin (PhyCys), which are involved in the regulation of metabolic processes (Eason et al. 2014). PhyCys' protective action under Cd stress extends to photosynthetic machinery enzymes (Rubisco), nitrogen use efficiency, and ROS scavengers enzymes (SOD and APX) (Per et al. 2016), as well as to S-assimilation enzymes to maintain higher levels of Cys and GSH for metal detoxification (Khan et al. 2009). In addition, PhyCys can act as a regulator of proteolysis during plant acclimatization, increasing tolerance to Cd (Per et al. 2016).

PhyCys is part of the cystatin superfamily and is a proteinase inhibitor that regulates proteolytic activity (Martínez et al. 2012; Kunert et al. 2015). In addition to functioning as the regulator of numerous metabolic processes, PhyCys is also involved in the formation of plant response to stress (Zhang et al. 2008). PhyCys gene expression (CsC and AtCYS1) was observed during cold and heat stresses, wounding, salinity, and drought (Pernas et al. 2000; Hwang et al. 2010). Overexpression of the AtCYS1 gene led to the prevention of cell death due to exposure to ROS (Belenghi et al. 2003). Overexpression of the BoCPI-1 protease inhibitor delays Chl destruction (Eason et al. 2014). Overexpression of PhyCys delays the destruction of the photosynthetic apparatus during senescence and significantly increases the amount of Rubisco protein (Prins et al. 2008). Ectopic expression of oryzacystatin enhances shoot branching and the accumulation of Chl in leaves (Quain et al. 2014).

15.7.3 Selenium Treatment

Selenium (Se) is not a necessary nutrient, but it can reduce the amount of free radicals in cells and thereby weaken the toxicity of Cd (Lazarus et al. 2006). The presence of Se prevents the absorption of Cd, neutralizes its toxicity, and activates antioxidant enzymes, thereby improving plant growth (Filek et al. 2008). The addition of Se to in vitro wheat cultures significantly improved the development and functioning of chloroplasts and reduced their degradation (Filek et al. 2009), as well as weakened Cd inhibition of photochemical processes (Filek et al. 2010).

Apparently, Se accelerates ETR in PSII, including antennas, which increases the number of active reaction centers and also affects the activity of OEC. By stimulating photosynthesis, Se helps maintain starch concentration, which decrease when exposed to Cd. Adding Se also reduces ROS formation (Filek et al. 2010).

15.7.4 Silicon Treatment

Silicon (Si) fertilization helps to mitigate abiotic stresses due to dilution effects, which leads to increased crop yields (Marschner 1995; Balakhnina et al. 2012). Deposition of Si in the leaves promotes tolerance to Cd, and also contributes to the preservation of water in the cells (Hattori et al. 2005).

A high Si content enhances plant resistance to stress through the activation of protective mechanisms (Mitani et al. 2009). The mechanism for reducing the toxicity of Cd with Si includes a decrease in the solubility of metals due to pH changes, the accumulation of phenols, and the formation of insoluble Cd–Si complexes (Gu et al. 2011). The degree of positive influence of Si during Cd pollution is dependent on plant species (Lukačová Kuliková and Lux 2010).

The addition of Si can alleviate the negative effects of Cd (Kaya et al. 2009; Broadhurst et al. 2013). Adding Si does not increase the production of net dry masses in normal conditions (Silva et al. 2017). However, it has been shown that under Cd stress conditions with prolonged exposure to Si, the net dry masses production increases (Zhang et al. 2008; Rizwan et al. 2012; Silva et al. 2017).

Suppression of absorption and transport of Cd, including through interaction with Si (Farooq et al. 2016), is considered as an effective protective mechanism against the toxic effects of Cd (Song et al. 2009). Adding Si to the soil reduces the availability of Cd, which reduces its absorption (Silva et al. 2017) and more effectively sequesters Cd in the roots (Vaculik et al. 2009, 2012), and also significantly reduces its movement into shoots (Song et al. 2009; Rizwan et al. 2012). Plant hyperaccumulators absorb Si using energy-dependent carriers (Ma et al. 2006). Silicon is able to integrate into the structure of the cell wall, which prevents the absorption of Cd by the roots and its movement into the aboveground organs (Lukačová et al. 2013). When transported to shoots, Si accumulates in the vascular system of the leaves in the form of a polymer, which prevents the movement of toxic ions (Mitani et al. 2005) and contributes to their coprecipitation (Gu et al. 2011). Apparently, Si hinders the transfer of Cd along the apoplastic pathway and contributes to its accumulation in the symplast (Ye et al. 2012).

Silicon can stimulate photosynthesis under conditions of cadmium stress by increasing φP_0 and Φ_{PSII}, decreases F_0, and increases F_v/F_m and qP (Nwugo and Huerta 2008; Feng et al. 2010). The Si use after the Cd stress onset can restore damage to the photosynthetic apparatus and improve Φ_{PSII} (Farooq et al. 2016), which is apparently not associated with a decrease in the content of Chl (Nwugo and Huerta 2008). Chl concentrations do not always change when Si is used under Cd stress conditions (Lukačová et al. 2013), although Feng et al. (2010) observed a higher Chl content with less damage to the thylakoid membranes on cucumber plants.

It should be noted that the Si-dependent blocking of the absorption and transport of Cd from the roots to the aboveground organs is not able to answer the question of why photosynthesis is restored after the end of Cd stress, although the concentration of Cd in the leaves did not change significantly. Apparently, the positive effect of introducing Si into aboveground tissues of the plants is due to the local effects of Si accumulation in the shoot, rather than the effect on Cd transport over long distances (Farooq et al. 2016).

Si-mediated metal stress tolerance also appears to be associated with improved antioxidant activity and high levels of ascorbate and glutathione (Ma and Yamaji 2006). On the other hand, the use of high doses of Si can cause an imbalance of nutrition and reduce the formation of dry matter in plants (Araújo et al. 2011). Si at high concentrations is likely to coprecipitate metals necessary for the functioning of photosynthesis, such as Fe and Cu (Gu et al. 2011).

Thus, the positive effects of Si under Cd stress can be accomplished through several mechanisms, namely, reducing Cd absorption and translocation, improving Cd compartmentation, retuning redox homeostasis, and increasing antioxidant capacity (Farooq et al. 2016).

15.7.5 Brassinosteroid Treatment

Brassinosteroids (BR) are polyhydroxysteroid phytohormones originally found in pollen from *Brassica napus* (Vardhini and Anjum 2015), but then they were found to be widespread throughout the plant because BRs are nontoxic, rapidly absorbed, and metabolized (Bajguz and Tretyn 2003). The classification of brassinosteroids consists in counting the number of carbon atoms in the molecular structure (C27, C28, or C29). Currently, more than 60 BRs have been identified (Haubrick and Assmann 2006), of which 24-epibrassinolide (EBR), 28-homobrassinolide, and brassinolide are biologically active (Vardhini and Anjum 2015).

Brassinosteroids are involved in the regulation of many processes at different levels of plant organization, including growth and productivity (Rao et al. 2002; Sasse 2003), gas exchange (Farooq et al. 2009), antioxidant enzymes (Sharma et al. 2010), and stimulation of chlorophyll synthesis (Fariduddin et al. 2003). In *Arabidopsis*, brassinosteroids stimulated plant growth, inducing cellulose formation, due to overexpression of its synthesis genes (Xie et al. 2011).

BRs participate in developing tolerance to various stresses (Vardhini et al. 2006; Hasan et al. 2011; Ahammed et al. 2012), such as high or low temperatures (Hayat et al. 2010a), moisture stress, drought (Yuan et al. 2010), salinization (Anuradha and Rao 2001; Alyemeni et al. 2013), damage by pesticides, polycyclic aromatic hydrocarbons (Ahammed et al. 2012), and Cd stress (Allagulova et al. 2015).

Brassinosteroids remove the negative influence of Cd stress in plants (Hasan et al. 2008, 2011; Ahammed et al. 2013). The use of BR mitigated the toxicity of Cd for plant growth (Anuradha and Rao 2009; Hayat et al. 2014; Santos et al. 2018). Treatment with EBR under Cd stress enlarged the relative water content in plants (Anuradha and Rao 2009; Hayat et al. 2007). BR reduced Cd in rapeseed plant tissue (Janeczko et al. 2005), cowpea plants (Santos et al. 2018), bean (Rady 2011), wheat (Kroutil et al. 2010), and *Chlorella vulgaris* (Bajguz 2000). EBR is likely to increase phytochelatin production in stress tissue cells (Bajguz 2011). This effect of EBR directly affects the decrease in values of the bioconcentration factor (BCF) and the translocation factor (TF), as well as the decrease in the rate of Cd translocation to the aerial organs (Santos et al. 2018).

Brassinosteroids can mitigate Cd exposure by improving the P_N of plants (Hayat et al. (2010b) by increasing g_s (Zhang et al. 2014). EBR increased the E of plants susceptible to Cd toxicity and simultaneously contributed to water absorption and root elongation (Santos et al. 2018). The increment in water-use efficiency in plants treated with EBR is inextricably related to the increase in the P_N and E (Santos et al. 2018). P_N/C_i values increased in EBR-treated *Vigna unguiculata* as a result of an increase in P_N and a synchronous decrease in C_i (Santos et al. 2018). An increase in the P_N/C_i ratio showed that EBR acted on Rubisco and enhanced CO_2 photoassimilation (Wahid et al. 2008).

EBR facilitated the effects of Cd treatment on the levels of other nutrient metals in plants, which reduced impairment of ionic homeostasis in tissues (Saidi et al. 2013). In *Vigna unguiculata*, EBR maintained the concentrations of Fe and Mn required for Chl biosynthesis (Lopes Júnior et al. 2014). EBR mitigated the toxic effects of Cd, contributing to an increase in Chl *a* and *b* in *Vigna* (Santos et al. 2018), Chl *b* in *Phaseolus* (Rady 2011) and total Chl in *Brassica juncea* (Hayat et al. 2007) and radish plants (Anuradha and Rao 2009).

BR mitigates the negative effects of Cd on fluorescence parameters, primarily by preventing the RC destruction and supporting TR_0/CS and ET_0/CS. The stimulatory effects of BR on F_v/F_m have been observed under various adverse conditions, namely, phenanthrene and pesticide contamination, as well as cooling (Cui et al. 2011). The EBR use in rape seedlings reduced the effects of inhibiting photochemical processes caused by Cd, reducing damage to photochemical RC and OEC, and also supporting efficient transport of the photosynthetic electron. EBR enhanced TR_0/CS, ET_0/CS, and φP_0, as well as Ψ_0. EBR limited the Cd-induced increase in dissipation of excitation energy (DI_0/CS), while at the same time protecting the OEC complex from a decrease in activity (Janeczko et al. 2005).

EBR mitigated the negative actions of Cd in the light phase of photosynthesis in plants *Vigna unguiculata* (Santos et al. 2018), *Triticum aestivum* (Hayat et al. 2014), *Phaseolus vulgaris* (Wael et al. 2015), and *Carthamus tinctorius* (Moradi and Ehsanzadeh 2015), minimizing negative effects on F_0, F_m, and F_v/F_m. Janeczko et al. (2005) revealed an increase in F_m after EBR treatment of plants subjected to Cd stress. However, with a high Cd concentration in *Zea mays*, a decrease in F_m values was observed (Wang et al. 2009). The use of EBR led to an increase in Φ_{PSII} and qP values in Cd-treated plants, which indicates an increase in photon absorption for use in photochemical reactions and an improvement in the ability of plants to absorb excitation energy in PSII reaction centers (Santos et al. 2018).

Epibrassinolide attenuates NPQ and the amount of excess energy of photosystem II in Cd-treated plants, thereby reducing thermal dissipation associated with excitation energy (Santos et al. 2018). This indicates an excessive excitation of photosystem II with an excess of light. In this case, excess energy can be eliminated by quenching to exclude the destruction of photosystem II (Silva et al. 2012). In plant photosystems, under the Cd influence, the electron transport rate decreases (Silveira et al. 2015). According to Santos et al. (2018), EBR treatment mitigated the negative effects of Cd on the ETR by increasing the redox efficiency of PQ.

Epibrassinolide treatment significantly increases photosynthetic assimilation of CO_2 (Anuradha and Rao 2009; Ahammed et al. 2012), contributing to an increase in dry weight of the plant (Hayat et al. 2000; Yu et al. 2004). BR increases the Chl content (Hayat et al. 2012), apparently as a result of the expression of genes synthesizing these pigments (Bajguz 2011). Epibrassinolide stimulates the activity of photosynthesis both by expressing genes and by increasing the enzyme activities of the Calvin cycle (Jiang et al. 2012).

In plants under Cd stress, a sharp reduction in the activity of carbonic anhydrase (EC 4.2.1.1) occurs (Anuradha and Rao 2009), which catalyzes the invertible conversion of HCO3 and CO_2 and thereby is able to regulate the CO_2 applicability for Rubisco (Badger and Price 1994). However, enzyme activity can be restored using EBR.

The molecular defense mechanism of photosynthetic reactions using EBR may enhance the activities of antioxidant systems (Rady 2011; Mazorra et al. 2002), which limit the development of Cd-induced oxidative stress (Ahammed et al. 2013). The use of EBR can reduce the content of ROS and MDA in affected plants, that is, BR can alleviate the effects of Cd stress (Hasan et al. 2008, 2011; Ahammed et al. 2012, 2013). Treatment with epibrassinolide reduces electrolyte leakage that occurs after treatment of plants with Cd (Allagulova et al. 2015; Santos et al. 2018). The decrease in oxidative stress is due to BR-induced enhancement of antioxidant activity and subsequent uptake of ROS (Cui et al. 2011).

Epibrassinolide increases the activities of glutathione S-transferase, peroxidase, and GR (Ahammed et al. 2012). The use of EBR under Cd stress can significantly increase the transcription of antioxidant enzyme genes (Ahammed et al. 2012, 2013). An increase in the activities of these enzymes can occur both by stimulating gene expression in de novo synthesis and by activating existing enzymes in response to BR treatment (Cui et al. 2011). Pretreatment of EBR radish seeds contributed to an increase in nitrate reductase activity under stress Cd (Anuradha and Rao 2009).

In addition, EBR treatment leads to the induction of secondary metabolism enzymes and also enhances their catalytic activity (Ahammed et al. 2013). The increased activity of phenylalanine ammonia lyase may contribute to the accumulation of phenols and flavonoids (Dixon and Paiva 1995), which can detoxify ROS (Wang et al. 2011). Activation of cinnamyl alcohol dehydrogenase means an increase in the cinnamic alcohol formation involved in the lignification process (Mitchell et al. 1994).

The efficiency of the protective effect of EBR increases in older tissues (Janeczko et al. 2005). This phenomenon may be due to a correlation between the increase in Cd toxicity and tissue age or the effects of heavy metals for a long time (Krupa and Moniak 1998). In plants subjected to simultaneous exposure to EBR and Cd, ETR/P_N value decrease, indicating that Mehler's reaction, photorespiration, and CO_2 assimilation used less photochemical energy (Fang et al. 2011). The ETR/P_N ratio can reflect the power of alternative electron sinks (Silva et al. 2010) and is used as a criterion for the rate of photorespiration as a defense system (Palliotti et al. 2015).

15.7.6 Decrease in Cd Toxicity Under Salt Stress

The effect of Cd on photosynthesis reactions can be largely indirect due to functional changes in other physiological processes (Burzyński and Kłobus 2004), for example, due to impaired absorption and distribution of nutrients (Krupa et al. 2002) and induction of ROS (Dietz et al. 1999). The disturbance of water metabolism observed in Cd stress (Poschenrieder and Barceló 1999) leads to an increase in stomatal resistance (Baryla et al. 2001) and, consequently, CO_2 absorption (He et al. 2008; Asgher et al. 2014). A decrease in the concentration required for the assimilation of intracellular CO_2 may lead to a decrease in the photosynthetic activity (Shi and Cai 2008; Ahammed et al. 2013; Xue et al. 2018).

The effect of Cd on photosynthesis occurs due to a change in the activity of reactions of the light and dark stages, as well as a decrease in the rate of Chl synthesis (Ebbs and Uchil 2008), and also by reducing the amount of the oxygen evolving complexes (Janeczko et al. 2005). The negative effects of Cd on Rubisco as the main CO2 fixation enzyme have been shown (Ishida et al. 1999).

The study of the effect of different concentrations of Cd in solution on wheat seedlings lacking the root system made it possible to exclude the effect of the root conducting system on metal absorption. Our studies have shown that Cd reduces the rate of photosynthesis (Table 15.1). The introduction of Cd into the solution caused a reduction in the ETR of chloroplasts, the maximum rate and efficiency of the carboxylation reaction, and the rate of utilization of triose phosphates.

Changes in the physiological parameters of the leaves were observed for 4 days using high (0.1 mM) and ultrahigh (1 and 5 mM) concentrations of Cd^{2+}. The use of 0.1 and 1 mM Cd^{2+} led to a gradual decline in the relative water content and Chl content in the leaves, as well as in the rate of photosynthesis, as assessed by the photosynthetic O_2 evolution rate (Figs. 15.1–15.3). At ultrahigh concentrations (5 mM) of Cd^{2+}, a significant decrease in photosynthetic activity occurred already during the first hours after treatment with Cd.

The violation of water metabolism of plants under the action of Cd occurred simultaneously with a decline in the water content in the leaves, which is very similar to the process observed at salinity. The simultaneous presence of Cd in a 50 mM NaCl solution led to the activation of anti-stress defense mechanisms. The presence of NaCl in solutions with a high concentration of Cd^{2+} (0.1 and 1 mM) had a paradoxically positive effect on the photosynthetic O_2 evolution rate. In the first 6 h of incubation, a sharp decrease in photosynthetic activity occurred. Subsequently, the rate of O_2 release in the presence of Cd + NaCl exceeded that of plants with one Cd (Fig. 15.1a, b), which may be due to the inclusion of protective mechanisms. The mechanism of this phenomenon is not yet clear. Given the rapid response of plants, it is possible that Na^+ has a direct effect on the oxygen evolving complex PSII, removing the inhibitory effect of Cd. The addition of NaCl had no noticeable effect on the relative content of water and Chl in the leaves of the plants, although their content decreased during the experiment (Figs. 15.2 and 15.3). The extremely high concentration of Cd^{2+} (5 mM) caused a rapid irreversible decline in photosynthetic activity despite the presence of NaCl (Fig. 15.1c).

Table 15.1 The P_N/C_i curve parameters of *Triticum aestivum* seedlings treated with 0.1 mM Cd^{2+}

Parameters	Control	0.1 mM Cd
The maximal rate of CO_2 uptake, μmol CO_2 m^{-2} s^{-1}	5.96 ± 0.22	3.84 ± 0.12
Rate of nonphotorespiratory CO_2 efflux in the light, μmol CO_2 m^{-2} s^{-1}	0.41 ± 0.02	0.46 ± 0.02
Efficiency of carboxylation, μmol CO_2 m^{-2} s^{-1} Pa^{-1}	0.17 ± 0.01	0.13 ± 0.01
The maximal rate of a carboxylation, μmol m^{-2} s^{-1}	6.15 ± 0.26	4.0 ± 0.22
Rate of electronic transport at a light saturation, μmol m^{-2} s^{-1}	15.9 ± 0.81	7.6 ± 0.32
Rate of recycling triosophosphates, μmol m^{-2} s^{-1}	1.27 ± 0.08	1.1 ± 0.05

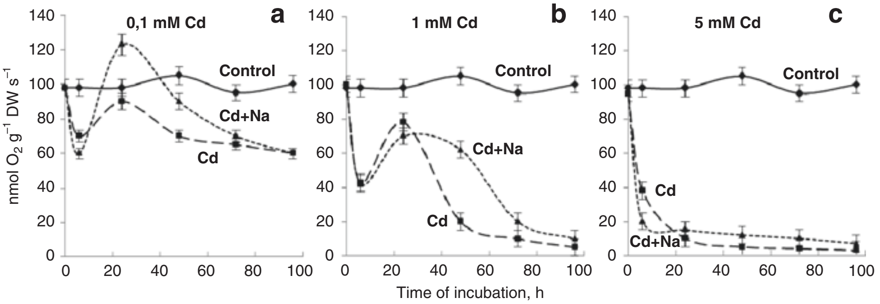

Fig. 15.1 Photosynthetic release of O_2 during incubation of wheat seedlings in Cd^{2+} solutions of various concentrations with the addition of 50 mM NaCl

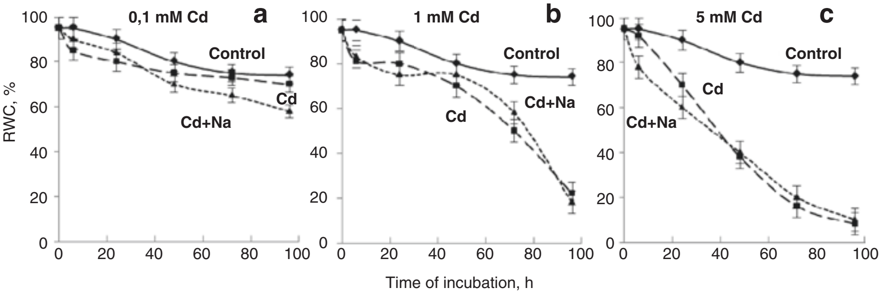

Fig. 15.2 Relative water content (RWC) of wheat seedlings in Cd^{2+}solutions of various concentrations with the addition of 50 mM NaCl

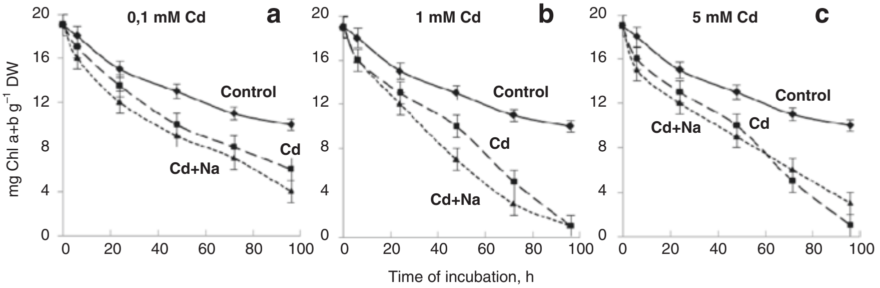

Fig. 15.3 The total chlorophyll content in leaves of wheat seedlings in Cd^{2+}solutions of various concentrations with the addition of 50 mM NaCl

15.8 Cd Effect on C-Metabolism

The carbohydrate metabolism of plants directly depends on the activity of the photosynthetic apparatus and its inhibition in the presence of Cd (Weigel 1985; Baszyński 1986). In the shoots of rice plants under the influence of Cd, the total content of carbohydrates increases, and the distribution of assimilates between organs also changes. Carbohydrate content increases in the stem and leaves, but remains unchanged in the roots (Moya et al. 1993). Large amounts of starch also accumulated in the cells of the microalga *Koliella antarctica* (La Rocca et al. 2009). Perhaps this is due to a sharp suppression of growth and a decrease in the nutritional need of cells (La Rocca et al. 2009). In contrast, sugar beet roots and shoots showed a decline in sugar after exposure to Cd (Greger and Bertell 1992).

In rice seedlings, treatment with 0.1 mM Cd blocked the movement of stored carbohydrates from seeds to the rest of the plant (Moya et al. 1993). A decrease in transport speed may result from the slowdown in several transport processes, including loading, transferring, and unloading (Samarakoon and Rauser 1979). A larger upbuilding of carbohydrates in the seeds may be associated with a lesser loading in the source areas. Blocking the movement of stored carbohydrates and reducing unloading in the final tissue explain the accumulation of substances in the stem, but not in the root.

On the other hand, the accumulation of carbohydrates may be associated with an increase in the glyoxylate pathway under the conditions of disturbance of the dark reactions of photosynthesis in Cd-treated plants. Indeed, under these conditions, the activation of glyoxylate pathway enzymes, namely isocitrate lyase and malate synthase, has been shown (Gillet et al. 2006). An increase in the activity of one of the glycolysis enzymes, phosphoglycerate mutase, was also noted. However, due to the reversibility of the reaction, under conditions of Cd stress, this enzyme is apparently involved in the process of gluconeogenesis and the synthesis of sugars from acetate.

Under conditions of Cd stress, a significant accumulation of starch occurred in rape culture (Shukla et al. 2003). In this regard, the reaction of the plant to the presence of Cd is similar to the reaction of photosynthetic plant tissues to darkness. Filek et al. (2010) suggested that starch accumulation may be due to the formation of a starch radical as a result of redox processes induced by Cd, when excess electrons are fixed on the starch polymer matrix.

On the other hand, during starch accumulation, Cd binds to SH groups of fructose 1,6-bisphosphatase in the cytosol, which inhibits the synthesis of sucrose and limits the recirculation of phosphates between the cytoplasm and chloroplasts (Sharkey 1990). Inhibition of P-metabolism enhances starch synthesis. Similar processes occur at high CO_2 or low temperatures in C3 plants (Pietrini et al. 2003).

At the same time, Gillet et al. (2006) observed an increase in uridine diphosphate (UDP)-glucose:protein transglucosylase activity (EC 2.4.1.112) involved in the synthesis of protein-bound alpha-glucan. The enzyme may be associated with reversible glycosylated polypeptides, which are highly conserved plant-specific proteins, which can perform self-glycosylation. This increase may be the reason for the accumulation of starch in Cd-treated plant cells (Nishikawa et al. 2003).

15.9 Cd Effect on N-Metabolism

Carbon dioxide is the final electron acceptor of the transport chain of photosystems. In conditions of CO_2 deficiency, for example, in the case of Cd stress, excess light energy is partially dissipated (Qiu et al. 2003), but can also be used to recover alternative electron acceptors (Eichelmann et al. 2011), for example, NO_2^-, the reduction of which occurs by means of a light-dependent nitrite reductase. Since eight electrons are required for the photoassimilation of each NO_2^- molecule into glutamate, compared to four electrons for CO_2 assimilation (Robinson 1986), photoreduction of carbon dioxide predominates under normal conditions. It would seem that under the conditions of CO_2 limiting under Cd stress, the main flow of the electron transport chain can be redirected to the restoration of alternative electron acceptors. Indeed, a decrease in photosynthetic activity under Cd stress is accompanied by an increase in demand for N-compounds in the plant, which may be due to the participation of N in the regulation of photosynthesis (Marschner 1995). However, in the plant there is a close relationship between C and N metabolism. There is a synchronous decrease in photosynthesis and photosynthetic nitrogen-use efficiency (Khan and Khan 2014). In turn, a correlation was found between the N content and photosynthesis activity (Iqbal et al. 2011), as well as the Rubisco content and S-metabolism (Iqbal et al. 2012). N limiting can lead to a high decrease in the photosynthetic efficiency (Resurreccion et al. 2001). In fact, treatment with high concentrations of Cd reduces the total N content, which leads to an imbalance between C, S, and N metabolism and, as a result, growth inhibition and a decrease in resistance to Cd stress (Gill et al. 2012).

It is assumed that a decrease in nitrogen use efficiency implies a lower N quota appropriated to the photosynthetic apparatus (Takashima et al. 2004). Indeed, in the presence of Cd, a decrease in the activity of nitrate reductase was observed (Anuradha and Rao 2009; Gill et al. 2012), a key enzyme for fixing inorganic N from the soil, reducing NO_3^- to NO_2^-. At relatively high Cd levels (100 µM), is decreased glutamine synthetase activity (Devriese et al. 2001), which catalyzes the synthesis of glutamine from glutamate and NH^{4+}. Gillet et al. (2006) suggested that low glutamine synthetase activity in the cytosol and chloroplasts under Cd stress may be associated with an inhibition at the expression level. Inhibition of glutamine synthetase may contribute to an increase in the level of glutamate required for the biosynthesis of proline, glutathione, and phytochelatins. This assumption is also confirmed by an increase in the activities of methionine synthetase, catalyzing the final stage of methionine biosynthesis, and S-adenosylmethionine synthetase, catalyzing the first stage of cysteine biosynthesis from methionine (Gillet et al. 2006). Cysteine can later be used for glutathione biosynthesis.

As a result of inhibition of photosynthetic activity due to Cd stress, it becomes necessary to obtain ATP from other sources. In this case, enzymatic pathways with a lower consumption of ATP per electron begin to prevail (Eichelmann et al. 2011), which is accompanied by the formation of additional ATP (Noctor and Foyer 1998), which can be used in the synthesis of secondary metabolism substances. In plants at Cd stress, ATP synthase activity may increase, leading to activation of ATP metabolism and consumption (Kalaji et al. 2014). Gillet et al. (2006) found that with Cd stress there is an increased expression of ATPases in various organelles, as well as inorganic pyrophosphatase. Nishikawa et al. (2003) revealed a correlation between P-metabolism and Cd detoxification during vacuolization.

15.10 Proline Accumulation

Cadmium toxicity can also be neutralized by proline accumulation (Siripornadulsil et al. 2002). In fact, the accumulation of nitrogen-containing compounds, including proline, is part of a general strategy for adapting plants to the negative effects of various stresses (Hare and Cress 1997). Cadmium is one of the strongest producers of proline among other heavy metals (Alia 1991). Increased resistance to Cd stress as a result of proline accumulation has been shown in several studies (Shevyakova et al. 2003; Moradi and Ehsanzadeh 2015). Synthesis of proline is carried out with the expenditure of a large amount of energy. However, under stressful conditions, these costs are justified, since in large quantities proline is able to maintain cell homeostasis (Hare and Cress 1997), stabilize the enzyme structure (Demiral and Türkan 2005), enhance membrane stability, and participate in ROS protection (Khan et al. 2007). An increase in the $NADP^+$/NADPH ratio as a result of proline biosynthesis stimulates the oxidative pentose phosphate pathway and, thus, provides precursors for the production of secondary metabolites (Hare and Cress 1997). In addition, proline can serve as an energy source in the restoration of plants after stress exposure (Hare and Cress 1997).

15.11 Conclusion

Various mechanisms of the toxic effect of cadmium on plant photosynthesis are presented. The action of Cd can be divided into a direct effect on the photosynthetic apparatus in chloroplasts and indirectly, with the participation of various physiological and metabolic processes localized both in the leaves and in other organs of the plant. It is shown that there are many local targets for the action of Cd on the photosynthetic apparatus, which to some extent affect the photosynthesis process, among which it is difficult to single out the main direction of the toxic action of the ion. Accordingly, it is difficult to develop general principles for counteracting Cd toxicity on the photosynthetic apparatus. The most effective way to avoid the effects of

Cd toxicity is to use plant species that are most resistant to the absorption of Cd from the soil. The remaining measures of protection against absorbed Cd are in the process of formation and study of the physiological and biochemical bases of the existing mechanisms. We hope that this review will help solve this problem.

References

Afkar E, Ababna H, Fathi AA (2010) Toxicological response of the green alga *Chlorella vulgaris* to some heavy metals. Am J Environ Sci 6:230–237

Aghaz M, Bandehagh A (2013) Phytotoxic effects of cadmium on photosynthesis pigments in dill (*Anethum graveolens*). Int J Farm Alli Sci 2:544–548

Ahammed GJ, Yuan HL, Ogweno JO, Zhou YH, Xia XJ, Mao WH, Shi K, Yu JQ (2012) Brassinosteroid alleviates phenanthrene and pyrene phytotoxicity by increasing detoxification activity and photosynthesis in tomato. Chemosphere 86:546–555

Ahammed GJ, Choudhary SP, Chen S, Xia X, Shi K, Zhou Y, Yu J (2013) Role of brassinosteroids in alleviation of phenanthrene–cadmium co-contamination-induced photosynthetic inhibition and oxidative stress in tomato. J Exp Bot 64:199–213

Ahmad I, Naeem M, Khan NA, Samiullah (2009) Effects of cadmium stress upon activities of antioxidative enzymes, in leaves and chloroplasts of wheat cultivars differing in yield potential. Photosynthetica 47:146–151

Ahmad P, Sarwat M, Bhat NA, Wani MR, Kazi AG, Tran LSP (2015) Alleviation of cadmium toxicity in *Brassica juncea* L. (Czern & Coss.) by calcium application involves various physiological and biochemical strategies. PLoS One 10:e0114571. https://doi.org/10.1371/journal.pone.0114571

Ahmed A, Tajmir-Riahi HA (1993) Interaction of toxic metal ions Cd^{2+}, Hg^{2+} and Pb^{2+} with light harvesting proteins of chloroplast thylakoid membranes. An FTIR studies. J Inorg Chem 50:235–243

Akhter MF, McGarvey B, Macfie SM (2012) Reduced translocation of cadmium from roots is associated with increased production of phytochelatins and their precursors. J Plant Physiol 169:1821–1829

Ali E, Maodzeka A, Hussain N, Shamsi IH, Jiang LX (2015) The alleviation of cadmium toxicity in oilseed rape (*Brassica napus*) by the application of salicylic acid. Plant Growth Regul 75:641–655

Alia SPP (1991) Proline accumulation under heavy metal stress. J Plant Physiol 138:554–558

Allagulova CR, Maslennikova DR, Avalbaev AM, Fedorova KA, Yuldashev RA, Shakirova FM (2015) Influence of 24-epibrassinolide on growth of wheat plants and the content of dehydrins under cadmium stress. Russ J Plant Physiol 62:465–471

Alyemeni MN, Hayat S, Wijaya L, Anaji (2013) A foliar application of 28-homobrassinolide mitigates salinity stress by increasing the efficiency of photosynthesis in *Brassica juncea*. Acta Bot Bras 27:502–505

Angadi S-B, Mathad P (1998) Effect of copper, cadmium and mercury on the morphological, physiological and biochemical characteristics of *Scenedesmus quadricauda* (Turp.) de Breb. J Environ Biol 19:119–124

Anjum SA, Tanveer M, Hussain S, Bao M, Wang L, Khan I, Ullah E, Tung SA, Samad RA, Shahzad B (2015) Cadmium toxicity in maize (*Zea mays* L.): consequences on antioxidative systems, reactive oxygen species and cadmium accumulation. Environ Sci Pollut Res 22:17022–17030

Anuradha S, Rao SSS (2001) Effects of brassinosteroids on salinity stress induced inhibition of germination and seedling growth of rice (*Oryza sa*tiva. L.). Plant Growth Regul 33:151–153

Anuradha S, Rao SSR (2009) Effect of 24-epibrassinolide on the photosynthetic activity of radish plants under cadmium stress. Photosynthetica 47:317–320

Araújo JCT, Nascimento CWA, Cunha Filho FF (2011) Availability of silicon and maize biomass in a lead contaminated soil treated with silicate. Ciênc Agrotec 35:878–883. [In Portuquese]

Asada K, Heber U, Schreiber U (1992) Pool size of electrons that can be donated to P700+ as determined in intact leaves: donation to $P700^+$ from stromal components via the intersystem chain. Plant Cell Physiol 33:927–932

Asgher M, Khan NA, Khan MIR, Fatma M, Masood A (2014) Ethylene production is associated with alleviation of cadmium-induced oxidative stress by sulfur in mustard types differing in ethylene sensitivity. Ecotoxicol Environ Saf 106:54–61

Atal N, Saradhi PP, Mohanty P (1991) Inhibition of chloroplast photochemical reactions by treatments of wheat seedlings with low concentration of cadmium: analysis of electron transport activities and changes in fluorescence yield. Plant Cell Physiol 32:943–951

Badger MR, Price GD (1994) The role of carbonic anhydrase in photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 45:369–392

Bajguz A (2000) Blockade of heavy metals accumulation in *Chlorella vulgaris* cells by 24-epibrassinolide. Plant Physiol Biochem 38:797–801

Bajguz A (2010) An enhancing effect of exogenous brassinolide on the growth and antioxidant activity in *Chlorella vulgaris* cultures under heavy metals stress. Environ Exp Bot 68:175–179

Bajguz A (2011) Suppression of *Chlorella vulgaris* growth by cadmium, lead and copper stress and its restoration by endogenous brassinolide. Arch Environ Contam Toxicol 60:406–416

Bajguz A, Hayat S (2009) Effects of brassinosteroids on the plant responses to environmental stresses. Plant Physiol Biochem 47:1–8

Bajguz A, Tretyn A (2003) The chemical characteristic and distribution of brassinosteroids in plants. Phytochemistry 62:1027–1046

Baker AJM (1981) Accumulators and excluders—strategies in response of plants to heavy metals. J Plant Nutr 3:643–654

Baker NR, Rosenquist E (2004) Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. J Exp Bot 55:1607–1621

Balakhnina TI, Matichenkov VV, Wlodarczyk T, Borkowska A, Nosalewicz M, Fomina IR (2012) Effects of silicon on growth processes and adaptive potential of barley plants under optimal soil watering and flooding. Plant Growth Regul 67:35–43

Barbosa MAM, Lobato AKS, Pereira TS, Viana GDM, Barbosa JRS, Coelho KNN, Sampaio LS, Filho BGS, Silveira JAG (2014) Photosynthesis-involvement in modulation of ascorbate and glutathione in *Euterpe oleracea* plants exposed to drought. Not Bot Hortic Agrobo 42:119–127

Barceló J, Poschenrieder C, Andreu I, Gunsé B (1986) Cadmium-induced decrease of water stress resistance in bush bean plants (*Phaseolus vulgaris* L. cv. Contender) I. Effects of Cd on water potential, relative water content, and cell wall elasticity. J Plant Physiol 125:17–25

Barceló J, Vazquez MD, Poschenrieder C (1988) Structural and ultrastructural disorders in cadmium-treated bush bean plants (*Phaseolus vulgaris* L.). New Phytol 108:37–49

Baryla A, Carrier P, Franck F, Coulomb C, Sahut C, Havaux M (2001) Leaf chlorosis in oilseed rape plants (*Brassica napus*) grown on cadmium-polluted soil, causes and consequences for photosynthesis and growth. Planta 212:696–709

Basa B, Lattanzio G, Solti Á, Tóth B, Abadía J, Fodor F, Sárvári É (2014) Changes induced by cadmium stress and iron deficiency in the composition and organization of thylakoid complexes in sugar beet (*Beta vulgaris* L.). Environ Exp Bot 101:1–11

Bashir H, Qureshi MI, Ibrahim MM, Iqbal M (2015) Chloroplast and photosystems: impact of cadmium and iron deficiency. Photosynthetica 53:321–335

Baszyński T (1986) Interference of Cd^{2+} in functioning of the photosynthetic apparatus of higher plants. Acta Soc Bot Pol 55:291–304

Baszyński T, Wajda L, Król M, Wolińska D, Krupa Z, Tukendorf A (1980) Photosynthetic activities of cadmium-treated tomato plants. Physiol Plant 48:365–370

Bauddh K, Singh RP (2012) Growth, tolerance efficiency and phytoremediation potential of *Ricinus communis* (L.) and *Brassica juncea* (L.) in salinity and drought affected cadmium contaminated soil. Ecotoxicol Environ Saf 85:13–22

Bazzaz MB, Govindjee (1974) Effects of cadmium nitrate on spectral characteristics and light reactions of chloroplasts. Environ Lett 6:1–12

Begović L, Mlilnarić S, Antunović Dunić J, Katanić Z, Lončarić Z, Lepedus H, Cesar V (2016) Response of *Lemna minor* L. to short-term cobalt exposure: the effect on photosynthetic electron transport chain and induction of oxidative damage. Aquat Toxicol 175:117–126

Bekasova OD, Brekhovskikh AA, Moskvina MI (2002) The mechanism of detoxication of cadmium-ions by cyano-bacterium *Nostoc muscorum* with the participation of extra-cellular polysaccharides. Biofizika 47:515–523. [In Russ]

Belenghi B, Acconcia F, Trovato M, Perazzolli M, Bocedi A, Polticelli F, Ascenzi P, Delledonne M (2003) AtCYS1, a cystatin from *Arabidopsis thaliana*, suppresses hypersensitive cell death. Eur J Biochem 270:2593–2604

Bhatt I, Tripathi BN (2011) Plant peroxiredoxins: catalytic mechanisms, functional significance and future perspectives. Biotechnol Adv 29:850–859

Björkman O, Demmig B (1987) Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170:489–504

Boisvert S, Joly D, Carpentier R (2006) Quantitative analysis of the experimental O–J–I–P chlorophyll fluorescence induction kinetics. Apparent activation energy and origin of each kinetic step. FEBS J 273:4770–4777

Bosabalidis AM, Kofidis G (2002) Comparative effects of drought stress on leaf anatomy of two olive cultivars. Plant Sci 163:375–379

Boutraa T, Akhkha A, Al-Shoaibi AA, Alhejeli AM (2010) Effect of water stress on growth and water use efficiency (WUE) of some wheat cultivars (*Triticum durum*) grown in Saudi Arabia. J Taibah Univ Sci 3:39–48

Broadhurst CL, Bauchan GR, Murphy CA, Tang YT, Pooley C, Davis AP, Chaney RL (2013) Accumulation of zinc and cadmium and localization of zinc in *Picris divaricata* Vant. Environ Exp Bot 87:1–9

Burzyński M, Kłobus G (2004) Changes of photosynthetic parameters in cucumber leaves under Cu, Cd, and Pb stress. Photosynthetica 42:505–510

Burzyński M, Żurek A (2007) Effects of copper and cadmium on photosynthesis in cucumber cotyledons. Photosynthetica 45:239–244

Cakmak L (2000) Possible roles of zinc in protecting plant cells from damage by reactive oxygen species. New Phytol 146:185–205

Cakmak I, Welch RM, Hart J, Norvell WA, Ozturk L, Kochian LV (2000) Uptake and retranslocation of leaf-applied cadmium (^{109}Cd) in diploid, tetraploid and hexaploid wheats. J Exp Bot 51:221–226

Castagna A, Di Baccio D, Tognetti R, Ranieri A, Sebastiani L (2013) Differential ozone sensitivity interferes with cadmium stress in poplar clones. Biol Plant 57:313–324

Chaneva G, Parvanova P, Tzvetkova N, Uzunova A (2010) Photosynthetic response of maize plants against cadmium and paraquat impact. Water Air Soil Pollut 208:287–293

Chaoui A, Mazhoudi S, Habib Ghorbal M, El Ferjani E (1997) Cadmium and zinc induction of lipid peroxidation and effects on antioxidant enzyme activities in bean (*Phaseolus vulgaris* L.). Plant Sci 127:139–147

Chen X, Wang J, Shi Y, Zhao MQ, Chi GY (2011) Effects of cadmium on growth and photosynthetic activities in pakchoi and mustard. Bot Stud 52:41–46

Cherif J, Derbel N, Nakkach M, Bergmann H, Jemal F, Lakhdar ZB (2012) Spectroscopic studies of photosynthetic responses of tomato plants to the interaction of zinc and cadmium toxicity. J Photochem Photobiol B 111:9–16

Cho U-H, Seo N-H (2005) Oxidative stress in *Arabidopsis thaliana* exposed to cadmium is due to hydrogen peroxide accumulation. Plant Sci 168:113–120

Choi Y-E, Harada E, Wada M, Tsuboi H, Morita Y, Kusano T, Sano H (2001) Detoxification of cadmium in tobacco plants: formation and active excretion of crystals containing cadmium and calcium through trichomes. Planta 213:45–50

Choppala G, Bolan N (2014) Cellular mechanisms in higher plants governing tolerance to cadmium toxicity. Crit Rev. Plant Sci 33:374–391

Chow WS, Hope AB (2004) Electron fluxes through photosystem I in cucumber leaf discs probed by far-red light. Photosynth Res 81:77–89

Christen D, Schönmann S, Jermini M, Strasser RJ, Dèfago G (2007) Characterization and early detection of grapevine (*Vitis vinifera*) stress responses to esca disease by in situ chlorophyll fluorescence and comparison with drought stress. Environ Exp Bot 60:504–514

Ci D, Jiang D, Dai T, Jing Q, Cao W (2009) Effects of cadmium on plant growth and physiological traits in contrast wheat recombinant inbred lines differing in cadmium tolerance. Chemosphere 77:1620–1625

Ci D, Jiang D, Wollenweber B, Dai T, Jing Q, Cao W (2010) Cadmium stress in wheat seedlings: growth, cadmium accumulation and photosynthesis. Acta Physiol Plant 32:365–373

Clemens S, Aarts MGM, Thomine S, Verbruggen N (2013) Plant science: the key to preventing slow cadmium poisoning. Trends Plant Sci 18:92–99

Cobbett CS (2000) Phytochelatins and their roles in heavy metal detoxification. Plant Physiol 123:825–832

Coleman J, Blake-Kalff M, Davies E (1997) Detoxification of xenobiotics by plants: chemical modification and vacuolar compartmentation. Trends Plant Sci 2:144–151

Costa ETS, Guilherme LRG, de Melo ÉEC, Ribeiro B, Inácio ESB, Severiano EC, Faquin V, Hale B (2012) Assessing the tolerance of castor bean to Cd and Pb for phytoremediation purposes. Biol Trace Elem Res 145:93–100

Cui JX, Zhou YH, Ding JG, Xia XJ, Shi K, Chen SC, Asami T, Chen ZX, Yu JQ (2011) Role of nitric oxide in hydrogen peroxide-dependent induction of abiotic stress tolerance by brassinosteroids in cucumber. Plant Cell Environ 34:347–358

Dafré AL, Sies H, Akerboom T (1996) Protein *S*-thiolation and regulation of microsomal glutathione transferase activity by the glutathione redox couple. Arch Biochem Biophys 332:288–294

Dalla Vecchia F, La Rocca N, Moro I, de Faveri S, Andreoli C, Rascio N (2005) Morphogenetic, ultrastructural and physiological damages suffered by submerged leaves of Elodea canadensis exposed to cadmium. Plant Sci 168:329–338

Dangl JL, Dietrich RA, Thomas H (2000) Senescence and programmed cell death. In: Buchanan BB, Gruissem W, Jones RL (eds) Biochemistry and molecular biology of plants. American Society of Plant Physiologists, Rockville, pp 1044–1100

Degl'Innocenti E, Castagna A, Ranieri A, Guidi L (2014) Combined effects of cadmium and ozone on photosynthesis of *Lycopersicon esculentum*. Photosynthetica 52:179–185

Demiral T, Türkan I (2005) Comparative lipid peroxidation, antioxidant defense systems and proline content in roots of two rice cultivars differing in salt tolerance. Environ Exp Bot 53:247–257

Deng G, Li M, Li H, Yin L, Li W (2014) Exposure to cadmium causes declines in growth and photosynthesis in the endangered aquatic fern (*Ceratopteris pteridoides*). Aquat Bot 112:23–32

Devriese M, Tsakaloudi V, Garbayo I, León R, Vílchez C, Vigara J (2001) Effect of heavy metals on nitrate assimilation in the eukariotic microalga *Chlamydomonas reinhardtii*. Plant Physiol Biochem 39:443–448

Di Cagno R, Guidi L, Stefani A, Soldatini GF (1999) Effects of cadmium on growth of Heliantus annus seedlings: physiological aspects. New Phytol 144:65–71

Di Cagno R, Guidi L, De Gara L, Soldatini GF (2001) Combined cadmium and ozone treatments affect photosynthesis and ascorbate-dependent defenses in sunflower. New Phytol 151:627–636

Dietz KJ, Baier M, Krämer U (1999) Free radicals and reactive oxygen species as mediators of heavy metal toxicity. In: Prasad MNV, Hagemayer J (eds) Heavy metal stress in plants. From molecules to ecosystems. Springer-Verlag, Berlin, pp 73–97

Dixit S, Singh DP (2015) Differential response of photosynthetic apparatus of cyanobacterium *Nostoc muscorum* to Pb and Cd toxicity. Photosynthetica 53:223–230

Dixon RA, Paiva NL (1995) Stress-induced phenylpropanoid metabolism. Plant Cell 7:1085–1097

Dominguez-Solis JR, Gutierrez-Alcala G, Romero LC, Gotor C (2001) The cytosolic O-actylserine(thiol)lyase gene is regulated by heavy metals and can function in cadmium tolerance. J Biol Chem 276:9297–9302

Dudkowiak A, Olejarz B, Łukasiewicz J, Banaszek J, Sikora J, Wiktorowicz K (2011) Heavy metals effect on cyanobacteria *Synechocystis aquatilis* study using absorption, fluorescence, flow cytometry, and photothermal measurements. Int J Thermophys 32:762–773

Eason JR, West PJ, Brummell DA, Watson LM, Somerfield SD, McLachlan ARG (2014) Overexpression of the protease inhibitor BoCPI-1 in broccoli delays chlorophyll loss after harvest and causes down-regulation of cysteine protease gene expression. Postharvest Biol Tecvnol 97:23–31

Ebbs S, Uchil S (2008) Cadmium and zinc induced chlorosis in Indian mutard [*Brassica juncea* (L.) Czern] involves preferential loss of chlorophyll *b*. Photosynthetica 46:49–55

Eichelmann H, Oja V, Peterson RB, Laisk A (2011) The rate of nitrite reduction in leaves as indicated by O_2 and CO_2 exchange during photosynthesis. J Exp Bot 62:2205–2215

Ekmekçi Y, Tanyolaç BD, Ayhan B (2008) Effects of cadmium on antioxidant enzyme and photosynthetic activities in leaves of two maize cultivars. J Plant Physiol 165:600–611

Ekvall L, Greger M (2003) Effects of environmental biomass producing factors on Cd uptake in two Swedish ecotypes of *Pinus sylvestris*. Environ Pollut 121:401–411

Ernst WHO, Verkleij JAC, Schat H (1992) Metal tolerance in plants. Acta Bot Neerland 41:229–248

Fagioni M, D'Amici GM, Timperio AM, Zolla L (2009) Proteomic analysis of multiprotein complexes in the thylakoid membrane upon cadmium treatment. J Proteome Res 8:310–326

Faller P, Kienzler K, Krieger-Liszkay A (2005) Mechanism of Cd^{2+} toxicity: Cd^{2+} inhibits photoactivation of photosystem II by competitive binding to the essential Ca^{2+} site. Biochim. Biophys Acta 1706:158–164

Fan KC, His HC, Chen CW, Lee HL, Hseu ZY (2011) Cadmium accumulation and tolerance of mahogany (*Swietenia macrophylla*) seedlings for phytoextraction applications. J Environ Manage 92:2818–2822

Fang XW, Turner NC, Li FM, Li WJ, Guo XS (2011) Caragana korshinskii seedlings maintain positive photosynthesis during short-term, severe drought stress. Photosynthetica 49:603–609

Fargaová A (2001) Phytotoxic effects of Cd, Zn, Pb, Cu and Fe on *Sinapis alba* L. seedlings and their accumulation in roots and shoots. Biol Plant 44:471–473

Fariduddin Q, Ahmad A, Hayat S (2003) Photosynthetic response of *Vigna radiata* to pre-sowing seed treatment with 28-homobrassinolide. Photosynthetica 41:307–310

Farooq M, Wahid A, SMA B, Islam-ud-Din (2009) Improving water relations and gas exchange with brassinosteroids in rice under drought stress. J Agron Crop Sci 195:262–269

Farooq MA, Detterbeck A, Clemens S, Dietz K-J (2016) Silicon-induced reversibility of cadmium toxicity in rice. J Exp Bot 67:3573–3585

Fediuc E, Erdei L (2002) Physiological and biochemical aspects of cadmium toxicity and protective mechanisms induced in *Phragmites australis* and *Typha latifolia*. J Plant Physiol 159:265–271

Feng J, Shi Q, Wang X, Wei M, Yang FJ, Xu HN (2010) Silicon supplementation ameliorated the inhibition of photosynthesis and nitrate metabolism by cadmium (Cd) toxicity in *Cucumis sativus* L. Sci Hortic 123:521–530

Fernández R, Bertrand A, Reis R, Mourato MP, Martins LL, González A (2013) Growth and physiological responses to cadmium stress of two populations of *Dittrichia viscosa* (L.) Greuter. J Hazard Mater 244–245:555–562

Fernandez-Piñas F, Mateo P, Bonilla I (1995) Ultrastructural changes induced by selected cadmium concentrations in the cyano-bacterium Nostoc UAM208. J Plant Physiol 147:452–456

Filek M, Keskinen R, Hartikainen H, Szarejko I, Janiak A, Miszalski Z, Golda A (2008) The protective role of selenium in rape seedlings subjected to cadmium stress. J Plant Physiol 165:833–844

Filek M, Zembala M, Hartikainen H, Mieszalski Z, Kornaś A, Wietecka-Posłuszny R, Walas P (2009) Changes in wheat plastid membrane properties induced by cadmium and selenium in presence/absence of 2, 4-dichlorophenoxyacetic acid. Plant Cell Tiss Org Cult 96:19–28

Filek M, Kościelniak J, Łabanowska M, Bednarska E, Bidzńska E (2010) Selenium-induced protection of photosynthesis activity in rape (*Brassica napus*) seedlings subjected to cadmium stress. Fluorescence and EPR measurements. Photosynth Res 105:27–37

Flower DJ, Ludlow MM (1986) Contribution of osmotic adjustment to the dehydration tolerance of water stressed pigeon pea (*Cajanus cajan* (L.) Millsp) leaves. Plant Cell Environ 9:33–40

Foyer CH, Noctor G (2005) Oxidant and antioxidant signaling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant Cell Environ 28:1056–1071

Foyer CH, Rennenberg H (2000) Regulation of glutathione synthesis and its role in abiotic and biotic stress. In: Rennenberg H, Brunold C, De Kok LJ, Stulen I (eds) Sulfur nutrition and sulfur assimilation in higher plants. SPB Academic, The Hague, pp 127–153

Franić M, Galić V, Mazur M, Šimić D (2017) Effects of excess cadmium in soil on JIP-test parameters, hydrogen peroxide content and antioxidant activity in two maize inbreds and their hybrid. Photosynthetica 56:660–669

Fuhrer J (1982) Ethylene biosynthesis and cadmium toxicity in leaf tissue of beans *Phaseolus vulgaris* L. Plant Physiol 70:162–167

Gallego SM, Pena LB, Barcia RA, Azpilicueta CE, Iannone MF, Rosales EP, Zawoznik MS, Groppa MD, Benavides MP (2012) Unravelling cadmium toxicity and tolerance in plants: insight into regulatory mechanisms. Environ Exp Bot 83:33–46

Geiken B, Masojidek J, Rizzuto M, Pompili ML, Giardi MT (1998) Incorporation of [35S] methionine in higher plants reveals that stimulation of the D1 reaction centre II protein turnover accompanies tolerance to heavy metal stress. Plant Cell Environ 21:1265–1273

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 48:909–930

Gill SS, Khan NA, Tuteja N (2012) Cadmium at high dose perturbs growth, photosynthesis and nitrogen metabolism while at low dose it up regulates sulfur assimilation and antioxidant machinery in garden cress (*Lepidium sativum* L.). Plant Sci 182:112–120

Gillet S, Decottignies P, Chardonnet S, Maréchal PL (2006) Cadmium response and redoxin targets in *Chlamydomonas reinhardtii*: a proteomic approach. Photosynth Res 89:201–211

Gonçalves JF, Becker AG, Cargnelutti D, Tabaldi AL, Pereira LB, Battisti V, Spanevello RM, Morsch VM, Nicoloso FT, Schetinger MRC (2007) Cadmium toxicity causes oxidative stress and induces response of the antioxidant system in cucumber seedlings. Braz J Plant Physiol 19:223–232

Gouia H, Ghorbal MH, Meyer C (2000) Effects of cadmium on activity of nitrate reductase and on other enzymes of the nitrate assimilation pathway in bean. Plant Physiol Biochem 38:629–638

Gratão PL, Monteiro CC, Tezotto T, Carvalho RF, Alves LR, Peters LP, Azevedo RA (2015) Cadmium stress antioxidant responses and root-to-shoot communication in grafted tomato plants. Biometals 28:803–816

Greger M, Bertell G (1992) Effects of Ca^{2+} and Cd^{2+} on the carbohydrate metabolism in sugar beet (*Beta vulgaris*). J Exp Bot 43:167–173

Greger M, Löfstedt M (2004) Comparison of uptake and distribution of cadmium in different cultivars of bread and durum wheat. Crop Sci 44:501–507

Grill E, Winnacker E-L, Zenk MH (1985) Phytochelatins: the principal heavy metal complexing peptides of higher plants. Science 230:674–676

Grill E, Löffler S, Winnacker EL, Zenk MH (1989) Phytochelatins, the heavy-metal-binding peptides of plants, are synthesized from glutathione by a specific γ-glutamylcysteine dipeptidyl transpeptidase (phytochelatin synthase). Proc Natl Acad Sci U S A 86:6838–6842

Gruszecki WI, Veeranjaneyulu K, Zelent B, Leblanc RM (1991) Energy transfer process during senescence: fluorescence and photoacoustic studies of intact pea leaves. Biochim Biophys Acta 1056:173–180

Gu H, Qui H, Tian T, Zhan SS, Deng THB, Chaney RL, Wang SZ, Tang YT, Morel JL, Qiu RL (2011) Mitigation effects of silicon rich amendments on heavy metal accumulation in rice (*Oryza sativa* L.) planted on multi-metal contaminated acidic soil. Chemosphere 83:1234–1240

Hajduch M, Rakwal R, Agrawal GK, Yonekura M, Pretova A (2001) High-resolution two-dimensional electrophoresis separation of proteins from metal-stressed rice (*Oryza sativa* L.) leaves: drastic reductions/fragmentation of ribulose-1,5-bisphosphate carboxylase/oxygenase and induction of stress-related proteins. Electrophoresis 22:2824–2831

Hall JL (2002) Cellular mechanisms for heavy metal detoxification and tolerance. J Exp Bot 53:1–11

Hare PD, Cress WA (1997) Metabolic implications of stress-induced proline accumulation in plants. Plant Growth Regul 21:79–102

Hasan SA, Hayat S, Ali B, Ahmad A (2008) 28-homobrassinolide protects chickpea (*Cicer arietinum*) from cadmium toxicity by stimulating antioxidants. Environ Pollut 151:60–66

Hasan SA, Hayat S, Ahmad A (2011) Brassinosteroids protect photosynthetic machinery against the cadmium induced oxidative stress in two tomato cultivars. Chemosphere 84:1446–1451

Hattori T, Inanaga S, Araki H, An P, Morita S, Luxová M, Lux A (2005) Application of silicon enhanced drought tolerance in Sorghum bicolor. Physiol Plant 123:459–466

Haubrick LL, Assmann SM (2006) Brassinosteroids and plant function: some clues, more puzzles. Plant Cell Environ 29:446–457

Hayat S, Ahmad A, Mobin M, Hussain A, Fariduddin Q (2000) Photosynthetic rate, growth, and yield of mustard plants sprayed with 28-homobrassinolide. Photosynthetica 38:469–471

Hayat S, Ali B, Hasan SA, Ahmad A (2007) Brassinosteroid enhanced the level of antioxidants under cadmium stress in *Brassica juncea*. Environ Exp Bot 60:33–41

Hayat S, Hasan SA, Yusuf M, Hayat Q, Ahmad A (2010a) Effect of 28-homobrassinolide on photosynthesis, fluorescence and antioxidant system in the presence or absence of salinity and temperature in *Vigna radiata*. Environ Exp Bot 69:105–112

Hayat S, Hasan SA, Hayat Q, Ahmad A (2010b) Brassinosteroids protect *Lycopersicon esculentum* from cadmium toxicity applied as shotgun approach. Protoplasma 239:3–14

Hayat S, Alyemeni MN, Hasan SA (2012) Foliar spray of brassinosteroid enhances yield and quality of *Solanum lycopersicum* under cadmium stress. Saudi J Biol Sci 19:325–335

Hayat S, Khalique G, Wani AS, Alyemeni MN, Ahmad A (2014) Protection of growth in response to 28-homobrassinolide under the stress of cadmium and salinity in wheat. Int J Biol Macromol 64:130–136

He J-Y, Ren Y-F, Zhu C, Yan Y-P, Jiang D-A (2008) Effect of Cd on growth, photosynthetic gas exchange, and chlorophyll fluorescence of wild and Cd-sensitive mutant rice. Photosynthetica 46:466–470

Horváth G, Droppa M, Oravecz A, Raskin VI, Marder JB (1996) Formation of the photosynthetic apparatus during greening of cadmium-poisoned barley leaves. Planta 199:238–244

Hsu YT, Kao CH (2007) Heat shock-mediated H_2O_2 accumulation and protection against Cd toxicity in rice seedlings. Plant and Soil 300:137–147

Hutchison RS, Groom Q, Ort DR (2000) Differential effects of chilling-induced photooxidation on the redox regulation of photosynthetic enzymes. Biochemistry 39:6679–6688

Hwang JE, Hong JK, Lim CJ, Chen H, Je J, Yang KA, Kim DY, Choi YJ, Lee SY, Lim CO (2010) Distinct expression patterns of two *Arabidopsis phytocystatin* genes, AtCYS1 and AtCYS2, during development and abiotic stresses. Plant Cell Rep 29:905–915

Iannelli MA, Pietrini F, Fiore L, Petrilli L, Massacci A (2002) Antioxidant response to cadmium in *Phragmites australis* plants. Plant Physiol Biochem 40:977–982

Ilangovan K, Cañizares-Villanueva RO, Gonzáles Moreno S, Voltolina D (1998) Effect of cadmium and zinc on respiration and photosynthesis in suspended and immobilized cultures of *Chlorella vulgaris* and *Scenedesmus acutus*. Bull Environ Contam Toxicol 60:936–943

Inouhe M, Ninomiya S, Tohoyama H, Joho M, Murayama T (1994) Different characteristics of roots in the cadmium-tolerance and Cd-binding complex formation between mono- and dicotyledonous plants. J Plant Res 107:201–207

Iqbal N, Masood A, Nazar R, Syeed S, Khan NA (2010) Photosynthesis, growth and antioxidant metabolism in mustard (*Brassica juncea* L.) cultivars differing in cadmium tolerance. Agric Sci China 9:519–527

Iqbal N, Nazar R, Syeed S, Masood A, Khan NA (2011) Exogenously-sourced ethylene increases stomatal conductance, photosynthesis, and growth under optimal and deficient nitrogen fertilization in mustard. J Exp Bot 62:4955–4963

Iqbal N, Khan NA, Nazar R, da Silva JAT (2012) Ethylene-stimulated photosynthesis results from increased nitrogen and sulfur assimilation in mustard types that differ in photosynthetic capacity. Environ Exp Bot 78:84–90

Irfan M, Ahmad A, Hayat S (2014) Effect of cadmium on the growth and antioxidant enzymes in two varieties of *Brassica juncea*. Saudi J Biol Sci 21:125–131

Ishida H, Makino A, Mae T (1999) Fragmentation of the large subunit of ribulose-1,5-bisphosphate carboxylase by reactive oxygen species occurs near Gly-329. J Biol Chem 274:5222–5226

Ishikita H, Knapp E-W (2005) Induced conformational changes upon Cd^{2+} binding at photosynthetic reaction centers. PNAS 102:16215–16220

Ito H, Tanaka A (1996) Determination of the activity of chlorophyll *b* to chlorophyll *a* conversion during greening of etiolated cucumber cotyledons by using pyrochlorophyllide *b*. Plant Physiol Biochem 34:35–40

Jain M, Pal M, Gupta P, Gadre R (2007) Effect of cadmium on chlorophyll biosynthesis and enzymes of nitrogen assimilation in greening maize leaf segments: role of 2-oxoglutarate. Indian J Exp Biol 45:385–389

Janeczko A, Kościelniak J, Pilipowicz M, Szarek-Łukaszewska G, Skoczowski A (2005) Protection of winter rape photosystem 2 by 24-epibrassinolide under cadmium stress. Photosynthetica 43:293–298

Janicka-Russak M, Kabala K, Burzynski M (2012) Different effect of cadmium and copper on H^+-ATPase activity in plasma membrane vesicles from *Cucumis sativus* roots. J Exp Bot 63:4133–4142

Januškaitienė I (2010) Impact of low concentration of cadmium on photosynthesis and growth of pea and barley. Environ Res Eng Manag 53:24–29

Jia L, Liu Z, Chen W, Ye Y, Yu S, He X (2015) Hormesis effects induced by cadmium on growth and photosynthetic performance in a hyperaccumulator, Lonicera japonica Thunb. J Plant Growth Regul 34:13–21

Jiang YP, Cheng F, Zhou YH, Xia XJ, Shi K, Yu JQ (2012) Interactive effects of CO_2 enrichment and brassinosteroid on CO_2 assimilation and photosynthetic electron transport in *Cucumis sativus*. Environ Exp Bot 75:98–106

Judy BM, Lower WR, Miles CD, Thomas MW, Krause GF (1990) Chlorophyll fluorescence of a higher plant as an assay for toxicity assessment of soil and water. In: Wang W, Gorsuch JW, Lower WL (eds) Plants for toxicity assessment. American Society for Testing and Materials, Philadelphia, pp 308–318

Kalaji HM, Łoboda T (2007) Photosystem II of barley seedlings under cadmium and lead stress. Plant Soil Environ 53:511–516

Kalaji HM, Oukarroum A, Alexandrov V, Kouzmanova M, Brestic M, Zivcak M, Samborska IA, Cetner MD, Allakhverdiev SI, Goltsev V (2014) Identification of nutrient deficiency in maize and tomato plants by in vivo chlorophyll *a* fluorescence measurements. Plant Physiol Biochem 81:16–25

Kalaji HM, Jajoo A, Oukarroum A, Brestic M, Zivcak M, Samborska IA, Cetner MD, Łukasik I, Goltsev V, Ladle RJ (2016) Chlorophyll *a* fluorescence as a tool to monitor physiological status of plants under abiotic stress conditions. Acta Physiol Plant 38:1–11

Kaya C, Tuna AL, Sonmez O, Ince F, Higgs D (2009) Mitigation effects of silicon on maize plants grown at high zinc. J Plant Nutr 32:1788–1798

Khan MIR, Khan NA (2014) Ethylene reverses photosynthetic inhibition by nickel and zinc in mustard through changes in PSII activity, photosynthetic nitrogen use efficiency, and antioxidant metabolism. Protoplasma 251:1007–1019

Khan MN, Siddiqui MH, Mohammad F, Khan MMA, Naeem M (2007) Salinity induced changes in growth, enzyme activities, photosynthesis, proline accumulation and yield in linseed genotypes. World J Agric Sci 3:685–695

Khan NA, Anjum NA, Nazar R, Iqbal N (2009) Increased activity of ATP-sulfurylase and increased contents of cysteine and glutathione reduce high cadmium-induced oxidative stress in mustard cultivar with high photosynthetic potential. Russ J Plant Physiol 56:670–677

Khoshmanesh A, Lawson F, Prince IG (1996) Cadmium uptake by unicellular green microalgae. Chem Eng J 62:81–88

Koelmans AA, Gillissen F, Lijklema L (1996) Influence of salinity and mineralization on trace metal sorption to cyano-bacteria in natural waters. Water Res 30:853–864

Kovalchuk O, Titov V, Hohn B, Kovalchuk I (2001) A sensitive transgenic plant system to detect toxic inorganic compounds in the environment. Nat Biotechnol 19:568–572

Krall JP, Edwards GE (1992) Relationship between photosystem II activity and CO_2 fixation in leaves. Physiol Plant 86:180–187

Krantev A, Yordanova R, Janda T, Szalai G, Popova L (2008) Treatment with salicylic acid decreases the effect of cadmium on photosynthesis in maize plants. J Plant Physiol 165:920–931

Krevešan S, Kiršek S, Kandrač J, Petrović N, Kelemen DJ (2003) Dynamics of cadmium distribution in the intercellular space and inside cells in soybean roots, stems and leaves. Biol Plant 46:85–88

Kroutil M, Hejtmánková A, Lachman J (2010) Effect of spring wheat (*Triticum aestivum* L.) treatment with brassinosteroids on the content of cadmium and lead in plant aerial biomass and grain. Plant Soil Environ 56:43–50

Krüger GHJ, Tsimili-Michael M, Strasser RJ (1997) Light stress provokes plastic and elastic modifications in structure and function of photosystem II in camellia leaves. Physiol Plant 101:265–277

Krupa Z, Baszynski T (1995) Some aspects of heavy metals toxicity towards photosynthetic apparatus–direct and indirect effects on light and dark reactions: a review. Acta Physiol Plant 17:177–190

Krupa Z, Moniak M (1998) The stage of leaf maturity implicates the response of the photosynthetic apparatus to cadmium toxicity. Plant Sci 138:149–156

Krupa Z, Öquist G, Hunter NPA (1993) The effects of cadmium on photosynthesis of *Phaseolus vulgaris* L.—a fluorescence analysis. Physiol Plant 88:626–630

Krupa Z, Siedlecka A, Skórzynska-Polit E, Maksymiec W (2002) Heavy metal influence on the light phase of photosynthesis. In: Prasad MNV, Strzałka K (eds) Physiology and biochemistry of metal toxicity and tolerance in plants. Kluwer Academic, Dordrecht, pp 287–303

Kumari A, Sheokand S, Swaraj K (2010) Nitric oxide induced alleviation of toxic effects of short term and long term Cd stress on growth, oxidative metabolism and Cd accumulation in chickpea. Braz J Plant Physiol 22:271–284

Kunert KJ, van Wyk SG, Cullis CA, Vorster BJ, Foyer CH (2015) Potential use of phytocystatins in crop improvement, with a particular focus on legumes. J Exp Bot 66:3559–3570

Küpper H, Küpper F, Spiller M (1998) In situ detection of heavy metal substituted chlorophylls in water plants. Photosynth Res 58:123–133

Küpper H, Šetlík I, Spiller M, Küpper FC, Prášil O (2002) Heavy metal-induced inhibition of photosynthesis: targets of in vivo heavy metal chlorophyll formation. J Phycol 38:429–441

Küpper H, Parameswaran A, Leitenmaier B, Trtílek M, Setlík I (2007) Cadmium-induced inhibition of photosynthesis and long-term acclimation to cadmium stress in the hyperaccumulator *Thlaspi caerulescens*. New Phytol 175:655–674

La Rocca N, Andreoli C, Giacometti GM, Rascio N, Moro I (2009) Responses of the Antarctic microalga *Koliella antarctica* (Trebouxiophyceae, Chlorophyta) to cadmium contamination. Photosynthetica 47:471–479

Lang M, Zhang Y, Chai T (2005) Identification of genes upregulated in response to Cd exposure, in *Brassica juncea* L. Gene 363:151–158

Larsson EH, Bornman JF, Asp H (1998) Influence of UV-B radiation and Cd^{2+} on chlorophyll fluorescence, growth and nutrient content in *Brassica napus*. J Exp Bot 49:1031–1039

Laspina NV, Groppa MD, Tomaro ML, Benavides MP (2005) Nitric oxide protects sunflower leaves against Cd-induced oxidative stress. Plant Sci 169:323–330

Laube VM, McKenzie CN, Kushner DJ (1980) Strategies of response to copper, cadmium and lead by a blue-green and a green alga. Can J Microbiol 26:1300–1311

Lazarus M, Orct T, Blanusa M, Kostial K, Pirsljin J, Beer-Ljubic B (2006) Effect of selenium pretreatment on cadmium content and enzymatic antioxidants in tissues of suckling rat. Toxicol Lett 164:191

Leborans GF, Novillo A (1996) Toxicity and bioaccumulation of cadmium in *Olisthodiscus luteus* (Raphidophyceae). Water Res 30:57–62

Les A, Walker RW (1984) Toxicity and binding of copper, zinc, and cadmium by the blue-green alga, *Chroococcus paris*. Water Air Soil Pollut 23:129–140

Leustek T (2002) Sulfate metabolism. In: Somerville CR, Meyrowitz EM (eds) The arabidopsis book. American Society of Plant Biologist, Rockville, MD

Leustek K, Saito K (1999) Sulfate transport and assimilation in plants. Plant Physiol 120:637–644

Li Q, Lu Y, Shi Y, Wang T, Ni K, Xu L, Liu S, Wang L (2013) Combined effects of cadmium and fluoranthene on germination, growth and photosynthesis of soybean seedlings. J Environ Sci (China) 25:1936–1946

Li S, Yang W, Yang T, Chen Y, Ni W (2015) Effects of cadmium stress on leaf chlorophyll fluorescence and photosynthesis of *Elsholtzia argyi*–a cadmium accumulating plant. Int J Phytoremediation 17:85–92

Li X, Zhou Q, Sun X, Ren W (2016) Effects of cadmium on uptake and translocation of nutrient elements in different welsh onion (*Allium fistulosum* L.) cultivars. Food Chem 194:101–110

Lichtenthaler HK, Buschmann C, Knapp M (2005) How to correctly determine the different chlorophyll fluorescence parameters and the chlorophyll fluorescence decrease ratio RFd of leaves with the PAM fluorometer. Photosynthetica 43:379–393

Linger P, Ostwald A, Haensler J (2005) *Cannabis sativa* L. growing on heavy metal contaminated soil: growth, cadmium uptake and photosynthesis. Biol Plant 49:567–576

Liu J, Qian M, Cai G, Yang J, Zhu Q (2007) Uptake and translocation of Cd in different rice cultivars and the relation with Cd accumulation in rice grain. J Hazard Mater 143:443–447

Liu K-L, Shen L, Wang J-Q, Sheng J-P (2008) Rapid inactivation of chloroplastic ascorbate peroxidase is responsible for oxidative modification to Rubisco in tomato (*Lycopersicon esculentum*) under cadmium stress. J Integr Plant Biol 50:415–426

Liu X, Peng K, Wang A, Lian C, Shen Z (2010) Cadmium accumulation and distribution in populations of *Phytolacca americana* L. and the role of transpiration. Chemosphere 78:1136–1141

Liu C, Guo J, Cui Y, Láo T, Zhang X, Shi G (2011) Effects of cadmium and salicylic acid on growth, spectral reflectance and photosynthesis of castor bean seedlings. Plant and Soil 344:131–141

Liu S, Yang R, Pan Y, Ma M, Pan J, Zhao Y, Cheng Q, Wu M, Wang M, Zhang M (2015) Nitric oxide contributes to minerals absorption, proton pumps and hormone equilibrium under cadmium excess in *Trifolium repens* L. plants. Ecotoxicol Environ Saf 119:35–46

Liu H, Wang H, Ma Y, Wang H, Shi Y (2016) Role of transpiration and metabolism in translocation and accumulation n of cadmium in tobacco plants (*Nicotiana tabacum* L.). Chemosphere 144:1960–1965

Liu L, Shang YK, Li L, Chen YH, Qin ZZ, Zhou LJ, Yuan M, Ding CB, Liu J, Huang Y, Yang RW, Zhou YH, Liao JQ (2018) Cadmium stress in Dongying wild soybean seedlings: growth, Cd accumulation, and photosynthesis. Photosynthetica 56:1346–1352

Lombi E, Tearall KL, Howarth JR, Zhao FJ, Hawesford MJ, McGrath SP (2002) Influence of iron status on cadmium and zinc uptake by different ecotypes of the hyperaccumulator *Thlaspi caerulescens*. Plant Physiol 128:1359–1367

Lopes Júnior CA, Mazzafera P, Arruda MAZ (2014) A comparative ionomic approach focusing on cadmium effects in sunflowers (*Helianthus annuus* L.). Environ Exp Bot 107:180–186

Lösch R (2004) Plant mitochondrial respiration under the influence of heavy metals. In: Prasad MNV (ed) Heavy metal stress in plants: from biomolecules to ecosystems, 2nd edn. Springer, Berlin, pp 182–200

Lu L, Tian S, Zhang M, Zhang J, Yang X, Jiang H (2010) The role of Ca pathway in Cd uptake and translocation by the hyperaccumulator *Sedum alfredii*. J Hazard Mater 183:22–28

Lukačová Kuliková Z, Lux A (2010) Silicon influence on maize, *Zea mays* L. hybrids exposed to cadmium treatment. B Environ Contam Toxicol 85:243–250

Lukačová Z, Švubová R, Kohanová J, Lux A (2013) Silicon mitigates the Cd toxicity in maize in relation to cadmium translocation, cell distribution, antioxidant enzymes stimulation and enhanced endodermal apoplasmic barrier development. Plant Growth Regul 70:89–103

Lux A, Martinka M, Vaculík M, White PJ (2011) Root responses to cadmium in the rhizosphere: a review. J Exp Bot 62:21–37

Lysenko EA, Klaus AA, Pshybytko NL, Kusnetsov VV (2015) Cadmium accumulation in chloroplasts and its impact on chloroplastic processes in barley and maize. Photosynth Res 125:291–303

Lysenko EA, Klaus AA, Alexander V, Kartashov AV, Kusnetsov VV (2019) Distribution of Cd and other cations between the stroma and thylakoids: a quantitative approach to the search for Cd targets in chloroplasts. Photosynth Res 139:337–358

Ma JF, Yamaji N (2006) Silicon uptake and accumulation in higher plants. Trends Plant Sci 11:392–397

Ma JF, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Ishiguro M, Murata Y, Yano M (2006) A silicon transporter in rice. Nature 440:688–691

Maksymiec W (2007) Signaling responses in plants to heavy metal stress. Acta Physiol Plant 29:177–187

Maksymiec W, Baszyński T (1996) Different susceptibility of runner bean plants to excess copper as a function of the growth stages of primary leaves. J Plant Physiol 149:217–221

Malik D, Sheoran IS, Singh R (1992) Carbon metabolism in leaves of cadmium treated wheat seedlings. Plant Physiol Biochem 30:223–229

Mallick N, Mohn FH (2003) Use of chlorophyll fluorescence in metal-stress research: a case study with green microalga *Scenedesmus*. Ecotoxicol Environ Saf 55:64–69

Maret W, Moulis J-M (2013) The bioinorganic chemistry of cadmium in the context of its toxicity. In: Sigel A, Sigel H, Sigel R (eds) Cadmium: from toxicity to essentiality. Metal ions in life sciences, vol 11. Springer, Dordrecht, pp 1–29

Maria SD, Puschenreiter M, Rivelli AR (2013) Cadmium accumulation and physiological response of sunflower plants to Cd during the vegetative growing cycle. Plant Soil Environ 59:254–261

Marschner H (1995) Mineral nutrition of higher plants. Academic Press, London

Martínez M, Cambra I, González-Melendi P, Santamaría ME, Díaz I (2012) C1A cysteine-proteases and their inhibitors in plants. Physiol Plant 145:85–94

Masood A, Iqbal N, Khan NA (2012) Role of ethylene in alleviation of cadmium-induced photosynthetic capacity inhibition by sulfur in mustard. Plant Cell Environ 35:524–533

Masuda T, Tanaka A, Melis A (2003) Chlorophyll antenna size adjustments by irradiance in *Dunaliella salina* involve coordinate regulation of chlorophyll a oxygenase (CAO) and Lhcb gene expression. Plant Mol Biol 51:757–771

Mazorra LM, Núñez M, Hechavarria M, Coll F, Sánchez-Blanco MJ (2002) Influence of brassinosteroids on antioxidant enzymes activity in tomato under different temperatures. Biol Plant 45:593–596

Mendoza-Cozalt D, Devars S, Loza-Tavera H, Moreno-Sanchez R (2002) Cadmium accumulation in the chloroplast of *Euglena gracilis*. Physiol Plant 115:276–283

Meng H, Hua S, Shamsi I, Jilani G, Li Y, Jiang L (2009) Cadmium-induced stress on the seed germination and seedling growth of *Brassica napus* L. and its alleviation through exogenous plant growth regulators. Plant Growth Regul 58:47–59

Mishra S, Srivastava S, Tripathi RD, Govindarajan R, Kuriakose SV, Prasad MNV (2006) Phytochelatin synthesis and response of antioxidants during cadmium stress in *Bacopa monnieri* L. Plant Physiol Biochem 44:25–37

Mitani N, Ma JF, Iwashita T (2005) Identification of the silicon form in xylem sap of rice (*Oryza sativa* L.). Plant Cell Physiol 46:279–283

Mitani N, Yamaji N, Ma JF (2009) Identification of maize silicon influx transporters. Plant Cell Physiol 50:5–12

Mitchell HJ, Hall JL, Barber MS (1994) Elicitor-induced cinnamyl alcohol-dehydrogenase activity in lignifying wheat (*Triticum aestivum* L) leaves. Plant Physiol 104:551–556

Miyazawa SI, Terashima I (2001) Slow development of leaf photosynthesis in an evergreen broad-leaved tree, *Castanopsis sieboldii*: relationships between leaf anatomical characteristics and photosynthetic rate. Plant Cell Environ 24:279–291

Mo CH, Cai QY, Tang SR, Zeng QY, Wu QT (2009) Polycyclic aromatic hydrocarbons and phthalic acid esters in vegetables from nine farms of the Pearl River Delta, South China. Arch Environ Contam Toxicol 56:181–189

Mobin M, Khan NA (2007) Photosynthetic activity, pigment composition and antioxidative response of two mustard (*Brassica juncea*) cultivars differing in photosynthetic capacity subjected to cadmium stress. J Plant Physiol 164:601–610

Mohamed AA, Castagna A, Ranieri A, Toppi LS (2012) Cadmium tolerance in *Brassica juncea* roots and shoots is affected by antioxidant status and phytochelatin biosynthesis. Plant Physiol Biochem 57:15–22

Moradi L, Ehsanzadeh P (2015) Effects of Cd on photosynthesis and growth of safflower (*Carthamus tinctorius* L.) genotypes. Photosynthetica 53:506–518

Moya JL, Ros R, Picazo I (1993) Influence of cadmium and nickel on growth, net photosynthesis and carbohydrate distribution in rice plants. Photosynth Res 36:75–80

Murthy SDS, Sabat SC, Mohanty P (1989) Mercury-induced inhibition of PS II activity and changes in the emission of fluorescence from phycobilisomes in intact cells of the cyanobacterium *Spirulina platensis*. Plant Cell Physiol 30:1153–1157

Nagel K, Adelmeier U, Voigt J (1996) Subcellular distribution of cadmium in the unicellular green alga *Chlamydomonas reinhardtii*. J Plant Physiol 149:86–90

Najeeb U, Jilani G, Ali S, Sarwar M, Xu L, Zhou W (2011) Insights into cadmium induced physiological and ultra-structural disorders in *Juncus effusus* L. and its remediation through exogenous citric acid. J Hazard Mater 186:565–574

Nakamura S, Suzui N, Nagasaka T, Komatsu F, Ishioka NS, Ito-Tanabata S, Kawachi N, Rai H, Hattori H, Chino M, Fujimaki S (2013) Application of glutathione to roots selectively inhibits cadmium transport from roots to shoots in oilseed rape. J Exp Bot 64:1073–1081

Nedjimi B, Daoud Y (2009) Cadmium accumulation in *Atriplex halimus* subsp. *schweinfurthii* and its influence on growth, proline, root hydraulic conductivity and nutrient uptake. Flora 204:316–324

Nishikawa K, Yamakoshi Y, Uemura I, Tominaga N (2003) Ultrastructural changes in *Chlamydomonas acidophila* (Chlorophyta) induced by heavy metals and polyphosphate metabolism. FEMS Microbiol Ecol 44:253–259

Nocito FF, Pirovano L, Cocucci M, Sacchi GA (2002) Cadmium-induced sulfate uptake in maize roots. Plant Physiol 129:1872–1879

Noctor G, Foyer CH (1998) Ascorbate and glutathione: keeping active oxygen under control. Annu Rev Plant Physiol Plant Mol Biol 49:249–279

Noctor G, Arisi A, Jouanin L, Kunert K, Rennenberg H, Foyer C (1998) Glutathione: biosynthesis, metabolism and relationship to stress tolerance explored in transformed plants. J Exp Bot 49:623–647

Noctor G, Gomez L, Vanacker H, Foyer CH (2002) Interactions between biosynthesis compartmentation and transport in the control of glutathione homeostasis and signaling. J Exp Bot 53:1283–1304

Nováková M, Matějová E, Sofrová D (2004) Cd^{2+} effect on photosynthetic apparatus in *Synechococcus elongatus* and spinach (*Spinacia oleracea* L.). Photosynthetica 42:425–430

Nwugo CC, Huerta AJ (2008) Effects of silicon nutrition on cadmium uptake, growth and photosynthesis of rice plants exposed to low-level cadmium. Plant and Soil 311:73–86

Nwugo CC, Huerta AJ (2011) The effect of silicon on the leaf proteome of rice (*Oryza sativa* L.) plants under cadmium-stress. J Proteome Res 10:518–528

Ohtsuka T, Ito H, Tanaka A (1997) Conversion of chlorophyll *b* to chlorophyll *a* and the assembly of chlorophyll with apoproteins by isolated chloroplasts. Plant Physiol 113:137–147

Österås AH, Ekvall L, Greger M (2000) Sensitivity to and accumulation of Cd in *Betula pendula*, Picea abies and *Pinus sylvestris* seedlings from different regions in Sweden. Can J Bot 78:1440–1449

Ow DW (1996) Heavy metal tolerance genes: prospective tools for phytoremediation. Res Conserv Recycl 18:135–149

Paddock M, Feler G, Okamura M (2003) Proton transfer pathways and mechanism in bacterial reaction centers. FEBS Lett 555:45–50

Pagliano C, Raviolo M, Dalla Vecchia F, Gabbrielli R, Gonnelli C, Rascio N, Barbato R, La Rocca N (2006) Evidence for PSII donor-side damage and photoinhibition induced by cadmium treatment on rice (*Oryza sativa* L.). J Photochem Photobiol B 84:70–78

Pál M, Horváth E, Janda T, Páldi E, Szalai G (2006) Physiological changes and defence mechanisms induced by cadmium stress in maize. J Plant Nutr Soil Sci 169:239–246

Palliotti A, Tombesi S, Frioni T, Silvestroni O, Lanari V, D'Onofrio C, Matarese F, Bellincontro A, Poni S (2015) Physiological parameters and protective energy dissipation mechanisms expressed in the leaves of two *Vitis vinifera* L. genotypes under multiple summer stresses. J Plant Physiol 185:84–92

Parmar P, Kumari N, Sharma V (2013) Structural and functional alterations in photosynthetic apparatus of plants under cadmium stress. Bot Stud 54:1–6

Per TS, Khan S, Asgher M, Bano B, Khan NA (2016) Photosynthetic and growth responses of two mustard cultivars differing in phytocystatin activity under cadmium stress. Photosynthetica 54:491–501

Pernas M, Sánchez-Monge R, Salcedo G (2000) Biotic and abiotic stress can induce cystatin expression in chestnut. FEBS Lett 467:206–210

Perreault F, Dionne J, Didur O, Juneau P, Popovic R (2011) Effect of cadmium on photosystem II activity in *Chlamydomonas reinhardtii*: alteration of O–J–I–P fluorescence transients indicating the change of apparent activation energies within photosystem II. Photosynth Res 107:151–157

Peters JS, Chin SK (2003) Inhibition of photosynthetic electron transport by palmitoleic acid is partially correlated by the loss of thylakoid membrane proteins. Plant Physiol Biochem 41:117–214

Pietrini F, Iannelli MA, Pasqualini S, Massacci A (2003) Interaction of cadmium with glutathione and photosynthesis in developing leaves and chloroplasts of *Phragmites australis* (Cav.) Trin. ex Steudel. Plant Physiol 133:829–837

Pietrini F, Zacchini M, Iori V, Pietrosanti L, Ferretti M, Massacci A (2010) Spatial distribution of cadmium in leaves and its impact on photosynthesis: examples of different strategies in willow and poplar clones. Plant Biol 12:355–363

Pinto AP, Mota AM, de Varennes A, Pinto FC (2004) Influence of organic matter on the uptake of cadmium, zinc, copper and iron by sorghum plants. Sci Total Environ 326:239–247

Pinzón-Torres JA, Schiavinato MA (2008) Growth, photosynthetic and water use efficiency in four tropical tree legume species. Hoehnea 35:395–404

Porra R-J, Schäfer W, Cmiel E, Katheder I, Scheer H (1994) The derivation of the formyl-group oxygen of chlorophyll *b* in higher plants from molecular oxygen. Achievement of high enrichment of the 7-formyl-group oxygen form $^{18}O_2$ in greening maize leaves. Eur J Biochem 219:671–679

Portis AR (2003) Rubisco activase: Rubisco's catalytic chaperone. Photosynth Res 75:11–27

Poschenrieder C, Barceló J (1999) Water relation in heavy metals stressed plants. In: MNV P, Hagemayer J (eds) Heavy metal stress in plants. From molecules to ecosystems. Springer-Verlag, Berlin, pp 207–231

Poschenrieder CH, Gunsé B, Barceló J (1989) Influence of cadmium on water relations, stomatal resistance and abscisic acid content in expanding bean leaves. Plant Physiol 90:1365–1371

Potters G, Pasternak TP, Guisez Y, Palme KJ, Jansen MAK (2007) Stress-induced morphogenic responses: growing out of trouble? Trends Plant Sci 12:98–105

Potters G, Pasternak TP, Guisez Y, Jansen MA (2009) Different stresses, similar morphogenic responses: integrating a plethora of pathways. Plant Cell Environ 32:158–169

Pourghasemian N, Ehsanzadeh P, Greger M (2013) Genotypic variation in safflower (*Carthamus* spp.) cadmium accumulation and tolerance affected by temperature and cadmium levels. Environ Exp Bot 87:218–226

Prasad TK (1996) Mechanisms of chilling-induced oxidative stress injury and tolerance in developing maize seedlings: changes in antioxidant system, oxidation of proteins and lipids, and proteases activities. Plant J 10:1017–1026

Prasad MNV, StrzaŁka K (1999) Impact of heavy metals on photosynthesis. In: Prasad MNV, Hagemeyer J (eds) Heavy metal stress in plants. Springer, Berlin, pp 117–138

Prasad SM, Zeeshan M (2005) UV-B radiation and cadmium induced changes in growth, photosynthesis, and antioxidant enzymes of cyanobacterium *Plectonema boryanum*. Biol Plant 49:229–236

Prins A, van Heerden PD, Olmos E, Kunert KJ, Foyer CH (2008) Cysteine proteinases regulate chloroplast protein content and composition in tobacco leaves: a model for dynamic interactions with ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) vesicular bodies. J Exp Bot 59:1935–1950

Przedpelska-Wasowicz EM, Wierzbicka M (2011) Gating of aquaporins by heavy metals in *Allium cepa* L. epidermal cells. Protoplasma 248:663–671

Qiu N, Lu Q, Lu C (2003) Photosynthesis, photosystem II efficiency and the xanthophyll cycle in the salt-adapted halophyte *Atriplex centralasiatica*. New Phytol 159:479–486

Quain MD, Makgopa ME, Márquez-García B, Comadira G, Fernandez-Garcia N, Olmos E, Schnaubelt D, Kunert KJ, Foyer CH (2014) Ectopic phytocystatin expression leads to enhanced drought stress tolerance in soybean (Glycine max.) and *Arabidopsis thaliana* through effects on strigolactone pathways and can also result in improved seed traits. Plant Biotechnol J 12:903–913

Rady MM (2011) Effect of 24-epibrassinolide on growth, yield, antioxidant system and cadmium content of bean (*Phaseolus vulgaris* L.) plants under salinity and cadmium stress. Sci Hortic 129:232–237

Ralph PJ, Burchett MD (1998) Photosynthetic response of *Halophila ovalis* to heavy metal stress. Environ Pollut 103:91–101

Ramos I, Esteban E, Lucena JJ, Garate A (2002) Cadmium uptake and subcellular distribution in plants of Lactica sp. Cd-Mn interaction. Plant Sci 162:761–767

Ranieri A, Castagna A, Scebba F, Careri M, Zagnoni I, Predieri G, Pagliari M, Sanità di Toppi L (2005) Oxidative stress and phytochelatin characterisation in bread wheat exposed to cadmium excess. Plant Physiol Biochem 43:45–54

Rao SSR, Vardhini BV, Sujatha E, Anuradha S (2002) Brassinosteroids. A new class of phytohormones. Curr Sci 82:1239–1245

Resurreccion AP, Makino A, Bennett J et al (2001) Effects of sulfur nutrition on the growth and photosynthesis of rice. Soil Sci Plant Nutr 47:611–620

Rhizopoulou S, Psaras GK (2003) Development and structure of drought-tolerant leaves of the Mediterranean shrub *Capparis spinosa* L. Ann Bot 92:377–383

Riaz S, Iqbal M, Hussain I, Rasheed R, Ashraf MA, Mahmood S, Younas M, Iqbal MZ (2014) Chronic cadmium induced oxidative stress not the DNA fragmentation modulates growth in spring wheat (*Triticum aestivum*). Int J Agric Biol 16:789–794

Rizwan M, Meunier J, Miche H, Keller C (2012) Effect of silicon on reducing cadmium toxicity in durum wheat (*Triticum turgidum* L. cv. Claudio W.) grown in a soil with aged contamination. J Hazard Mater 209:326–334

Robinson JM (1986) Carbon dioxide and nitrite photoassimilatory processes do not intercompete for reducing equivalents in spinach and soybean leaf chloroplasts. Plant Physiol 80:676–684

Rodríguez-Serrano M, Romero-Puertas MC, Pazmiño DM, Testillano PS, Risueño MC, Luis A, Sandalio LM (2009) Cellular response of pea plants to cadmium toxicity: cross talk between reactive oxygen species, nitric oxide, and calcium. Plant Physiol 150:229–243

Romanowska E, Igamberdiev A, Parys E, Gardestron P (2002) Stimulation of respiration by Pb^{2+} ions in detached leaves and mitochondria of C3 and C4 plants. Physiol Plant 116:148–154

Romero-Puertas MC, Palm JM, Gómez M, del Río LA, Sandalio LM (2002) Cadmium causes the oxidative modification of proteins in pea plants. Plant Cell Environ 25:677–686

Romero-Puertas MC, Rodríguez-Serrano M, Corpas FJ, Gomez M, del Rio LA, Sandalio LM (2004) Cadmium-induced subcellular accumulation of $O_2.-$ and H_2O_2 in pea leaves. Plant Cell Environ 27:1122–1134

Saeidi G, Rickauer M, Gentzbittel L (2012) Tolerance for cadmium pollution in a core-collection of the model legume, *Medicago truncatula* L. at seedling stage. Aust J Crop Sci 6:641–648

Saidi I, Ayouni M, Dhieb A, Chtourou Y, Chaïbi W, Djebali W (2013) Oxidative damages induced by short-term exposure to cadmium in bean plants: Protective role of salicylic acid. S Afr J Bot 85:32–38

Samani Majd S, Taebi A, Afyuni M (2007) Lead and cadmium distribution in urban roadside soils of Isfahan, Iran. J Environ Stud 33:1–10

Samarakoon AB, Rauser WE (1979) Carbohydrate levels and photoassimilate export from leaves of *Phaseolus vulgaris* exposed to excess cobalt, nickel and zinc. Plant Physiol 63:1165–1169

Sandalio LM, Dalurzo HC, Gómez M, Romero-Puertas MC, Del Río LA (2001) Cadmium-induced changes in the growth and oxidative metabolism of pea plants. J Exp Bot 52:2115–2126

Sanità di Toppi L, Gabbrielli R (1999) Response to cadmium in higher plants. Environ Exp Bot 41:105–130

Santos LR, Batista BL, Lobato AKS (2018) Brassinosteroids mitigate cadmium toxicity in cowpea plants. Photosynthetica 56:591–605

Sarry JE, Kuhn L, Ducruix C, Lafaye A, Junot C, Hugouvieux V, Jourdain A, Bastien O, Fievet JB, Vailhen D, Amekraz B, Moulin C, Ezan E, Garin J, Bourguignon J (2006) The early responses of *Arabidopsis thaliana* cells to cadmium exposure explored by protein and metabolite profiling analyses. Proteomics 6:2180–2198

Sárvári É (2005) Effects of heavy metals on chlorophyll-protein complexes in higher plants: causes and consequences. In: Pessarakli M (ed) Handbook of photosynththesis. CRC, Boca Raton, FL, pp 865–888

Sas KN, Kovács L, Zsiros O, Gombos Z, Garab G, Hemmingsen L, Danielsen E (2006) Fast cadmium inhibition of photosynthesis in cyanobacteria in vivo and in vitro studies using perturbed angular correlation of γ-rays. J Biol Inorg Chem 11:725–734

Sasse JM (2003) Physiological Actions of Brassinosteroids: an update. J Plant Growth Regul 22:276–288

Sayed OH (2003) Chlorophyll fluorescence as a tool in cereal crop research. Photosynthetica 41:321–330

Schafer HJ, Haag-Kerwer A, Rausch T (1998) cDNA cloning and expression analysis of genes encoding GSH synthesis in roots of the heavy-metal accumulator *Brassica juncea* L. Evidence for Cd-induction of a putative mitochondrial γ glutamylecysteine synthetase isoform. Plant Mol Biol 37:87–97

Schansker G, Toth SZ, Strasser RJ (2005) Methylviologen and dibromothymoquinone treatments of pea leaves reveal the role of photosystem I in the Chl *a* fluorescence rise OJIP. Biochim Biophys Acta 1706:250–261

Scheumann V, Schoch S, Ruediger W (1998) Chlorophyll *a* formation in the chlorophyll *b* reductase reaction requires reduced ferredoxin. J Biol Chem 273:35102–35108

Schürmann P, Jacquot J-P (2000) Plant thioredoxin systems revisited. Annu Rev Plant Biol 51:371–400

Seemann JR, Critchley C (1985) Effects of salt stress on the growth, ion content, stomatal behaviour and photosynthetic capacity of a salt-sensitive species, *Phaseolus vulgaris* L. Planta 164:151–162

Šeršeň F, Kráľová K (2001) New facts about $CdCl_2$ action on the photosynthetic apparatus of spinach chloroplasts and its comparison with $HgCl_2$ action. Photosynthetica 39:575–580

Shah K, Ritambhara GK, Verma S, Dubey RS (2001) Effect of cadmium on lipid peroxidation, suoperoxide anion generation and activities of antioxidant enzymes in growing rice seedlings. Plant Sci 161:1135–1144

Sharkey TD (1990) Feedback limitation of photosynthesis and the physiological role of ribulose bisphosphate carboxylase carbamylation. Bot Mag Tokyo 2:87–105

Sharma I, Pati PK, Bhardwaj R (2010) Regulation of growth and antioxidant enzyme activities by 28-homobrassinolide in seedlings of *Raphanus sativus* L. under cadmium stress. Indian J Biochem Biophys 47:172–177

Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot 2012:217037

Sheoran IS, Singhal HR, Singh R (1990) Effect of cadmium and nickel on photosynthesis and the enzymes of the photosynthetic carbon reduction cycle in pigeonpea (*Cajanus cajan* L.). Photosynth Res 23:345–351

Shevyakova NI, Netronina IA, Aronova EE, Kuznetsov VV (2003) Compartmentation of cadmium and iron in *Mesembryanthemum crystallinum* plants during the adaptation to cadmium stress. Russ J Plant Physiol 50:678–685

Shi GR, Cai QS (2008) Photosynthetic and anatomic responses of peanut leaves to cadmium stress. Photosynthetica 46:627–630

Shi GX, Xu QS, Xie KB, Xu N, Zhang XL, Zeng XM, Zhou HW, Zhu L (2003) Physiology and ultrastructure of *Azolla imbricata* as affected by Hg^{2+} and Cd^{2+} toxicity. Acta Bot Sin 45:437–444

Shukla UC, Singh J, Joshi PC, Kakkar P (2003) Effect of bioaccumulation of cadmium on biomass productivity, essential trace elements, chlorophyll biosynthesis, and macromolecules of wheat seedlings. Biol Trace Elem Res 92:257–273

Siedlecka A, Baszynski T (1993) Inhibition of electron flow around photosystem I in chloroplasts of Cd-treated maize plants is due to Cd-induced iron deficiency. Physiol Plant 87:199–202

Siedlecka A, Krupa Z (1999) Cd/Fe interaction in higher plants—its consequences for the photosynthetic apparatus. Photosynthetica 36:321–331

Siedlecka A, Samuelsson G, Garderström P, Kleczkowski LA, Krupa Z (1998) The "activatory model" of plant response to moderate cadmium stress—relationship between carbonic anhydrase and Rubisco. In: Garab G (ed) Photosynthesis: mechanisms and effects, vol IV. Kluwer Academic, Dordrecht, pp 2677–2680

Sigfridsson KGV, Bernat G, Mamedov F, Styring S (2004) Molecular interference of Cd^{2+} with Photosystem II. Biochim Biophys Acta 1659:19–31. https://doi.org/10.1016/j.bbabio.2004.07.003

Silva EN, Ribeiro RV, Ferreira-Silva SL, Viégas RA, Silveira JAG (2010) Comparative effects of salinity and water stress on photosynthesis, water relations and growth of *Jatropha curcas* plants. J Arid Environ 74:1130–1137

Silva EN, Ribeiro RV, Ferreira-Silva SL, Vieira SA, Ponte LFA, Silveira JAG (2012) Coordinate changes in photosynthesis, sugar accumulation and antioxidative enzymes improve the performance of *Jatropha curcas* plants under drought stress. Biomass Bioenergy 45:270–279

Silva JRR, Fernandes AR, Perez DV (2014) Phytoextraction of heavy metals from a landfill in the metropolitan region of Belém-Pará-Brazil. Rev Ciênc Agrar 57:429–438

Silva AJ, Nascimento CWA, Gouveia-Neto AS (2017) Assessment of cadmium phytotoxicity alleviation by silicon using chlorophyll *a* fluorescence. Photosynthetica 55:648–654

Silva JRR, Fernandes AR, Silva Junior ML, Santos CRC, Lobato AKS (2018) Tolerance mechanisms in *Cassia alata* exposed to cadmium toxicity—potential use for phytoremediation. Photosynthetica 56:495–504

Silveira FS, Azzolini M, Divan JAM (2015) Scanning cadmium photosynthetic responses of *Elephantopus mollis* for potential phytoremediation practices. Water Air Soil Pollut 226:359

Šimić D, Mladenović Drinić S, Zdunić Z, Jambrović A, Ledencan T, Brkić J, Brkić A, Brkić I (2012) Quantitative trait loci for biofortification in maize grain. J Hered 103:47–54

Singh PK, Tewari RK (2003) Cadmium toxicity induced changes in plant water relations and oxidative metabolism of *Brassica juncea* L. plants. J Environ Biol 24:107–112

Singh DP, Sharma SK, Bisen PS (1993) Differential action of Hg^{2+} and Cd^{2+} on the phycobilisomes and chlorophyll a fluorescence, and photosystem II dependent electron transport in the cyanobacterium *Anabaena flos-aquae*. Biometals 6:125–132

Singh S, Eapen S, D'souza SF (2006) Cadmium accumulation and its influence on lipid peroxidation and antioxidative system in an aquatic plant, *Bacopa monnieri* L. Chemosphere 62:233–246

Singh S, Khan NA, Nazar R, Anjum NA (2008) Photosynthetic traits and activities of antioxidant enzymes in blackgram (*Vigna mungo* L. Hepper) under cadmium stress. Am J Plant Physiol 3:25–32

Siripornadulsil S, Traina S, Verma DPS, Sayre RT (2002) Molecular mechanisms of proline-mediated tolerance to toxic heavy metals in transgenic microalgae. Plant Cell 14:2837–2847

Skórzyńska E, Baszyński T (1993) The changes in PSII complex polypeptides under cadmium treatment—are they of direct or indirect nature? Acta Physiol Plant 15:263–269

Skórzyńska-Polit E, Baszyński T (1997) Differences in sensitivity of photosynthetic apparatus in Cd-stressed runner bean plants in relation to their age. Plant Sci 128:11–21

Skórzyńska-Polit E, Drazkiewicz M, Krupa Z (2010) Lipid peroxidation and antioxidative response in *Arabidopsis thaliana* exposed to cadmium and copper. Acta Physiol Plant 32:169–175

Song A, Li Z, Zhang J, Xue G, Fan F, Liang Y (2009) Silicon-enhanced resistance to cadmium toxicity in *Brassica chinensis* L. is attributed to Si-suppressed Cd uptake and transport and Si-enhanced antioxidant defense capacity. J Hazard Mater 172:74–83

Song Y, Jin L, Wang X (2017) Cadmium absorption and transportation pathways in plants. Int J Phytoremediation 19:133–141

Sorić R, Ledenčan T, Zdunić Z, Jambrović A, Brkić I, Lončarić Z, Kovačević V, Šimić D (2011) Quantitative trait loci for metal accumulation in maize leaf. Maydica 56:323–329

Soudek P, Petrová Š, Vanková R, Song J, Vanek T (2014) Accumulation of heavy metals using Sorghum sp. Chemosphere 104:15–24

Sterckeman T, Redjala T, Morel JL (2011) Influence of exposure solution composition and of plant cadmium content on root cadmium short-term uptake. Environ Exp Bot 74:131–139

Stirbet A, Govindjee (2011) On the relation between the Kautsky effect (chlorophyll *a* fluorescence induction) and photosystem II: Basics and applications of the OJIP fluorescence transient. J Photochem Photobiol B 104:236–257

Strasser RJ, Srivastava A, Tsimilli-Michael M (2000) The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: Yunus M, Pathre U, Mohanty P (eds) Probing photosynthesis: mechanism, regulation and adaptation. Taylor and Francis, London, pp 445–483

Strasser RJ, Srivastava A, Tsimilli-Michael M (2004) Analysis of the chlorophyll a fluorescence transient. In: Govindjee PG (ed) Chlorophyll fluorescence a signature of photosynthesis, advances in photosynthesis and respiration. Kluwer, Dordrecht, pp 321–362

Subrahmanyam D, Rathore VS (2000) Influence of manganese toxicity on photosynthesis in ricebean (*Vigna umbellata*) seedlings. Photosynthetica 38:449–453

Sundberg MD (1986) A comparison of stomatal distribution and length in succulent and non-succulent desert plants. Phytomorphology 36:53–66

Takahashi R, Ishimaru Y, Senoura T, Shimo H, Ishikawa S, Arao T, Nakanishi H, Nishizawa NK (2011) The OsNRAMP1 iron transporter is involved in Cd accumulation in rice. J Exp Bot 62:4843–4850

Takashima T, Hikosaka K, Hirose T (2004) Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. Plant Cell Environ 27:1047–1054

Talarico L (2002) Fine structure and X-ray microanalysis of a red macrophyte cultured under cadmium stress. Environ Pollut 120:813–821

Tang L, Ying RR, Jiang D, Zeng X-W, Morel J-L, Tang Y-T, Qiu R-L (2013) Impaired leaf CO_2 diffusion mediates Cd-induced inhibition of photosynthesis in the Zn/Cd hyperaccumulator *Picris divaricate*. Plant Physiol Biochem 73:70–76

Tausz M, Sircelj H, Grill D (2004) The glutathione system as a stress marker in plant ecophysiology: is a stress response concept valid? J Exp Bot 55:1955–1962

Terashima I (1992) Anatomy of non-uniform leaf photosynthesis. Photosynth Res 31:195–212

Thapar R, Srivastava AK, Bhargava P, Mishra Y, Rai LC (2008) Impact of different abiotic stresses on growth, photosynthetic electron transport chain, nutrient uptake and enzyme activities of Cu-acclimated *Anabaena doliolum*. J Plant Physiol 165:306–316

Tian YL, Zhang HY, Guo W, Wei XF (2015) Morphological responses, biomass yield, and bioenergy potential of sweet sorghum cultivated in cadmium-contaminated soil for biofuel. Int J Green Energy 12:577–584

Timperio AM, D'Amici GM, Barta C, Loreto F, Zolla L (2007) Proteomic, pigment composition, and organization of thylakoid membranes in iron-deficient spinach leaves. J Exp Bot 58:3695–3710

Tran TA, Popova LP (2013) Functions and toxicity of cadmium in plants: recent advances and future prospects. Turk J Bot 37:1–13

Tripathi BC, Bhatia B, Mohanty P (1981) Inactivation of chloroplast photosynthetic electron transport activity by Ni2. Biochem Biophys Acta 638:217–224

Tuba Z, Saxena DK, Srivastava K, Kalaji MH (2010) Chlorophyll *a* fluorescence measurements for validating the tolerant bryophytes for heavy metal (Pb) biomapping. Curr Sci 98:1505–1508

Turnau K, Anielska T, Ryszka P, Gawroński S, Ostachowicz B, Jurkiewicz A (2008) Establishment of arbuscular mycorrhizal plants originating from xerothermic grasslands on heavy metal rich industrial wastes—new solution for waste revegetation. Plant and Soil 305:267–280

Vaculik M, Lux A, Luxová M, Tanimoto E, Lichtscheidl I (2009) Silicon mitigates cadmium inhibitory effects in young maize plants. Environ Exp Bot 67:52–58

Vaculik M, Landberg T, Greger M, Luxová M, Stoláriková M, Lux A (2012) Silicon modifies root anatomy, and uptake and subcellular distribution of cadmium in young maize plants. Ann Bot 110:433–443

Valentovičová K, Halušková L, Huttová J, Mistrík I, Tamás L (2010) Effect of cadmium on diaphorase activity and nitric oxide production in barley root tips. J Plant Physiol 167:10–14

Van Assche F, Clijsters H (1990) Effects of metals on enzyme activity in plants. Plant Cell Environ 13:195–206

Váňová L, Kummerová M, Klemš M, Zezulka Š (2009) Fluoranthene influences endogenous abscisic acid level and primary photosynthetic processes in pea (*Pisum sativum* L.) plants in vitro. Plant Growth Regul 57:39–47

Vardhini BV, Anjum NA (2015) Brassinosteroids make plant life easier under abiotic stresses mainly by modulating major components of antioxidant defense system. Front Environ Sci 2:67

Vardhini BV, Anuradha S, Rao SSR (2006) Brassinosteroids-a great potential to improve crop productivity. Indian J Plant Physiol 11:1–12

Vassilev A, Berova M, Stoeva N, Zlatev Z (2005) Chronic Cd toxicity of bean plants can be partially reduced by supply of ammonium sulphate. J Cent Eur Agric 6:389–396

Verma K, Singh DP (1995) Differential regulation of high light tolerance in the mutant and wild type *Anacystis nidulans* cells. Curr Microbiol 30:373–379

Vido K, Spector D, Lagniel G, Lopez S, Toledano MB, Labarre J (2001) A proteome analysis of the cadmium response in *Saccharomyces cerevisiae*. J Biol Chem 276:8469–8474

Wael MS, Mostafa MR, Taia AAEM, Saad MH, Magdi TA (2015) Alleviation of cadmium toxicity in common bean (*Phaseolus vulgaris* L.) plants by the exogenous application of salicylic acid. J Hortic Sci Biotech 90:83–91

Wahid A, Ghani A, Javed F (2008) Effect of cadmium on photosynthesis, nutrition and growth of mungbean. Agron Sustain Dev 28:273–280

Wan G, Najeeb U, Jilani G, Naeem MS, Zhou W (2011) Calcium invigorates the cadmium-stressed *Brassica napus* L. plants by strengthening their photosynthetic system. Environ Sci Pollut R 18:1478–1486

Wang X, Liu Y, Zeng G, Chai LY, Song XC, Min ZY, Xiao X (2008) Subcellular distribution and chemical forms of cadmium in *Bechmeria nivea* (L.) Gaud. Environ Exp Bot 62:389–395

Wang H, Zhao SC, Liu RL, Zhou W, Jin JY (2009) Changes of photosynthetic activities of maize (*Zea mays* L.) seedlings in response to cadmium stress. Photosynthetica 47:277–283

Wang C, Lu J, Zhang SH, Wang PF, Hou J, Qian J (2011) Effects of Pb stress on nutrient uptake and secondary metabolism in submerged macrophyte *Vallisneria natans*. Ecotoxicol Environ Saf 74:1297–1303

Wang Y, Jiang X, Li K, Wu M, Zhang R, Zhang L, Chen G (2014) Photosynthetic responses of *Oryza sativa* L. seedlings to cadmium stress: physiological, biochemical and ultrastructural analyses. Biometals 27:389–401

Wang L, Cui X, Cheng H, Chen F, Wang J, Zhao X, Lin C, Pu X (2015) A review of soil cadmium contamination in China including a health risk assessment. Environ Sci Pollut Res 22:16441–16452

Wang X, Chen C, Wang J (2017) Cadmium phytoextraction from loam soil in tropical southern China by Sorghum bicolor. Int J Phytoremediation 19:572–578

Watanabe M, Henni K, Ogawa K, Suzuki T (2003) Cadmium-dependent generation of reactive oxygen species and mitochondrial DNA breaks in photosynthetic and non-photosynthetic strains of *Euglena gracilis*. Comp Biochem Physiol Pt C 134:227–234

Wei B, Yang L (2010) A review of heavy metal contaminations in urban soils, urban road dusts and agricultural soils from China. Microchem J 94:99–107

Weigel HJ (1985) Inhibition of photosynthetic reactions of isolated intact chloroplast by cadmium. J Plant Physiol 119:179–189

Wodala B, Eitel G, Gyula TN, Ördög A, Horváth F (2012) Monitoring moderate Cu and Cd toxicity by chlorophyll fluorescence and P_{700} absorbance in pea leaves. Photosynthetica 50:380–386

Wu FB, Zhang GP, Yu JS (2003) Genotypic differences in effect of Cd on photosynthesis and chlorophyll fluorescence of barley (*Hordeum vulgare* L.). Bull Environ Contam Toxicol 71:1272–1281

Wu JW, Shi Y, Zhu YX, Wang YC, Gong HJ (2013) Mechanisms of enhanced heavy metal tolerance in plants by silicon: a review. Pedosphere 23:815–825

Xiang C, Werner BL, Christensen EM, Oliver DJ (2001) The biological functions of glutathione revisited in *Arabidopsis* transgenic plants with altered glutathione levels. Plant Physiol 126:564–574

Xie L, Yang C, Wang X (2011) Brassinosteroids can regulate cellulose biosynthesis by controlling the expression of CESA genes in *Arabidopsis*. J Exp Bot 62:4495–4506

Xiong ZT, Peng YH (2001) Response of pollen germination and tube growth to cadmium with special reference to low concentration exposure. Ecotoxicol Environ Saf 48:51–55

Xu D, Chen Z, Sun K, Yan D, Kang M, Zhao Y (2013) Effect of cadmium on the physiological parameters and the subcellular cadmium localization in the potato (*Solanum tuberosum* L.). Ecotoxicol Environ Saf 97:147–153

Xue ZC, Gao HY, Zhang LT (2013) Effects of cadmium on growth, photosynthetic rate and chlorophyll content in leaves of soybean seedlings. Biol Plant 57:587–590

Xue ZC, Li JH, Li DS, Li SZ, Jiang CD, Liu LA, Wang SY, Kang WJ (2018) Bioaccumulation and photosynthetic activity response of sweet sorghum seedling (*Sorghum bicolor* L. Moench) to cadmium stress. Photosynthetica 56:1422–1428

Yamakura F, Suzuki K (1980) Cadmium, chromium and manganese replacement for iron-superoxide dismutase for *Pseudomonas ovalis*. J Biochem 88:191–196

Ye J, Yan C, Liu J, Lu H, Liu T, Song Z (2012) Effects of silicon on the distribution of cadmium compartmentation in root tips of *Kandelia obovata* (S. L.) Yong. Environ Pollut 162:369–373

Yi H, Meng Z (2003) Genotoxicity of hydrated sulfur dioxide on root tips of *Allium sativum* and *Vicia faba*. Mutat Res 537:109–114

Yoon J, Cao X, Zhou Q, Ma LQ (2006) Accumulation of Pb, Cu, and Zn in native plants growing on a contaminated Florida site. Sci Total Environ 368:456–464

Yu JQ, Huang LF, Hu WH, Zhou YH, Mao WH, Ye SF, Nogues S (2004) A role for brassinosteroids in the regulation of photosynthesis in *Cucumis sativus*. J Exp Bot 55:1135–1143

Yuan GF, Jia CG, Li Z, Sun B, Zhang LP, Liu N, Wang QM (2010) Effect of brassinosteroids on drought resistance and abscisic acid concentration in tomato under water stress. Sci Hortic 126:103–108

Zhang FQ, Shi WY, Jin ZX, Shen ZG (2003) Response of antioxidative enzymes in cucumber chloroplasts to cadmium toxicity. J Plant Nutr 26:1779–1788

Zhang X, Liu S, Takano T (2008) Two cysteine proteinase inhibitors from *Arabidopsis thaliana*, AtCYSa and AtCYSb, increasing the salt, drought, oxidation and cold tolerance. Plant Mol Biol 68:131–143

Zhang S, Zhang H, Qin R, Jiang W, Liu D (2009) Cadmium induction of lipid peroxidation and effects on root tip cells and antioxidant enzyme activities in *Vicia faba* L. Ecotoxicology 18:814–823

Zhang X, Gao B, Xia H (2014) Effect of cadmium on growth, photosynthesis, mineral nutrition and metal accumulation of bana grass and vetiver grass. Ecotoxicol Environ Saf 106:102–108

Zhao FJ, Hamon RE, Lombi E, McLaughlin MJ, McGrath SP (2002) Characteristics of cadmium uptake in two contrasting ecotypes of the hyperaccumulator *Thlaspi caerulescens*. J Exp Bot 368:535–543

Zhao K, Liu X, Xu J, Selim HM (2010) Heavy metal contaminations in a soil-rice system: identification of spatial dependence in relation to soil properties of paddy fields. J Hazard Mater 181:778–787

Zhou JL, Huang PL, Lin RG (1998) Sorption and desorption of Cu and Cd by macroalgae and microalgae. Environ Pollut 101:67–75

Zribi L, Fatma G, Fatma R, Salwa R, Hassan N, Néjib RM (2009) Application of chlorophyll fluorescence for the diagnosis of salt stress in tomato *Solanum lycopersicum* (variety Rio Grande). Sci Hortic 120:367–372

Żurek G, Rybka K, Pogrzeba M, Krzyżak J, Prokopiuk K (2014) Chlorophyll *a* fluorescence in evaluation of the effect of heavy metal soil contamination on perennial grasses. PLoS One 9:e91475

Chapter 16
Ecophysiology and Stress Responses of Aquatic Macrophytes Under Metal/Metalloid Toxicity

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Abstract Many metal elements are essential for plant growth at low concentrations but their excessive levels in the rhizosphere may cause phytotoxicity depending upon the fact that metals are easily absorbed and translocated in soil–plant systems. Nonessential metals/metalloids, i.e., Pb, Cr, Cd, As, Hg, etc., initiate a series of consecutive and/or parallel events at morphological, physiological, and molecular levels in aquatic plants depending on the nature of element and plant species. This chapter emphasizes the responses of aquatic macrophytes to metals/metalloids, with possible implementation in phytoremediation techniques. Metal-triggered growth inhibition, alterations in enzyme activities, inhibition of photosynthesis, changes in nutrient acquisition and metabolism, and the formation of free radicals are the major components reviewed in this book chapter. Discussion about the metal toxicity avoidance strategies like fluctuations in rhizospheric environments, plasma membrane exclusion, cell wall immobilization, phytochelatin-based sequestration and compartmentalization processes, stress proteins, and metallothioneins is also within the scope of this chapter. Metal tolerance in aquatic plants is more likely involved in an integrated network of multiple response processes generally described as "fan-shaped response" rather than several isolated functions described above. Plant tolerance to metals/metalloids is mainly determined from its transport across plasma membrane and tonoplast in plant. The appropriate understanding of metal-triggered ecophysiological responses of aquatic plants may make it promising to use them for treatment of metal polluted waters and soils.

Keywords Aquatic plants · Defense mechanisms · Ecophysiological responses · Metals/metalloids · Phytofilteration · Phytostabilization · Tolerance

16.1 Introduction

Heavy metals (HMs) are continuously added into the water reservoirs and aquatic bodies by both anthropogenic and natural processes such as household sewage and industrial effluent liberations, mining, electronic waste, farming, and fluctuations in natural climatic events like storms and floods (Tanwir et al. 2015). This results in a rapid increase of metal content of aquatic reservoirs, which directly are available to aquatic animals such as a wide variety of fishes and aquatic invertebrates living inside it. It is also initiating a comprehensive array of negative biological effects on growth of aquatic fauna and flora, ranging from being vital for living organisms to those being fatal, respectively. The presence of low concentrations of metals in water reservoirs is required for different species of plants and animals living in the aquatic environment. These includes micronutrients (Zn, Cu, Fe, Co, Mn, Cr, Mo) and macronutrients (Mg, Ca, P, N, S, K), but in case of increase of these metals from threshold level, they will cause fatal effects leading not only to reduction in growth but also to reduced rate of metabolic processes together with reproduction, with concern on the whole trophic chain comprising humans (Asati et al. 2016). In addition, metals having no essential role in plant metabolisms, such as Cd, Pb, As, Ni, and Hg, accelerate the global poisonous effect on organisms at very low concentrations. High concentration of metals in aquatic bodies could be highly dangerous for natural diversity and also to human health. This is because of the long persistence in water, toxic properties, bioaccumulation in living organisms, and biomagnification in the food chain (Javed et al. 2019). Toxic metal contamination is an international problem; thus, international rules and regulations are demanded for maintenance of water quality at specified limits of the WHO in freshwater, marine water, and groundwater and also in biota (Gheorghe et al. 2017). At present, according to the European Water Framework Directive (EUWFD, 2000/60/EC), five major characteristics including biological parameters, such as macrophytes, phytoplankton, benthic invertebrates, phyto-benthos, and fishes, concern hydro-morphological water quality and chemical properties, which are required for the assessment of ecological status of water bodies. The effect of metals on biotic life of water reservoirs is an important indicator of water quality (Javed et al. 2019). Fishes and mollusks are important aquatic organisms which are used as indicators of water quality due to the metals in water bodies. Aquatic plants give important information to forecast the rank of oceanic environment, because they are immobile and quickly attain equilibrium with their surrounding environment. Aquatic plants can take up large amounts of heavy metals in their tissues. Many studies have been published on the use of aquatic plants for the elimination of heavy metals from contaminated water reservoirs (Mishra and Tripathi 2009). Normally resilient and progressive associations have been present among metal concentrations in plants and water and/or between sedimented metal concentration in soil and aquatic plants (Bonanno and Giudice 2010).The maximum metal uptake (bioconcentration factors [BCF]) was reported for nickel and cadmium uptake by *Typha* sp. (BCF = 0.8 and 1.3, respectively) and for zinc increase in *Juncus* sp. (BCF = 4.8) (Ladislas et al. 2012).

Various physical and chemical methods are used to remove the metals from water bodies but most of them are not appropriate due to high cost and less performance. The chemical processing of wastes also produces a large amount of chemical sludge that increases the cost of the project (Rakhshaee et al. 2009). Thermal and chemical processing of wastewater is a difficult process at a large scale, since it is too costly and also degrades the valuable components of water and soil (Gaur and Adholeya 2004). Recent increase in concerns regarding the heavy metal contamination of water reservoirs has originated an increase of suitable technologies to calculate the presence and mobility of metals in water, soil, and wastewater. Currently, phytoremediation is one of the effective and cheap solutions which are used to remove inactive metals and other metallic pollutants from polluted water and soil (Javed et al. 2017, 2018, 2019). Phytoremediation is the use of hyperaccumulating plants to take up large amounts of contamination from water, sediments, and soil. This technology does not harm the environment and is cost-effective. Hyperaccumulators are those plants which are capable of taking up large amounts of toxic metals (Cho-Ruk et al. 2006). Phytoremediation is successful because it uses the natural system of exclusive and selective accumulation abilities of plants, such as translocation to different parts of the plant body, bioaccumulation, and degradation of contaminants by the plant body (Tangahu et al. 2011). Many plant species are successfully used for absorbing heavy metals and metalloids such as cadmium, lead, arsenic, chromium, and numerous radionuclides from water and soils. One unique type of phytoremediation is phytoextraction, which can be used to remove metallic contaminants from soil of those having known biological function inside the plant body (Fe, Zn, Mn, Mg, Cu, Ni, Mo) or those having no specific known function in the plant body (Cd, Pb, Cr, Ag, Co, Hg) (Tangahu et al. 2011).

Phytofiltration is another type of phytoremediation that can be suitable in site plantation of hyperaccumulating plants in contaminated water bodies and is frequently appropriate for aquatic plant species (Olguín and Sánchez-Galván 2012). Aquatic macrophytes are capable of absorbing heavy metals not only from the water, but also from the surrounding soil. Normally, aquatic plants can hyperaccumulate high quantities of heavy metals. Due to that characteristic, these plants are used to eliminate toxic substances from the water environment and they also serve in biomonitoring of polluted water bodies (Cardwell et al. 2002). Aquatic plants exhibit phytofilteration under diverse contaminated water conditions and heavy metal presence.

Some plants have an additional ability to take up metals which have no known biological functions inside the plant body. Aquatic plants are among these plants and are able to accumulate higher concentrations of different metallic contaminants such as Pb, Cd, Hg, Cr, Ar, Ni, Zn, Cu, and Fe from wastewaters (Duman et al. 2010; Rai 2010; Rahman and Hasegawa 2011). Macrophytes are a type of aquatic plants that grow inside or near water bodies and are classified into three major groups (submerged, emergent, and floating plants). Aquatic plants have different roles in different situations and these roles are reported by diverse studies such as the ability to remove toxic metals (Skinner et al. 2007), act as bio-monitors of metallic contents in water bodies (Pajevic et al. 2004), and capacity to act as biological filters. The aquatic environment is different from terrestrial ones, because higher uptake by plants is enabled by dissolution of contaminants in water, which may increase the accumulation of metallic contaminants (Javed et al. 2019). Hence, aquatic macrophytes often face the first connection to metal contaminants of aquatic bodies. The main mechanisms behind the hyperaccumulation of toxic metal substances by aquatic plant are the existence of their strong antioxidant machinery (Israr et al. 2006) and production of nontoxic metallic complexes (Malec et al. 2009).

16.2 Heavy Metals or Metalloids and Their Availability in the Plant–Soil System

Heavy metals consist of a large and heterogeneous group of elements generally different from each other in their biological functions and chemical characteristics. Heavy metals are generally included in the environmental pollutants' group of metals because of their toxic effects on the growth and metabolism of animals, plants, and human beings. Various anthropic events such as smelting and mining processes and use of sewage water for agriculture resulted in a locally increased concentration of heavy metals such as Cd, Pd, Cr, As, Ni, and Co in soil up to unsafe levels (Javed et al. 2017). These metals are highly persistent in the natural environment; therefore, they are transferred into water, soil, and plant bodies. Humans can consume the plants as food which results in indirect intake of heavy metals from food, which can cause severe health issues. Aquatic organisms are affected by these metals due to their leaching from different point sources, giving rise to accidental mixing of toxicants in the environment (Javed et al. 2019). Due to this, metal pollution poses a great danger to aquatic flora and fauna, particularly to fishes, a major source of protein for humans (Rajeswari and Sailaja 2014).

Heavy metals are a diverse group including 19 elements which show many similar chemical and physical characteristics and are different from all other known 98 elements. Cadmium, lead, and mercury are the most toxic heavy metals and have no known biological function. The heavy metals including Cu, Cr, Mn, Sn, Zn, and Ni are nonbiodegradable, and once diffused into the water bodies, they cause permanent toxicity. Due to the nonbiodegradability of these metals, their toxicity causes severe types of damage to biological systems (Tanwir et al. 2015). Heavy metals including Pb, Cd, Hg, and Co are different from others because they are easily taken up by living tissues, resulting in various kinds of dangerous disorders and diseases even at very small quantities (Rajeswari and Sailaja 2014).

The term heavy metal arise from the classification of Gamelan in 1817; he divided the known elements into light metals, heavy metals, and nonmetals. "A metal with high specific gravity and higher atomic weight is called heavy metal." The specific gravity of heavy metals ranges from 5.30 to 22.00 and the atomic number is always higher than 20 (Rajeswari and Sailaja 2014).

16.2.1 Lead (Pb)

Lead (Pb) is a heavy metal in group fourteen of the periodic table. The atomic mass of lead is 207.2, with atomic number 82 and specific density 11.4 g cm^{-3}. Lead has a high boiling point (1749 °C) and low melting point (327.40 °C). Sulfur is capable of combining with lead to produce PbS and $PbSO_4$. Oxygen also chemically reacts with lead to give rise to $PbCO_3$ whose concentration ranges from 9.5 to 30 mg kg^{-1} in the upper layer of the earth (Javed et al. 2017). Lead is obtained from rocks and commonly used as bearings, solders, cable covers, caulking, pigments, plumbing, ammunition, Sb and Sn sleeve bearings, high-detail castings, and flex printing. Ionic lead, lead oxides, Pb (II), lead–metal oxyanion complexes, and lead hydroxides are the common forms of lead that diffuse into the soil, surface waters, and groundwater by industrialization processing. Lead hydroxyl complexes and Pb (II) are the two most stable form of lead. Lead (II) is also the most reactive form of Pb which is involved in the formation of mononuclear and polynuclear hydroxides and oxides. Lead hydroxides and lead sulfides are the most stable ores in the soil, which increase the soil sulfide levels by reduction (Rajeswari and Sailaja 2014).

16.2.2 Chromium (Cr)

Elemental chromium (Cr) is a heavy metal with atomic mass 51.99 and atomic number 24.00 which is naturally found in the earth's crust. The specific density of chromium is 7.19 g cm^{-3} and it has three oxidation states which extend from Cr (II) to Cr (VI) (Jacobs and Testa 2005). Chromium produces stable compounds in trivalent [Cr (III)] form and naturally occurring ores contain the state ferrochromite. Cr (VI) is the second most stable form (Patlolla et al. 2009). Industries are the major source of anthropogenic release of chromium to water, soil, and air but it also is released due to the natural leaching processes of metals. Tanneries, chromate production, metal processing, chrome and ferrochrome pigment production, and stainless steel welding are the major industrial units which release chromium as a waste product (Tchounwou et al. 2012). Chromium is always released in the soil and water in hexavalent state [Cr (VI)] (Jacobs and Testa 2005). Hexavalent chromium [Cr (VI)] is a highly dangerous toxin released due to industrial processes and causes carcinoma production in human beings (Velma et al. 2009). Naturally Cr (VI) concentration was recently found at 50 μg per liter in drinking water which is above the World Health Organization permitted limit for water (Velma et al. 2009). Chromium is used in several industrial practices and occurs in all kinds of ecosystems (Wang et al. 2006). Major factors leading to the harmful effects of Cr complexes are the solubility and oxidation state.

16.2.3 Nickel (Ni)

Nickel (Ni) is a white silvery toxic heavy metal at high concentrations with atomic mass 58.69 and atomic number 28 and is ranked 24th among the most abundant metals in the upper surface of the earth. It comprises about 3% of total matter on earth. The density of nickel is 8.9 g cm^{-3} and is also ranked as the fifth element on earth by weight after Fe, O_2, Mg, and Si. Nickel belongs to the transition series of group 10 in the modern periodic table along with other elements. It is a corrosion-resistant metal, but it can easily dissolve in weak oxidizing acids. Naturally occurring nickel is a blend of five different stable isotopes. However, it is also present in 19 other unstable isotopic forms. Though nickel can occur in numerous oxidation states (−1, +1, +3, and + 4), the widespread oxidation state under environmental situations is Ni (II). Nickel is a universal trace metal and released in the air, soil, and water samples in the biosphere by anthropic and natural sources. Various nickel compounds are used in different industrial units such as nickel carbonate, nickel acetate, nickel oxide, and nickel hydroxide (Hall et al. 2015). These complexes leach into the soil and environment and are ultimately taken up by plant tissues. They can enter into the food chain via plants and generate toxic effects on the health of animals and human (Cempel and Nikel 2006). In water reservoir, Ni enters by solubilization of nickel and biological cycles and sedimentation by natural processes. pH is an important factor which controls the solubilization of nickel in soil. At pH 6.5, Ni compounds are present in soluble form, while at pH 6.7, Ni is found as insoluble hydroxides. Nickel is a metabolically vital micronutrient for normal plant growth and an important component of the enzyme urease which plays a vital role in nitrogen metabolism. It is highly phytotoxic when present in higher concentrations (Hall et al. 2015). The annual global addition of Ni to the human environment is almost 150,000 to 180,000 metric tons per annum.

16.2.4 Cadmium (Cd)

Cadmium is located in the second group of the transition elements. Cadmium's atomic mass is 112.4, atomic number 48, and specific density 8.65 g cm^{-3}. It is highly toxic in its ionic form. Cadmium is mostly emitted into the natural environment by burning of coal in industries. Other important sources of Cd are emission from industrial paints and manufacturing of batteries (Nazar et al. 2012). Detergents, fertilizers, pesticides, biosolids, and refined petroleum materials also contain some Cd. Cadmium is used as an electrode in Ni–Cd batteries (Agency for Toxic Substances and Disease Registry (ATSDR) 2012). Therefore, it is important to study and control the potential consequences of application of sewage sludge to soils used for crops, as it could contain toxic amounts of cadmium. A common indicator of Cd uptake in human beings is painful osteomalacia.

16.2.5 Arsenic (As)

Arsenic is a global element with atomic number 33 and atomic mass 74.92; it is always present only at low concentration in all sorts of environments. Trivalent and pentavalent states of inorganic arsenite and arsenate naturally exist and its density is 5.72 g cm^{-3}, while three organic substances also exist in the form of methylated metabolites: trimethylarsine oxide, dimethylarsinic acid (DMA), and monomethylarsonic acid (MMA). Natural leaching of arsenic takes place through various kinds of natural phenomenon like soil erosion, volcanic eruptions, and human activities (ATSDR 2012). Industries are also another important source of arsenic compound production which may cause the increase of arsenic in the natural ecosystem such as algicides, insecticides, fungicides, herbicides, dyestuffs, wood preservatives, and sheep dips. Arsenic is also used in different kinds of veterinary medicines which are used for the abolition of tapeworms in cattle and sheep (Centeno et al. 2005). Arsenic is still used in drugs in Africa for the treatment of amoebic dysentery, African sleeping sickness, black head in chicken and turkeys, and filariasis in dogs (Centeno et al. 2005).

16.2.6 Mercury (Hg)

Mercury is another important heavy metal present in group IV and row VI of the modern periodic table. Mercury has an atomic weight of 200.6, atomic number of 80, and specific density of 13.60 g cm^{-3}. It is typically produced as a by-product of metal refining processes. It is also liberated in the ecosystems by liberation of coal and its products in industries causing contamination of the natural environment (Driscoll et al. 2013). Another important source of mercury contamination is at sideways of gas and oil pipelines. In the natural environment, mercury is present in different forms like elemental form (Hg), mercuric ion form (Hg^{2+}), and alkylated mercurous form (methyl- or ethyl-Hg^{2+}). Mercurous and mercury are the two most important and highly stable forms in oxidizing conditions. The most noxious form of mercury is its alkylated forms which are highly volatile in air and readily soluble in water. The elimination of mercury in solution form contamination sites is possible by the use of some techniques like sorption to soils, humic materials, and sedimentation (Rajeswari and Sailaja 2014).

16.3 Aquatic Plants

Plants that grow in aquatic environment are called aquatic plants. Aquatic plants are divided into four major groups based on the growth form (submerged, floating, floating leaved, and emergent) (Materac and Sobiecka 2017):

- Submerged plants: these plants typically grow inside water bodies and are rooted in mud present at the bottom.
- Floating leaved: these plants have anchoring roots on the soil surface and leaves floating on the water surface.
- Floating: the roots, branches, leaves, and stems of such plants are floating submerged in water and they do not have any anchoring in soil.
- Emergent: these plants spread their leaves and shoots in the air from the water surface, although keeping their roots below the surface.

Some examples of wetland plant species are shown in Table 16.1 (Ikram et al. 2013; Javed et al. 2019).

16.4 Uptake and Translocation of Metals/Metalloids in Aquatic Plants

Aquatic plants have two major types, as "accumulators" and "excluders." Accumulators are those plants which can survive in the presence of high amount of toxic agents in their apical tissues (Sinha et al. 2004). They are capable of deforming toxic substances into less toxic ones in leaves and stems. Plants have modified themselves to take up essential micronutrients from soil with high efficiency when they are present even at low concentration. They have developed various kinds of metabolic processes such as producing chelating chemicals, redox reactions, and encouraging pH changes in the root zone that would solubilize micronutrients from insoluble precipitates to soluble ones. They also have developed extremely specific mechanisms for the storage and translocation of micronutrients. The toxic chemical substances like heavy metals have no specific mechanisms of accumulating in plant tissues. Toxic elements use the same mechanisms for its translocation, uptake, and storage in plant tissues which are used by essential micronutrients, because they have common chemical characteristics. Therefore, the mechanisms of essential micronutrients are important for phytoremediation. There are particular proteins present in the plasma membrane of plant cells which are involved in the uptake of ions and accumulation in tissues. They are: (1) proton pumps (ATPases are proton pumps that use energy and produce electrochemical gradients), (2) cotransporters and anti-transporters (these are proteins that are able to use electrochemical differences by protons produced by ATPase pumps to facilitate the active uptake of ions), and (3) transport channels (these are also group of proteins that enable the transfer of ions into and out of the cells in a passive way). All mechanisms are used for the transport of various kinds of ions across the membrane. The main problem behind the uptake of metal contaminants is the interaction between different kinds of ions. First, plant roots take up ions from soil and then translocate these ions into the stems and leaves. Plants normally take up a small concentration of trace elements ranging from 10 to 15 ppm for its metabolic requirements and these ions are not usually stored in high concentrations (Tanwir et al. 2015). But the hyperaccumulator plants are capable of uptake and

Table 16.1 Aquatic plants which are important for phytoremediation

Sr. no	Types of aquatic plant	Common name	Scientific name	Family
1	*Submerged*	Curly-leaf pondweed	*Potamogeton crispus*	Potamogetonaceae
		Marsh spike-rush	*Eleocharis palustris*	Cyperaceae
		Hornwort	*Ceratophyllum demersum* L.	Ceratophyllaceae
		Water weed	*Elodea canadensis* L.	Hydrocharitaceae
		Water milfoil	*Myriophyllum oliganthum* L.	Haloragaceae
		Celery leaf buttercup	*Ranunculus sceleratus* L.	*Ranunculaceae*
		Water celery	*Vallisneria americana* L.	Hydrocharitaceae
2	*Floating leaved*	Crested floating heart	*Nymphoides cristata*	Menyanthaceae
		American water lotus	*Nelumbo lutea* L.	Nelumbonaceae
		White water lily	*Nymphaea odorata* L.	Nymphaeaceae
		Water velvet	*Azolla pinnata*	Azollaceae
		Duckweed	*Lemna aequinoctialis*	Lemnaceae
		Water snowflake	*Nymphoides indica*	Menyanthaceae
		Pepperwort. Water clover	*Marsilea quadrifoliata*	Marsileaceae
		Lotus, sacred lotus	*Nelumbo nucifera*	Nelumbonaceae
		Water lettuce	*Pistia stratiotes*	Araceae
		Indian pondweed	*Potamogeton nodosus*	Potamogetonaceae
		Purple-fringed riccia	*Ricciocarpus natans*	Ricciaceae
		Giant duck weed	*Spirodela polyrrhiza*	Lemnaceae
3	*Floating*	Swollen duckweed	*Lemna gibba Linn.*	Lemnaceae
		Common duckweed	*Lemna minor*	Lemnaceae
		Hydrilla	*Hydrilla verticillata*	Hydrocharitaceae
		Water meal	*Wolffia* spp.	Nymphaeaceae
		Water lettuce	*Pistia spathulata Michaux*	*Araceae*
		Water hyacinth	*Eichhornia crassipes* L.	Pontederiaceae
4	*Emergents*	Cooper's reed	*Typha latifolia*	Typhaceae
		Narrow leaf cattails	*Typha angustifolia* L.	Typhaceae
		Elephant grass	*Typha elephantina*	Typhaceae
		Cattails	*Typha* spp.	Typhaceae
		Whip grass	*Hemarthria compressa*	Poaceae
		Wooly bulrush	*Scirpus cyperinus* L.	Cyperaceae
		Reed canary grass	*Phalaris arundinacea* L.	Poaceae
		Frogfruit	*Verbena nodiflora* L.	Verbenaceae

storage of these toxic heavy metals up to thousands of ppm. How hyperaccumulating plants can take up toxic metals, store them in the tissue, and survive under high toxicity is a matter of concern. There are various toxicity avoidance mechanisms but the storage of toxic ions in the vacuole seems to be a major one (Javed et al. 2019).

Uptake of ions into the roots and transport to the shoot of hyperaccumulator plants are facilitated by evapotranspiration which generates a force to absorb essential and nonessential elements together with other substances present in the soil into the plant. This mechanism is also responsible for the transport of contaminants into the plant tissues (Salido et al. 2003). Metal-accumulating plants can store metals like Zn, Cd, Pb, Ni, Mn, and Co at a concentration 1000 times higher than non-accumulator plants can. The microorganism communities present in the rhizosphere like bacteria and fungi are helpful in the mobilization of essential and toxic ions into bioavailable forms (Erdei et al. 2005). The major mechanisms involved in the phytoremediation-based removal of toxic heavy metals from the soil and water bodies are phytoextraction, phytostabilization, and rhizofiltration.

16.4.1 Phytoextraction

Phytoextraction is a technique of toxic heavy metal removal from the soil and water with the help of plants. In this technique, plants can take up, absorb, and translocate heavy metals through roots into the aboveground tissues. The plants can be harvested and burnt to obtain energy and ash and can be used for recycling of metals (Erakhrumen 2007).

16.4.2 Phytostabilization

Phytostabilization is a phytoremediation technique in which specific plant species are used which can immobilize the toxic metals into the water and soil using different mechanisms like absorption, accumulation in different plant parts, adsorption on root surface, or precipitation in root zone that will help in the prevention of toxic metals from their transformation in soil, deflation, and transportation by erosion (Erakhrumen 2007). Specific species of plants can be used for the phytostabilization of specific metals. This idea was supported by a comparative study in which two aquatic plants, *Typha domingensis* and *Phragmites australis*, were successfully used for the stabilization of Hg and As. However, these two species are inefficient in case of phytostabilization of other toxic and essential metals (Bonanno 2013).

16.4.3 Rhizofiltration

Rhizofiltration is a technique used for the phytoremediation of toxicants present in aquatic bodies. Such plants are used that can precipitate the toxic metals onto roots, or take up and sequester or compartmentalize the metals into roots of plants. This technique is commonly used for the detoxification of wastewater present in constructed wetlands (Erakhrumen 2007). Many species of aquatic plants are reported which are involved in the phytofilteration of pollutants. *Eichhonia crassipes* is an aquatic macrophyte that is used for the absorption of Pb, Cu, Zn, and Ni in water reservoirs. This plant is able to accumulate higher concentration of metals in roots than in shoots, due to the tap and fibrous root system found in this plant, which is involved in phytofiltration (Thayaparan 2013).

Many scientists have concluded that aquatic macrophytes act as a sink for heavy metals in the aqueous environment (Xing et al. 2013), and diverse aquatic plants take up variable quantities of diverse heavy metals. For example, various studies have exposed that floating aquatic plants like *Eichhornia crassipes* (Newete et al. 2016), emergent aquatic plant species like *Typha latifolia* (Duman et al. 2016), and aquatic submerged plants like *Ceratophyllum demersum* and *Hydrilla verticillata* (Xue et al. 2012) and *Potamogeton malaianus* (Romero-Oliva et al. 2015) are capable of accumulating high concentrations of heavy metals. Due to this characteristic of aquatic plants, various species are used for the removal of toxic heavy metals from wastewater. The accumulation of toxic contaminants in tissues usually decreases by efflux from submerged to floating and then finally to emergent aquatic plants, but this arrangement is sometimes influenced by the aquatic water and type of plants (Peng et al. 2008). Ultimately, it will also depend on the concentrations of metals in the water reservoir, while surface sedimentation also is a vital pool of contaminants in the aquatic ecosystem. There is still a gap of knowledge about the ability of several aquatic plant species to take up and accumulate heavy metals, the relations among the aquatic plants, and the level of metal contamination in water and sediments (Romero-Oliva et al. 2015).

16.5 Morphophysiological Responses of Aquatic Macrophytes to Metal/Metalloid Stress

16.5.1 Effect on Growth

The growth of plants is an important component to sustain life on this planet. Nutrient availability in soil and water, air quality, and plant genotype are the major factors behind the normal external and internal growth of aquatic macrophytes (Jacoby et al. 2017). The increasing concentration of Ni in the ecosystem harshly disturbs the growth and other metabolic activities of plants. The higher concentration of Ni and other heavy metals in the aquatic environment negatively affects the normal growth of plants, which is an important character which is used to assess the toxicity level (Ashfaque et al. 2016). The different processes of reduction of plant growth and metabolism by Ni^{2+} are inadequately elucidated. Besides causing overall metabolic disorder, heavy metals reduce the flexibility of cell walls, possibly by directly binding to pectins and by preventing peroxidase action in the cell walls and intercellular space; these peroxidases are required for lignification and connections among polysaccharides comprising ferulic acid. It is incidental that plant growth reduction by Ni and other heavy metals causes inhibition of metabolic procedures and stunted development, which lead to decrease of normal cell divisions. It is not known if the Ni is capable of entering the cell nucleus and if it is able to react with the nuclear protein and DNA or not (Ashfaque et al. 2016).

Heavy metals also affect other metabolic processes, plant physiology, and biochemical properties of plants, and the most detrimental effects are growth inhibition, necrosis, chlorosis, changed stomatal action, leaf rolling, efflux of cations, decreased water potential, alterations in membrane functions, retardation of photosynthesis, altered metabolism, respiration, and enzyme activities (Dubey 2011). In plants, aquaporin damage due to the presence of heavy metals greatly affects the plant–water relation. Under heavy metal stress of two aquatic plants, *Myriophyllum spicatum* and *Ceratophyllum demersum*, aquaporin-related membrane transport is negatively affected (Georgiadou et al. 2018). Chatterjee and Chatterjee (2000) reported that under Cr toxicity, the transpiration rate and water potential were decreased due to an increase in relative water content and diffusion resistance in cauliflower. Likewise, excess of Zn, Cu, and Mg constrains the germination of seeds and vegetative growth in barley, wheat, and rice (Mahmood et al. 2007). On the other hand, a high accumulation of Pb, Fe, and Cu resulted in abrupt decrease in germination at seedling stage of tomato (Mami et al. 2011). *Lamina minor* is a highly tolerant species and can tolerate Pb and Zn at 4 and 10 mg/L, respectively. Lead is the most toxic heavy metal when it is present at 8 mg/L in water or soil. Pb and Zn at higher concentration showed severe damage to photosynthetic pigments and soluble proteins (Jayasri and Suthindhiran 2017).

Heavy metals are extremely dangerous if they accumulate into the cytosol. They then retard cell respiration, the rate of photosynthesis, and nitrogen metabolism. Also the oxidative damage increases, which may result in stunted growth (Maksymiec et al. 2007). The heavy metals disturb the PSI and PSII of the photosystem, altering the stomatal function that results in photosynthesis inhibition (Appenroth 2010). These metals can directly affect the activity of major enzymes of the photosynthetic pathway, like RuBisCO and PEPC. The cadmium ion decreases the activity of RuBPC and breaks down the Mg^{2+}-complex structure. This may cause oxygenation of RuBisCO (Krantev et al. 2008). In *Lemna minor,* chlorophyll *a* is more affected by heavy metals than chlorophyll *b*, as a decrease of chlorophyll *a* reduces photosynthesis more than chlorophyll *b* (Jayasri and Suthindhiran 2017). At high levels of As and Al, nitrate reductase, glutamine synthetase, and nitrite reductase activities were decreased (Sharma and Dubey 2005). Ghani (2010) reported that the accumulation of nitrogen in roots and shoots is affected by the metal levels. However, protein content of *Lemna minor* decreased with increasing cadmium levels.

16.5.2 Alterations in Enzymatic Activities

Similar to other heavy metals, Ni affects various physiological processes in plants, such as several enzyme activities. Results indicated that the toxicity of Ni is associated with oxidative stress in plants (Gajewska et al. 2009).The production of H_2O_2 in living plant tissues is influenced by various enzymatic and nonenzymatic antioxidants. Nickel toxicity in wheat causes a decrease in superoxide dismutase (SOD) production and slightly increases the release of ascorbate peroxidase (APX) in leaves of plant. APX is an important enzyme that is likely involved in the reduction of H_2O_2 in wheat leaves under Ni stress, because the increase in the production of APX always coincides with reduction of H_2O_2 concentration. At the same level of heavy metal pollution, plants showed different responses towards enzyme production in both in vivo and in vitro conditions (Marquez-Garcia and Cordoba 2010). This difference may be due to the presence of physiological barriers that retard the translocation of heavy metals into the cytoplasmic region of the cell or due to the detoxification mechanism present in cells to cope with the heavy metal stresses. It is evident from different studies that Ni^{2+} stress enhances the activity of Mg^{2+}-bound ATPases in the plasmalemma of *Oryza sativa* shoots (Seregin and Ivanov 2001). Fluctuation in the Ni ion concentration can either enhance or degrade enzymatic production in different tissues of aquatic macrophytes. In aquatic plants, the production of SOD, CAT, glutathione reductase (GR), and ascorbate peroxidase (APX) showed different responses at different levels of toxic heavy metals (Shi et al. 2006). SOD and CAT production was increased due to the increased sludge in water bodies in *Hemarthria compressa* and *Typha angustifolia*. The increased production of CAT and SOD in plant tissues may be due to the presence of antioxidant defense against metal toxicity, as reported by Marquez-Garcia and Cordoba (2010). The increase in the production of antioxidant enzymes in *Salvinia natans* and *Phragmites* sp. was also reported (Dhir et al. 2009). *Lemna trisulca, Phragmites australis, Salvinia minima,* and *Ceratophyllum demersum* show a higher increase in the production of antioxidant enzymes when they are grown in a water with high concentration of Cu and Cd (Hou et al. 2007). However, enzymes other than SOD and CAT are less influenced by metallic toxicity. In two separate studies, Shanker et al. (2005) and Duarte et al. (2012) proved that plants growing under Cr stress showed rapid decline in CAT activity, which is due to the Cr-dependent inhibition of this enzyme system. Increase in the production of ROS ($O_2^{\bullet-}$, $OH^{\bullet}$) resulted in the inactivation of CAT due to the inactivation of a heme group binding with enzymes (Aravind and Prasad 2005).

16.5.3 Photosynthesis Inhibition

Heavy metals are toxic for aquatic plants and show nonspecific reduction of photosynthesis by numerous direct and indirect ways. The reduction in photosynthesis rate may be due to one or more reasons like obstructed chlorophyll production, disruption of chloroplast structure, disordered electron transport, lack of CO_2, inhibition of enzymes of the Calvin cycle, or closure of stomata. The *Lemna minor* planted under Ni toxicity showed a decline in photosynthetic rate due to the reduction in the number and size of chloroplasts; degradation of the ultrastructure of the chloroplast, which showed reduced number of thylakoid and grana; degradation of the construction of plasto globuli; and variations in membrane lipid composition (Jayasri and Suthindhiran 2017). These changes in the photosynthetic machinery may be the result of decreased cell moisture or peroxidation of lipids present in cell membrane by oxidative stress produced in response to Ni stress. Nickel is also involved in the inhibition of electron transport from pheophytin through plastoquinone QA and QB by modifying the carriers' structures (plastoquinone QB, proteins of reaction center).

16.5.4 Effect on Nutrient Acquisition and Water Balance

Heavy metals alter the nutrients inside the aquatic plant body both positively or negatively (Xue et al. 2010). Nutrient ions and heavy metal ions can compete with each other for the binding on common transporter proteins due to the similarity in structure of nuclei which ultimately reduces the uptake of nutrient ions. One example of this mechanism is the decrease of Fe^{2+}, Zn^{2+}, and Mg^{2+} in root tissues of plants due to increase in the concentration of Ni^{2+}. The reason behind the decrease in nutrient acquisition is the Ni^{2+}-induced disorders in metabolic process which affects the enzymatic structure of the cell membrane. In shoots of *Oryza sativa*, the composition of phospholipid and sterol in the plasma membrane was altered together with ATPase activity due to the presence of Ni^{2+} and other ions. Cadmium inhibits both passive and active uptake of K, by binding to the plasma membrane ATPase in sugar beet (Lindberg and Wingstrand 1985). Actually, these deviation changes the membrane permeability, which in response alters the ionic balance in the cytoplasm of plant cells (Romero-Oliva et al. 2015). The effect of heavy metals on nutrient acquisition in plants depends upon their concentration in the environment. A study on ryegrass plants elaborated the effect of Ni and other toxic ions on the uptake of Fe. The iron concentration in root tissues increased with low Ni in the root zone of soil and decreased with increasing Ni concentration (Xing et al. 2013). A 50 to 200 mg g^{-1} soil Ni content reduced the uptake of Mg, Cu, and Mg in caryopses and Ca and Mg in the aerial parts of *Triticum aestivum. H. verticillata,* a common aquatic plant, can be able to take up different heavy metals like Pb, Cd, Hg, Ni, Cu, As, and Cr, which can compete with essential nutrient ions by using the same transporter which transports nutrients (Xue et al. 2010; Romero-Oliva et al. 2015).

16.5.5 Formation of Free Radical

Molecular species which contain unpaired electrons in their valence shell are capable of autonomous existence and are called free radical. These species are extremely reactive and can both receive or donate an electron from one molecular structure to another molecule. They can perform redox reaction in which oxidation and reduction take place at the same time. However, free radicals have a short life span up to 10^{-6} s in biological systems due to its high reactivity (Engwa 2018). Some ROS containing oxygen are not capable of taking part in a chemical reaction but they generate free radicals. Frequent inflow and production of ROS from exogenous and endogenous sources may result in oxidative injury which leads to damage of several cellular functions. Damage to enzymes, proteins, DNA, and lipid membrane takes place due to oxidative injury (Dietz et al. 1999).

The most vulnerable target to oxidative damage is the plasma membrane, which contains high concentrations of unsaturated fatty acid. The lipid damage by ROS activity, usually known as lipid peroxidation, takes place in three steps (Rahman et al. 2012). The first stage is initiation; it includes the action of a ROS metabolite which is able to remove a hydrogen atom from a methylene present in the lipid due to the presence of a double bond. However, the residual fatty acid molecule accepts one electron from the surrounding, and by forming a conjugated diene, it stabilizes the molecular structure by rearrangement. In the second stage, which is called propagation stage, fatty acid radicals combine with oxygen to convert it into a peroxyl radical ($ROO^{\bullet}$). The $ROO^{\bullet}$ is able to extract the second hydrogen atom from a close fatty acid molecule, which once again yields another fatty acid radical. Plant proteins are the target superoxide radicals ($RO^{\bullet}$), hydroxyl ($OH^{\bullet}$), and reactive radicals of ROS which trigger injury in tissues. Superoxide radicals and hydrogen peroxide radicals can both positively and negatively impair those plant proteins which have thiol (-SH) groups, while others show a fragile effect. These interactions of radicals and ROS can cause direct protein injury by changing an amino acid structure or a specific part of an amino acid, also showing indirect damage by fragmentation, peroxidation, and degradation of amino acids. Due to this protein damage, plants undergo loss of cellular functions together with degradation of important metabolic enzymes. Oxidation of protein produces keto, carbonyl compounds, and aldehydes. The peroxynitrite radical ($ONOO^{\bullet}$) together with other nitrogen radicals undergoes chemical oxidation to produce 3-nitrotyrosine, which is an important detectable marker used for the oxidation of protein. Oxidation of protein originates from many variations in their functions, like chemical fragmentation, inactivation, and enhanced proteolytic deprivation (Engwa 2018). ROS can also attack DNA even if it is a highly stable molecule and can cause different kinds of serious damage to DNA like single- and double-strand DNA disruptions, injury to purines, alteration of DNA bases, destruction of deoxyribose sugar, breakage of cross-linkages in the DNA protein, and injury to DNA repair. Hydroxyl radical ($OH^{\bullet}$) is the supreme harmful ROS that disturbs nucleic acids (Engwa 2018). The hydroxyl radical can produce injury to adenine and guanine and undergo oxidation to produce 8-hydroxyadenine and hydroxydeoxyguanosine separately. It can also attack pyrimidine bases leading to the foundation of 5-(hydroxymethyl)uracyl, thymine glycols, thymine peroxide, and many other products. Superoxide radical ($O_2^{\bullet -}$) and hydrogen peroxide H_2O_2 do not have any detrimental effects on the physiological concentrations of DNA because they are less reactive. Transition heavy metals like iron that is able to bind easily with DNA sites and can undergo a catalization process to produce an $OH^{\bullet}$ radical in response can damage DNA. *Salvinia natans* showed a similar kind of response when grown under heavy metal stress (Dhir et al. 2012).

16.6 Metal/Metalloid Toxicity Avoidance Mechanism in Aquatic Plants

16.6.1 Fluctuations in Rhizospheric Environments

Aquatic plants are capable of absorbing, translocating, and accumulating high concentrations of heavy metals and heavy metals chemical complexes present in their environment. In order to sustain their electric gradient, the roots of plants release protons when they take up higher amounts of cations than anions and uptake protons when the reverse occurs (Javed et al. 2019). In that way, the rhizosphere pH changes are due to the activities of plant roots. The pH changes due to activities of roots have discrete influence on the accessibility of many nutrients in the rhizosphere and highly toxic heavy metals comprising Cr, Cd, and Hg. The induction of acidosis in the rhizosphere ultimately solubilizes Zn- and Al-containing complexes, which in response increase the endorsement of Zn or Al in plant tissues (Calba et al. 2004). In contrast, the increased pH negatively alters the Cu solubility in the soil (Chaignon et al. 2002).

The rhizosphere pH fluctuation also takes place in aquatic plants, and due to this, they are able to tolerate higher concentrations of various heavy metals in water bodies. Zeng et al. (2008) experimentally proved that the roots of rice plant can increase the rhizospheric pH when cultivated under high levels of Cr and predominantly at 50 μM or above. The submerged aquatic plant *Elodea canadensis* L. also imparts significant effects on rhizospheric pH in the presence of Cd. Stoltz and Greger (2002) experimentally demonstrated the capability of *Eriophorum scheuchzeri* L. and *Eriophorum angustiflium* L. living in wetlands to increase rhizospheric pH, even when they were growing in highly acidic wastewater (Javed et al. 2017).

The rhizospheric pH is composed of three major components (Song et al. 2004):

I. The anion and cation absorption difference between root and soil
II. Rhizospheric respiration which produces CO_2
III. The root-associated secretion of H^+, organic acids, and various other chemical compounds from roots

The release of buffering agents from plant roots (CO_3^{2-}, OH^-) also may result in a change of rhizospheric pH. The buffering agents are released in response to the fluctuation in cation/anion balance due to the uptake of nitrogenous source (Tanwir et al. 2015). The uptake of NH_4^+ ion significantly decreases pH, while, on the other hand, accumulation of NO_3^- ion may increase the pH, but the decrease was more prominent as compared to increase. The pH value of soil in the root zone decreased by 1.1 units when treated with ammonium and increase of 0.25 units when recorded in the presence of nitrate. Furthermore, release of organic acids from roots is also involved in pH change, i.e., an anion in the form of citrate is produced which is capable of consuming protons, which in response increases soil pH.

Cadmium stress in aquatic plants generates oxidative stress which alters the activity of ATPase present in the plasma membrane. The decrease of ATPase activity by cadmium may result in pH increase of apoplast (Lindberg and Wingstrand 1985). The ATPase activity also retarded the proton efflux which in response changed the rhizospheric pH (Astolfi et al. 2005).

Increase in rhizospheric pH may enhance the precipitation of metal oxyhydroxide and hydroxides (Vanloon and Duffy 2000). The pH changes also affect the binding of toxic metals with soil organic matter (Marschner 1995).

Eriophorum angustifolium growing in low concentrations of toxic heavy metals showed pH basification in the rhizosphere (Tariq Javed et al. 2013). Growing roots of maize in hydroponics under controlled conditions with different levels of Cd toxicity displayed varying changes in pH at high and low levels of toxicity (Tanwir et al. 2015). The increase in mucilage pH at lower level of applied Cd is possibly activated by Cd, which is due to the inhibition of proton pumps activity present in cell membrane (Janicka-Russak et al. 2008). A significant decrease in rhizospheric pH was also reported in *Z. mays* cultivated in a mixture of heavy metals (Blossfeld et al. 2010). A similar kind of study also reported the release of organic acids at low and high levels of applied Cd in a hot pepper plant (Xin et al. 2015). Organic acids are released by anion channels in the form of anions (Zhu et al. 2011), and the discharge of anions is managed with the co-efflux of cations/proton under metal stress in a poplar plant (Qin et al. 2007). In case of *Cucumis sativus*, H^+-ATPase pumping activity was altered due to a decreased proton efflux (Janicka-Russak et al. 2008).

16.6.2 Formation of Redox Barriers

The root-associated microorganisms and plant roots produce a redox barrier by oxidizing activities. Aquatic plants, such as *Spartina alterniflora*, *Oryza sativa*, *Typha latifolia* and *Phragmites communis*, are capable of oxidizing a highly soluble form of Fe (II) to a sparingly soluble form of Fe (III) whose toxicity also is reduced, and due to this, an iron plaque is formed in their roots.

16.6.3 Phytochelatin-Based Sequestration and Compartmentalization

Phytochelatins (PCs) are a group of metal-binding peptides which have a specific general structure n-Gly here $n = 2–11$ and they are produced in response to heavy metals. These metals (Hg, Cd, Ag, Ni Cu, Zn, Pb, and Au) are responsible for the biosynthesis of PCs. The key functions of phytochelatins are the induction of tolerance and detoxification of heavy metals in plants by forming metal chelates, especially in case of Cd (Yadav 2010). Formation of phytochelatins takes place in the cell cytosol, they bind to Cd, and then the Cd–PC complex is synthesized, which crosses the tonoplast with the help of an ATP-binding transporter. Production of isophytochelatins primarily depends upon the available concentration of glutathione synthetase or Gly in the plant cell at the time of heavy metal stress (Rea 2012).

It was evident from the study of Lindberg et al. (2004) that pretreated protoplasts with Cd showed reduced Cd uptake. An efflux of Cd from the cytosol is due to two main mechanisms; one of them is the transport of the Cd–PC complex and the other is Cd^{2+}/H^+ antiporter. *Arabidopsis* plants growing in high concentration of Cd^{2+} produced PCs rapidly, but at lower Cd^{2+} concentration, PCs were not only reduced but their production was inhibited (Li et al. 2017). Increase in Cd concentration in *Nitzschia palea* may induce phytochelatins binding with metallic ion (Figueira et al. 2014). The PCs can temporarily bind with Cd and reduce its toxicity in the cytosol of plants (Sylwia et al. 2010). *S. alfredii*, a Cd-tolerant plant, can tolerate high concentrations of Cd due to its binding to maleic acid (an organic acid produced by plant) in the cytosol (Tian et al. 2011). Phytochelatins are temporary blockers of heavy metals and they have no specific role in the chief intracellular mechanisms for the detoxification of toxic metals in aquatic plants (Liu et al. 2015).

16.6.4 Stress Coping Proteins

There are low-molecular weight polypeptide proteins with high concentration of cysteine residue which do not contain histidine and any aromatic amino acid. They are also composed of a large concentration of metallic ions and plenty of Cys-X-Cys amino acid arrangements where X is not equal to cysteine (Lu et al. 2003). Metallothioneins (MTs) are low-molecular-weight proteins ranging from 2 to 16 kDa and composed of a structure based on three major classes (Liu et al. 2015). These metallic proteins are capable of binding to both toxic (Pb, Cd, As) and essential (Zn, Cu) metallic ions with the help of a thiol group (-SH) containing an active site (Choudhary et al. 2010). Some aquatic plants also carry MT genes, which increase the metal-tolerant capacity of these plants (Shestivska et al. 2011).

16.7 Metal/Metalloid Transport Across Plasma Membrane and Tonoplast of Aquatic Plants

One of the basic reasons behind the abiotic stress in plants is the increasing heavy metal toxicity in the environment. Although plants have conventional approaches to compensate for the critical uptake of salts in cellular cytosol, the tonoplast and cellular membrane-associated proton-driven Na disseminate systems permit exclusion of sodium both into the vacuole and apoplast. The molecular mechanism behind the sodium exclusion into the apoplast is well described. This mechanism is called salt overly sensitive (SOS) pathway and is mainly composed of three proteins: the Na^+/H^+ antiporter is the first component (SOS1), the second is kinase protein (SOS2) which controls the activity of SOS1, and the third one is the calcium-binding protein (SOS3) which controls the SOS2 (Neuhaus and Trentmann 2014).

16.8 Fan-Shaped Ecophysiological Responses in Aquatic Plants Under Metal/Metalloid Stress

Aquatic plants have a well-developed mechanism to mitigate the harmful effects of toxic heavy metals on growth and metabolism. However, higher concentrations of metals result in reduction in photosynthetic activity (Rai 2016). It was reported that in *Quercus ilex* alteration in photosynthetic activity does not take place under metal contamination and production of polycyclic aromatic hydrocarbons (PAHs) acts as an indicator of metal pollution. The heavy metal toxicity is obtained due to its binding to active sites of enzymes, and heavy metals can also interfere with nucleic acids and proteins and change the cell metabolism (Rai 2016). Aquatic plants also produce various kinds of biochemical and physiological changes in cell growing in metal contaminants (Singh et al. 2015). Fenton reaction and auto-oxidation are the two processes that increase the production of reactive oxygen species (ROS), which in response block the transport of essential biomolecules. Crossing the membrane and intracellular movement of toxic metal with the help of these biomolecules is the main mode of heavy metal increase in plant tissues (Rai 2016). Additionally, in the modern molecular era, the study of proteomics in an organism is necessary to understand protein expression in plants via its genome (Liu et al. 2013). Furthermore, plant adaptations to tolerate metallic ions and plant stress responses are closely related with modifications in plant proteomics.

Aquatic plants have various mechanisms at all parts and stages of life to cope with heavy metal stress and all these mechanisms are collectively called as “fan-shaped ecophysiological response of aquatic plants” (Fig. 16.1). Plants respond to heavy metal stress at the root, shoot, and leaf at a cellular level. At root level, plants reduce uptake of metallic contaminants by various mechanisms such as root exudates, pH modulation, mucilage secretion, mycorrhizal association, active ion efflux, and installation of a redox barrier. All these mechanisms operate simultaneously to

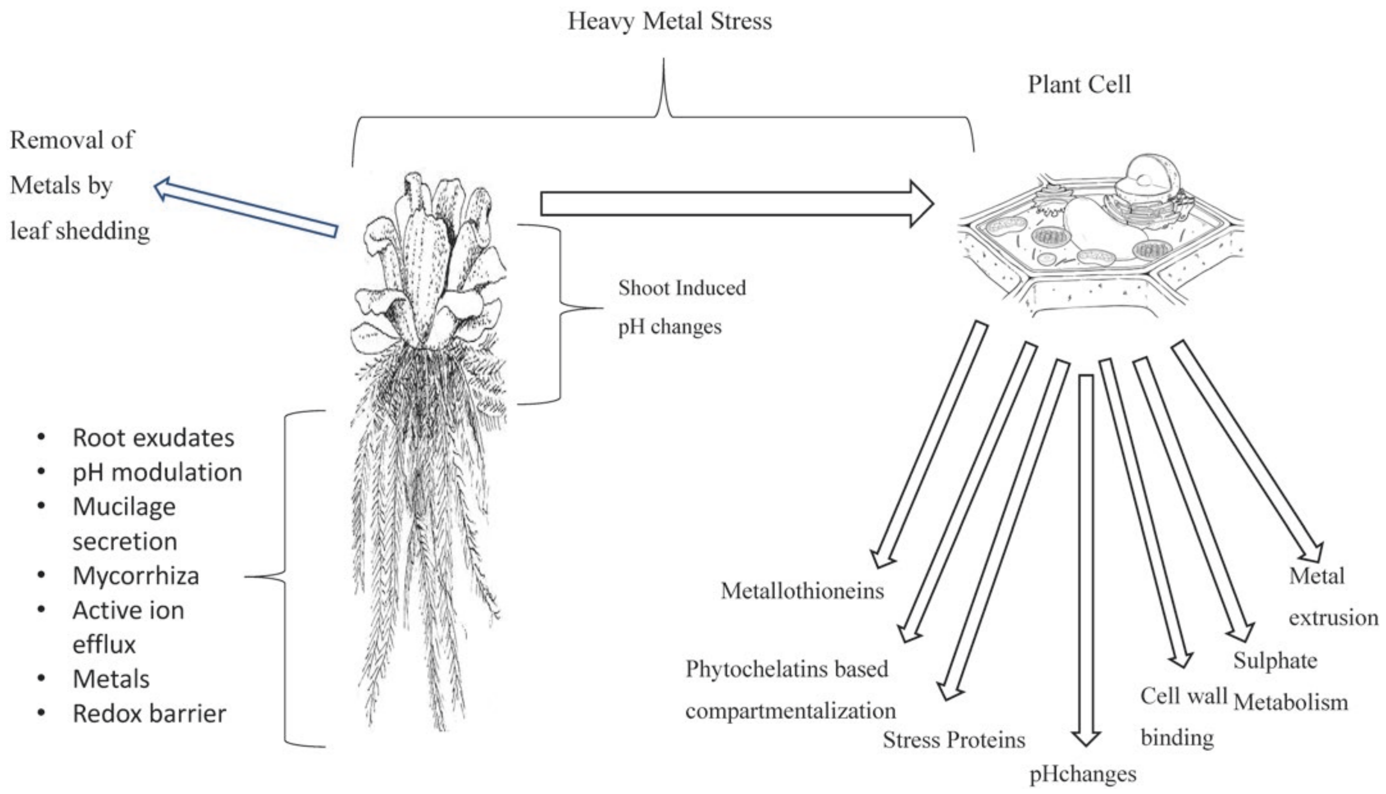

Fig. 16.1 Metal stress avoidance strategies in aquatic plants (left-hand side) and metal tolerance mechanisms as highlighted by "rays of fan" (right-hand side)

stabilize the toxic metals in the plant rhizosphere or in the root tissues of plants. Leaves also take part in the removal of heavy metals by premature shedding of leaves. In shoot tissues of aquatic plants, pH modulation operates to compartmentalize metals in vacuole or reduce translocation from roots to shoot which facilitates the plant to take up higher concentrations of toxic metals and retain them into the roots. Aquatic plants also operate with various mechanisms of metallic stress coping at cellular levels such as production of metallothionein, phytochelatin-based sequestration, production of stress coping proteins, cell wall binding, sulfate metabolism, and metal extrusion. All these mechanisms make aquatic plants suitable for phytoremediation of heavy metals and especially hyperaccumulating plants, which can survive in many types of environment.

16.9 Conclusion

Phytoremediation is a modern technique that is used to eliminate toxic chemical substances from the environment in a biological way. Aquatic plants are capable of taking up heavy metals in large concentration, they have specific mechanism by which they absorb heavy metals, and they tolerate the effects of these toxicants on plant metabolism. Aquatic plants are easy to grow and harvest in a polluted wastewater area. Their metal-accumulating capacity and stress coping activity are higher than other plants due to a unique fan-shaped response mechanism. So the use of aquatic plants is highly recommended for the detoxification or removal of heavy metals from wastewater reservoirs and water surrounding soils. Actually, these methods are important steps for vitally refining the efficacy of phytoremediation in a large scale, for industrial and field applications.

References

Agency for Toxic Substances and Disease Registry (ATSDR) (2012) Toxicological profile for arsenic TP-92/09. Center for Disease Control, Atlanta, GA

Appenroth KJ (2010) Definition of "heavy metals" and their role in biological systems. In: Soil heavy metals. Springer, Berlin, pp 19–29

Aravind P, Prasad MNV (2005) Modulation of cadmium-induced oxidative stress in *Ceratophyllum demersum* by zinc involves ascorbate-glutathione cycle and glutathione metabolism. Plant Physiol Biochem 43:107–116

Asati A, Pichhode M, Nikhil K (2016) Effect of heavy metals on plants: an overview. Int J Innov Eng Res Manag 5(3):56–66

Ashfaque F, Inam A, Sahay S, Iqbal S (2016) Influence of heavy metal toxicity on plant growth, metabolism and its alleviation by phytoremediation—a promising technology. Int J Agric Ecol Res Int 6:1–19

Astolfi S, Zuchi S, Passera C (2005) Effect of cadmium on H^+-ATPase activity of plasma membrane vesicles isolated from roots of different S-supplied maize (*Zea mays* L.) plants. Plant Sci 169:361–368

Blossfeld S, Perriguey P, Sterckeman T, Morel J, Losch R (2010) Rhizosphere pH dynamics in trace-metal-contaminated soils monitored with planar pH optodes. Plant and Soil 330:173–184

Bonanno G (2013) Comparative performance of trace element bioaccumulation and biomonitoring in the plant species *Typha domingensis, Phragmites australis* and *Arundo donax*. Ecotoxicol Environ Saf 97:124–130

Bonanno G, Giudice RL (2010) Heavy metal bioaccumulation by the organs of *Phragmites australis* (common reed) and their potential use as contamination indicators. Ecol Indic 10(3):639–645

Calba H, Cazevieille PC, Poss R, Jaillard B (2004) The dynamics of protons, aluminium and calcium in the rhizosphere of maize cultivated in tropical acid soils, experimental study and modelling. Plant and Soil 260:33–46

Cardwell AJ, Hawker DW, Greenway M (2002) Metal accumulation in aquatic macrophytes from southeast Queensland, Australia. Chemosphere 48:653–663

Cempel M, Nikel G (2006) Nickel: a review of its sources and environmental toxicology. Pol J Environ Stud 15(3):375–382

Centeno JA, Tchounwou PB, Patlolla AK, Mullick FG, Murakat L, Meza E, Gibb H, Long Fellow D, Yedjou CG (2005) Environmental pathology and health effects of arsenic poisoning a critical review. In: Naidu R, Smith E, Smith J, Bhattacharya P (eds) Managing arsenic in the environment from soil to human health. CSIRO, Adelaide

Chaignon V, Bedin F, Hinsinger P (2002) Copper bioavailability and rhizosphere pH changes as affected by nitrogen supply for tomato and oilseed rape cropped on an acidic and a calcareous soil. Plant and Soil 243:635–639

Chatterjee J, Chatterjee C (2000) Phytotoxicity of cobalt, chromium and copper in cauliflower. Environ Pollut 109:69–74

Cho-Ruk K, Kurukote J, Supprung P, Vetayasuporn S (2006) Perennial plants in the phytoremediation of lead contaminated soils. Biotechnology 5(1):1–4

Choudhary SP, Bhardwaj R, Gupta BD, Dutt P, Gupta RK, Biondi S, Kanwar M (2010) Epibrassinolide induces changes in indole-3-acetic acid, abscisic acid and polyamine concentrations and enhances antioxidant potential of radish seedlings under copper stress. Physiol Plant 140(3):280–296

Dhir B, Sharmila P, Saradhi P (2009) Potential of aquatic macrophytes for removing contaminants from the environment. Crit Rev Environ Sci Technol 39:1–28

Dhir B, Nasim SA, Samantary S, Srivastava S (2012) Assessment of osmolyte accumulation in heavy metal exposed *Salvinia natans*. Int J Bot 8:153–158

Dietz KJ, Baier M, Krämer U (1999) Free radicals and reactive oxygen species as mediators of heavy metal toxicity in plants. In: Heavy metal stress in plants. Springer, Berlin, pp 73–97

Driscoll CT, Mason RP, Chan HM, Jacob DJ, Pirrone N (2013) Mercury as a global pollutant: sources, pathways, and effects. Environ Sci Technol 47(10):4967–4983

Duarte BN, Silva V, Cac-ador I (2012) Hexavalent chromium reduction, uptake and oxidative biomarkers in *Halimione portulacoides*. Ecotoxicol Environ Saf 83:1–7

Dubey RS (2011) Metal toxicity, oxidative stress and antioxidative defense system in plants. In: Gupta SD (ed) Reactive oxygen species andante oxidants in higher plants. CRC, Boca Raton, FL, pp 177–203

Duman F, Cicek M, Sezen G (2010) Biological responses of duckweed (*Lemna minor* L.) exposed to the inorganic arsenic species As (III) and As (V): effects of concentration and duration of exposure. Ecotoxicology 19:983–993

Duman RS, Aghajanian GK, Sanacora G, Krystal JH (2016) Synaptic plasticity and depression: new insights from stress and rapid-acting antidepressants. Nat Med 22:238–249

Engwa GA (2018) Free radicals and the role of plant phytochemicals as antioxidants against oxidative stress-related diseases. In: Phytochemicals-source of antioxidants and role in disease prevention. IntechOpen, Rijeka

Erakhrumen AA (2007) State of forestry research and education in Nigeria and sub-saharan Africa: implications for sustained capacity building and renewable natural resources development. J Sustain Dev 9(4):133–151

Erdei L, Mezosi G, Mecs I, Vass I, Foglein Fand Bulik L (2005) Phytoremediation as a program for decontamination of heavy-metal polluted environment. Acta Biol 49(1–2):75–76

Figueira E, Freitas R, Guasch H, Almeida SP (2014) Efficiency of cadmium chelation by phytochelatins in *Nitzschia palea*(Kutzing) W. Smith. Ecotoxicology 2(3):285–292

Gajewska E, Wielanek M, Bergier K, Skłodowska M (2009) Nickel-induced depression of nitrogen assimilation in wheat roots. Acta Physiol Plant 3(1):1291–1300

Gaur A, Adholeya A (2004) Prospects of arbuscular mycorrhizal fungi in phytoremediation of heavy metal contaminated soils. Curr Sci 86(4):528–534

Georgiadou EC, Kowalska E, Patla K, Kulbat K, Smolinska B, Leszczynska J, Fotopoulos V (2018) Influence of heavy metals (Ni, Cu and Zn) on nitro-oxidative stress responses, proteome regulation and allergen production in basil (*Ocimum basilicum* L.) plants. Front Plant Sci 9:862

Ghani A (2010) Toxic effects of heavy metals on plant growth and metal accumulation in maize (*Zea mays* L.). Iran J Toxicol 3(3):325–334

Gheorghe S, Stoica C, Vasile GG, Nita-Lazar M, Stanescu E, Lucaciu IE (2017) Metals toxic effects in aquatic ecosystems: modulators of water quality. In: Water quality. Intech Open, Rijeka

Hall DS, Lockwood DJ, Bock C, MacDougall BR (2015) Nickel hydroxides and related materials: a review of their structures, synthesis and properties. Proc R Soc A Math Phys Eng Sci 471(2174):20140792

Hou W, Chen X, Songm G, Wangm QC, Chang C (2007) Effects of copper and cadmium on heavy metal polluted water body restoration by duckweed (*Lemna minor*). Plant Physiol Biochem 45:62–69

Ikram S, Parvaiz M, Ahmed M, Ilyas U, Khalid A, Munir M, Anwar S, Afzal H (2013) Aquatic plants of Sialkot district, Pakistan. World Appl Sci J 28(6):884–896

Israr M, Sahi SV, Jain J (2006) Cadmium accumulation and antioxidative responses in the *Sesbania drumondiiallus*. Arch Environ Contam Toxicol 50:121–127

Jacobs JA, Testa SM (2005) Overview of chromium (VI) in the environment background and history. In: Guertin J, Jacobs JA, Avakian CP (eds) Chromium (VI) handbook. CRC, Boca Raton, FL, pp 1–22

Jacoby R, Peukert M, Succurro A, Koprivova A, Kopriva S (2017) The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions. Front Plant Sci 8:1617

Janicka-Russak M, Kabala K, Burzynski M, Klobus G (2008) Response of plasma membrane H+-ATPase to heavy metal stress in *Cucumis sativus* root. J Exp Bot 5(9):3721–3728

Javed MT, Akram MS, Tanwir K, Chaudhary HJ, Ali Q, Stoltz E, Lindberg S (2017) Cadmium spiked soil modulates root organic acids exudation and ionic contents of two differentially Cd tolerant maize (*Zea mays* L.) cultivars. Ecotoxicol Environ Saf 141:216–225

Javed MT, Akram MS, Habib N, Tanwir K, Ali Q, Niazi NK, Iqbal N (2018) Deciphering the growth, organic acid exudations, and ionic homeostasis of *Amaranthus viridis* L. and *Portulaca oleracea* L. under lead chloride stress. Environ Sci Pollut Res 25(3):2958–2971

Javed M, Tanwir KT, Akram MS, Shahid M, Niazi NK, Lindberg S (2019) Phytoremediation of cadmium-polluted water/sediment by aquatic macrophytes: role of plant-induced pH changes. In: Cadmium toxicity and tolerance in plants. Academic, New York, pp 495–529

Jayasri MA, Suthindhiran K (2017) Effect of zinc and lead on the physiological and biochemical properties of aquatic plant *Lemna minor*: its potential role in phytoremediation. Appl Water Sci 7(3):1247–1253

Krantev A, Yordanova R, Janda T, Szalai G, Popova L (2008) Treatment with salicylic acid decreases the effect of cadmium on photosynthesis in maize plants. Plant Physiol J 165:920–931

Ladislas S, El-Mufleh A, Gérente C, Chazarenc F, Andrès Y, Béchet B (2012) Potential of aquatic macrophytes as bioindicators of heavy metal pollution in urban stormwater runoff. Water Air Soil Pollut 223(2):877–888

Li B, Liang P, Wei D, Lei M, Liu B, Lin Y, Li Z, Jidong G (2017) Enhanced flocculation and sedimentation of trace cadmium from irrigation water using phosphoric fertilizer. Sci Total Environ 601–602:485–492

Lindberg S, Wingstrand G (1985) Mechanism for Cd2+ inhibition of (K+ + Mg2+)ATPase activity and K+ (86Rb+) uptake join roots of sugar beet (Beta vulgaris). Physiol Plant 63(2):181–186

Lindberg S, Landberg T, Greger M (2004) A new method to detect cadmium uptake in protoplasts. Planta 219:526–532

Liu W, Zhang X, Liang L, Chen C, Wei S, Zhou O (2015) Phytochelatin and oxidative stress under heavy metal stress tolerance in plants. In: Gupta DK et al (eds) Reactive oxygen species and oxidative damage in plants under stress. https://doi.org/10.1007/978-3-319-20421-5_8

Lu T, Liu JY, Zhang RQ, Zhao NM (2003) Modeling rice rgMT as a plant metallothionein-like protein by the distance geometry and homology methods. Acta Bot Sin 45:1297–1306

Mahmood T, Islam KR, Muhammad S (2007) Toxic effects of heavy metals on early growth and tolerance of cereal crops. Pak J Bot 3(9):451–464

Maksymiec W, Wójcik M, Krupa Z (2007) Variation in oxidative stress and photochemical activity in *Arabidopsis thaliana* leaves subjected to cadmium and excess copper in the presence or absence of jasmonate and ascorbate. Chemosphere 6(6):421–427

Malec P, Maleva MG, Prasad MNV, Strzalka K (2009) Identification and characterization of Cd induced peptides in *Egeria densa* (Water Weed): putative role in Cd detoxification. Aquat Toxicol 95:213–221

Mami Y, Ahmadi G, Shahmoradi M, Ghorbani HR (2011) Influence of different concentration of heavy metals on the seed germination and growth of tomato. Afr J Environ Sci Technol 5:420–426

Marschner H (1995) Mineral nutrition of higher plants. Academic press, New York, Boston, London

Marquez-Garcia B, Cordoba F (2010) Antioxidative system in wild populations of Erica and evalensis. Environ Exp Bot 68:58–65

Materac M, Sobiecka E (2017) The efficiency of macrophytes for heavy metals removal from water. Biotechnol Food Sci 81(1):35–40

Mishra VK, Tripathi BD (2009) Accumulation of chromium and zinc from aqueous solutions using water hyacinth (*Eichhornia crassipes*).J. Hazard Mater 164(2–3):1059–1063

Nazar R, Iqbal N, Masood A, Iqbal M, Khan R, Syeed S, Khan NA (2012) Cadmium toxicity in plants and role of mineral nutrients in its alleviation. Am J Plant Sci 3:1476–1489

Neuhaus HE, Trentmann O (2014) Regulation of transport processes across the tonoplast. Front Plant Sci 5:460

Newete SW, Erasmus BF, Weiersbye IM, Byrne MJ (2016) Sequestration of precious and pollutant metals in bio mass of cultured water hyacinth (*Eichhorniacrassipes*). Environ Sci Pollut Res 2(3):20805–20818

Olguín EJ, Sánchez-Galván G (2012) Heavy metal removal in phytofiltration and phycoremediation: the need to differentiate between bioadsorption and bioaccumulation. N Biotechnol 30(1):3–8

Pajevic S, Kevresan Z, Vuckovic M, Radulovic D, Frontasayeva M, Pavlov S, Galinskaya Y (2004) Aquatic macrophytes as biological resources for monitoring the impacts of heavy metals on the aquatic environment. Int Assoc Danube Res 35:323–330

Patlolla A, Barnes C, Yedjou C, Velma V, Tchounwou PB (2009) Oxidative stress, DNA damage and antioxidant enzyme activity induced by hexavalent chromium in Sprague Dawley rats. Environ Toxicol 24(1):66–73

Peng K, Luo C, Lou L, Li X, Shen Z (2008) Bioaccumulation of heavy metals by the aquatic plants *Potamogeton pectinatus* L and *Potamogeton malaianus* Miq and their potential use for contamination indicators and in wastewater treatment. Sci Total Environ 392:22–29

Qin R, Hirano Y, Brunner I (2007) Exudation of organic acid anions from poplar roots after exposure to Al, Cu and Zn. Tree Physiol 27:313–320

Rahman MJ, Hasegawa H (2011) Aquatic arsenic: phytoremediation using floating macrophytes. Chemosphere 83:633–646

Rahman T, Hosen I, Islam TM, Shekhar HU (2012) Oxidative stress and human health. Adv Biosci Biotechnol 3:997–1019

Rai PK (2010) Microcosme investigation on phytoremediation of Cr using *Azolla pinnata*. Int J Phytol 2:96–104

Rai PK (2016) Impacts of particulate matter pollution on plants: implications for environmental biomonitoring. Ecotoxicol Environ Saf 129:120–136

Rajeswari TR, Sailaja N (2014) Impact of heavy metals on environmental pollution. Chem Pharm J Res 3:175–181

Rakhshaee R, Giahi M, Pourahmad A (2009) Studying effect of cell wall's carboxyl-carboxylate ratio change of *Lemna minor* to remove heavy metals from aqueous solution.J. Hazard Mater 163(1):165–173

Rea PA (2012) Phytochelatin synthase of a protease a peptide polymerase made. Physiol Plant 145:154–164

Romero-Oliva CS, Contardo-Jara V, Pflugmacher S (2015) Time dependent uptake, bioaccumulation and biotransformation of cell free crude extract microcystins from Lake Amatitlán, Guatemala by *Ceratophyllum demersum*, *Egeria densa* and *Hydrilla verticillata*. Toxicon 105:62–73

Salido AL, Hasty KL, Lim JM, Butcher DJ (2003) Phytoremediation of arsenic and lead in contaminated soil using Chinese Brake ferns (*Pteris vittata*) and Indian mustard (*Brassica juncea)*. Int J Phytoremediation 5(2):89–103

Seregin IV, Ivanov VB (2001) Physiological aspects of cadmium and lead toxic effects on higher plants. Russ J Plant Physiol 48(4):523–544

Shanker AK, Cervantes C, Loza-Tavera H, Avudainayagam S (2005) Chromium toxicity in plants—a review. Environ Int 31:739–753

Sharma P, Dubey RS (2005) Modulation of nitrate reductase activity in rice seedlings under aluminium toxicity and water stress; role of osmolytes as enzyme protectant. J Plant Physiol 162:854–864

Shestivska V, Adam V, Prasek J, Macek T, Mackova M, Havel L, Diopan V, Zehnalek J, Hubalek J, Kizek R (2011) Investigation of the antioxidant properties of metallothionein in transgenic tobacco plants using voltammetry at a carbon paste electrode. Int J Electrochem Sci 6:2869–2883

Shi Q, Bao Z, Zhu Z, Ying Q, Qian Q (2006) Effects of different treatments of salicylic acid on heat tolerance, chlorophyll fluorescence, and antioxidant enzyme activity in seedlings of *Cucumis sativa* L. Plant Growth Regul 48:127–135

Singh S, Parihar P, Singh R, Singh VP, Prasad SM (2015) Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics and ionomics. Front Plant Sci 6:1143

Sinha RK, Herat S, Tandon PK (2004) Phytoremediation role of plants in contaminated site management. In: Book of environmental bioremediation technologies. Springer, Berlin, pp 315–330

Skinner K, Wright N, Porter-Goff E (2007) Mercury uptake and accumulation by four species of aquatic plants. Environ Pollut 145:234–237

Song FQ, Yang GT, Meng FR, Tian XJ, Dong AR (2004) The rhizospheric niche of seedlings of populus ussuriensis colonized by arbuscular mycorrhizal (AM) fungi. Ecol Environ 13:211–216

Stoltz E, Greger M (2002) Cottongrass effects on trace elements in submersed mine tailings. J Environ Qual 31(5):1477–1483

Sylwia W, Anna R, Ewa B, Stephan C, Danuta MA (2010) The role of subcellular distribution of cadmium and phytochelatins in the generation of distinct phenotypes of AtPCS1- and CePCS3-expressing tobacco. J Plant Physiol 167:981–988

Tangahu BV, Abdullah S, Rozaimah S, Basri H, Idris M, Anuar N, Mukhlisin M (2011) A review on heavy metals (As, Pb, and Hg) uptake by plants through phytoremediation. Int J Chem Eng. https://doi.org/10.1155/2011/939161

Tanwir K, Akram SA, Masood S, Chaudhary HJ, Lindberg S, Javed MT (2015) Cadmium-induced rhizospheric pH dynamics modulated nutrient acquisition and physiological attributes of maize (Zea mays L.). Environ Sci Pollut Res 22(12):9193–9203

Tariq Javed M, Stoltz E, Lindberg S, Greger M (2013) Changes in pH and organic acids in mucilage of Eriophorum angustifolium roots after exposure to elevated concentrations of toxic elements. Environ Sci Pollut Res 20(3):1876–1880

Tchounwou PB, Yedjou CG, Patlolla AK, Sutton DJ (2012) Heavy metals toxicity and the environment. EXS 101:133–164

Thayaparan M (2013) Rhizofiltration of Pb by *Azolla Pinnata*. Int J Environ Sci 3(6):1811

Tian S, Lu L, Labavitch J, Yang X, He Z, Hu H, Sarangi R, Newville M, Commisso J, Brown P (2011) Cellular sequestration of cadmium in the hyperaccumulator plant species. Plant Physiol 157(4):1914–1925

VanLoon GW, Duffy SJ (2000) Environmental chemistry – A global perspective. Oxford University Press, New York, pp 366–385

Velma V, Vutukuru SS, Tchounwou PB (2009) Ecotoxicology of hexavalent chromium in freshwater fish: a critical review. Rev Environ Health 24(2):129–145

Wang XF, Xing ML, Shen Y, Zhu X, Xu LH (2006) Oral administration of Cr (VI) induced oxidative stress, DNA damage and apoptotic cell death in mice. Toxicology 228:16–23

Zeng F, Chen S, Miao Y, Wu F, Zhang G (2008) Changes of organic acid exudation and rhizosphere pH in rice plants under chromium stress. Environ Pollut 155(2):284–289

Zhu XF, Cheng Z, Hu YT, Jiang T, Yu L, Dong NY, Yang JL, Zheng SJ (2011) Cadmium-induced oxalate secretion from root apex is associated with cadmium exclusion and resistance in Lycopersicon esulentum. Plant Cell Environ 34(7):1055–1064

Xin J, Huang B, Dai H, Zhou W, Yi Y, Peng L (2015) Roles of rhizosphere and root derived organic acids in Cd accumulation by two hot pepper cultivars. Environ Sci Pollut Res 22(8):6254–6261

Xing W, Wu H, Hao B, Huang W, Liu G (2013) Bioaccumulation of heavy metals by submerged macrophytes: looking for hyper accumulators in eutrophic lakes. Environ Sci Technol 47:4695–4703

Xue PY, Li GX, Liu WJ, Yan CZ (2010) Copper uptake and translocation in a submerged aquatic plant *Hydrilla verticillata* (L.f.) Royle. Chemosphere 81:1098–1103

Xue P, Yan C, Sun G, Luo Z (2012) Arsenic accumulation and speciation in the submerged macrophyte *Ceratophyllum demersum* L. Environ Sci Pollut Res 19:3969–3976

Yadav SK (2010) Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. S Afr J Bot 76(2):167–179

Chapter 17
Physiological, Biochemical, and Molecular Responses of the Plants Against Enhanced Ultraviolet B and Heavy Metal Stress

Deepanshi Jaiswal, Avantika Pandey, and S. B. Agrawal

Contents

Abstract Ultraviolet-B (UV-B) radiation and heavy metals (HMs) are well-known stress factors for plants. UV-B is a part of incoming solar radiation reaching to the earth surface and its intensity is regulated by the stratospheric ozone layer, which in recent time had shown a significant depletion due to several natural and anthropogenic factors. HMs have also increased in the environment due to the industrial discharge, emissions from vehicle exhaust and improper disposal of wastes in soil and water, which directly or indirectly influence all types of vegetation. It is impor-

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tant to identify physiological, biochemical, and molecular changes in plants against stress factors and plant's strategy to survive successfully under such harsh environment. This review primarily focuses on how UV-B and HMs individually or in combination elicit plant responses, their survival and various adaptation mechanisms in combating stress. Both stresses affect various physiological and biochemical processes at cellular and molecular levels in plants. Induction of several important metabolites such as N-containing compounds, phenolic compounds, terpenes, and essential oils is the major secondary response in plants for long-term stress adaptation under UV-B stress whereas sequestration of HMs by the formation of metal–ligand complex and the antioxidant defense systems are the most important detoxification mechanism used by plants against HMs-induced stress. Based on the outcomes, it will be possible to identify important traits, plants, and various defensive or adaptive mechanisms in plants to cope up with UV-B and metal tolerance.

Keywords Supplemental UV-B · Heavy metals · Antioxidative enzymes · Secondary metabolites

Abbreviations

APX	Ascorbate peroxidase
CAT	Catalase
C_i	Internal CO_2
DAG	Days after germination
DAS	Days after sowing
DAT	Days after treatment
ETR	Electron transport rate
F_v/F_m	Maximum photochemical efficiency of photosystem II
GPX	Glutathione peroxidase
GR	Glutathione reductase
g_s	Stomatal conductance
GSH	Non-oxidized sulfydryl form of glutathione
GSSG	Oxidized form of glutathione
H_2O_2	Hydrogen peroxide
HMs	Heavy metals
MDA	Malondialdehyde
MTs	Metallothioneins
NR	Nitrate reductase
PAL	Phenylalanine ammonia lyase
PCs	Phytochelatins
Pn	Net photosynthetic rate

POX	Peroxidase
PS I and PS II	Photosystem I and II
qP	Photochemical quenching
ROS	Reactive oxygen species
SOD	Superoxide dismutase
sUV-B	Supplemental ultraviolet-B
T_r	Transpiration rate
UVR8	UV resistance locus 8
ϕPS II	Effective quantum yield of photosystem II

17.1 Introduction

As sessile organism, plants are continuously exposed to various abiotic and biotic stresses in their environment. From the beginning of the earth, sunlight functions as a driving force for photosynthetic organisms as well as plants. At that time, all types of radiation, including very harmful ultraviolet radiation, were reaching the earth, but due to evolution of oxygen-producing photosynthetic organisms, a gaseous layer of ozone (O_3) forms in the stratosphere. From that time to now, this layer protects all living beings from the harmful ultraviolet (UV) radiations. Increasing industrialization and anthropogenic activities led to depletion of this O_3 layer, which was first detected in 1980s. It was due to the excess use of chlorine and bromine hydrocarbons, which work as potent damaging molecules for O_3 destruction. Nowadays, there are some other factors such as aerosols, hydrocarbons, and greenhouse gases involved in depletion of O_3 layer and increasing the amount of solar UV radiation. Sensitivity of plants to UV-B radiation varies among species; some are sensitive while other species are non-affected by enhanced UV-B radiation (Teramura and Sullivan 1994). As a stress for plant, it may cause morphogenetic effects which may affect the growth and morphology of plants (Rozema et al. 1997). The well-known sensitive targets of UV-B in plant cell are macromolecules (deoxyribonucleic acid (DNA), proteins) and membranes which affect the normal growth of plants (Jansen et al. 1998). Plants exposed to elevated UV-B radiation developed antioxidant defense response with increased activities of catalase (CAT), superoxide dismutase (SOD), peroxidase (POX), and glutathione peroxidase (GPX) (Costa et al. 2002; Kumari et al. 2010). Radiation-related negative impacts on photosynthetic process involve degradation of PS II proteins (Sullivan et al. 2003), reduced photosynthetic pigments (Surabhi et al. 2009), Rubisco activity (Yu et al. 2013), and stomatal functioning (Cooley et al. 2000; Kataria et al. 2014). Non-damaging level of UV-B induces defense responsive genes in plants. Brown et al. (2005) reported that UV-B stimulates UV RESISTANCE LOCUS 8 (UVR8) (UV-B-specific signaling component) that modulates the expression of a range of genes involved in protection of plants against UV-B. Defense adaptation of plants led to accumulation of

UV-B screening compounds such as flavonoids (Kumari et al. 2009a, b), phenols, alkaloids, and essential oil.

Heavy metals (HMs) are one of the main abiotic factors that hampered the development, growth and productivity of plants. HMs contamination of the environment due to increased anthropogenic activities, modern agricultural practices and rapid industrialization has become a matter of concern worldwide. Although many HMs occur naturally in earth crusts but due to various natural and/or anthropogenic activities, they released into the environment and contribute to undesirable toxic accumulation of HMs in the environment (Chandra and Kang 2016), which causes toxicity to the living organisms (Eapen and D'souza 2005). HMs belong to a group of incessant, non-biodegradable, inorganic chemical constituent with the density higher than 5 g cm^{-3} that have cytotoxic, mutagenic, and genotoxic effects on both ends of food chain, that is, plants and animals through contamination of soil, water, and surrounding atmosphere (Emamverdian et al. 2015). The term HMs includes several metals and metalloids such as Fe, Zn, Cu, Cd, Cr, Pb, Hg, As, Ni, Co, and Mn among which Fe, Zn, Cu, Ni, Co, and Mn are referred as essential micronutrients that are required at certain concentration for the normal growth and development of plants, although excess concentration of these HMs becomes detrimental to plants, and other HMs such as Cr, Cd, Pb, As, and Hg are referred as non-essential with unknown biological and physiological functions and are toxic even at low concentration (Gill et al. 2012; Shahid et al. 2014; Singh et al. 2016b). In plants, HMs exert their toxicity through four possible mechanisms: (1) HMs compete with nutrient cations and oxyanions for the absorption at root surface due to their similarity with cations and oxyanions, (2) disrupt structure and functions of several proteins by direct interaction with sulfhydryl (−SH) group of functional proteins and render them inactive, (3) displace essential cations from the specific binding sites in enzymes and signaling proteins thereby disrupting their functions, and (4) generate reactive oxygen species (ROS) that induces oxidative stress (DalCorso et al. 2013), which ultimately affects various physiological and biochemical processes in plants at cellular and molecular levels (Singh et al. 2016b).

17.2 UV-B as a Stress Factor for Plants: Morphology, Physiology, and Biochemistry

As a harmful radiation, ultraviolet-B generates oxidative stress in plants that affect plant life both positively and negatively by targeting DNA, photosynthetic machinery, membranes, antioxidant enzymes, phytohormones, and secondary metabolites in plants (Jansen et al. 1998; Takshak and Agrawal 2019) (Fig. 17.1). UV-B radiation functions as a stress for plant as it has harmful effects on growth and development of plant, with a reduction in growth at a higher dose of supplemental Ultraviolet-B (sUV-B) irradiation (Kumari et al. 2009a, b; Takshak and Agrawal 2019). As a stress, UV-B induces antioxidative defense in form of increased enzy-

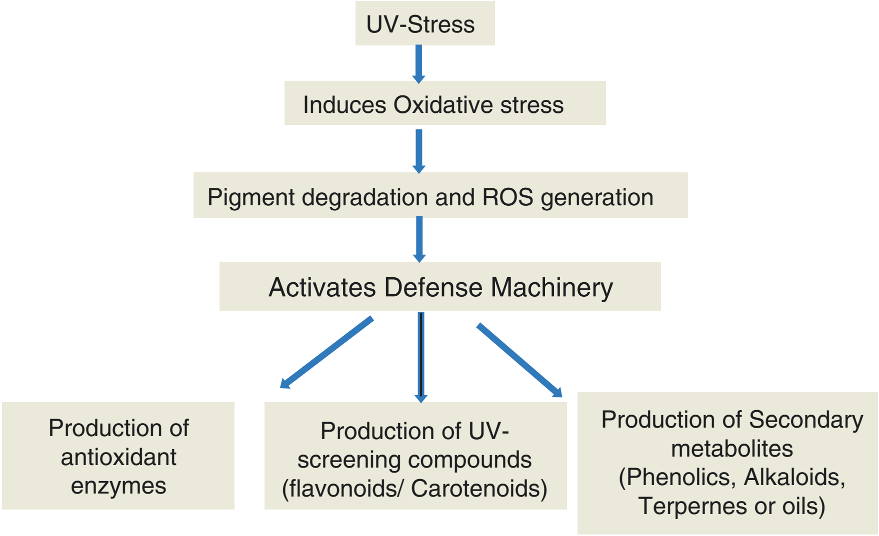

Fig. 17.1 A general outline of defense response in presence of ultraviolet-B.

matic and non-enzymatic antioxidant activities such as superoxide dismutase, catalase, ascorbate peroxidase (APX), POX, and glutathione reductase (GR) to reduce oxidative stress and to scavenge ROS (Kumari et al. 2010). Apart from the stress, UV-B induces secondary metabolites pathways through activating the enzymes of phenyl propanoid pathway (Takshak and Agrawal 2014; Kumari and Agrawal 2011). UV-B induced the defense through activation of free radical scavenging activities, which depicts plant organs effectively perform to reduce the stress (Takshak and Agrawal 2015a). This subsection discusses the UV-B-induced changes in growth, morphology, physiology, and biochemistry of plants.

17.2.1 Morphological Changes

Several morphological changes occur in response of UV-B such as the reduction of plant height and leaf length/area, increased auxiliary branching, leaf bronze, glazing, chlorosis, and necrotic spots (Kataria et al. 2014). A study with mulberry plants showed negative effects of sUV-B (3.78 kJ m^{-2} day^{-1}) on plant morphology in form of stunted growth, leaf length, width, and petiole length with non-significant differences between male and female plants (Chen et al. 2016). Fraser et al. (2017) reported that UV-B with low-dose R: FR (Red: Far red) induced compactness in coriander in form of longer petiole formation, whereas in combination with white light it did not have effect on petiole length. It can be suggested that UV-B used as a method for increasing compactness in commercially cultivated plants. Contrary to this, UV-B imposed inhibition on low R: FR-induced hypocotyls elongation. UV-B-induced growth pattern has been varied among species. As revealed by Bassman et al. (2003), plant height of *Pinus ponderosa* followed similar trend in both ambient and two times ambient UV-B, whereas three times ambient UV-B reduced the height with an increase at final stage as compared to other two treatments. sUV-B exposure of initial 6 months increased the seedlings height of *Pseudotsuga menziesii* while non-significant differences found at the later stage. Higher dose of UV-B (3×) reduced the plant height in *Picea engalmanni* whereas non-significant changes were found between lower dose (2×) and ambient. Another study commences that higher dose of UV-B deleteriously affects plant growth (plant height, biomass of leaves and shoot except root) as compared to lower dose and controls (Bassman et al. 2003). Hamid et al. (2018) also reported the negative impact of UV-B on plant height and number of tillers at early growth stages in *Heteropogon contortus*, whereas root length, number of leaves and biomass were mostly affected at the later stage of growth. Kakani and co-authors reported a significant decrease in leaf area (30%) and plant height (47%) after 16 h of exposure in *Gossypium hirsutum*. Early development of necrotic patches was found under UV-B exposed plants as compared to the control (Kakani et al. 2003a, b). Initial exposure of UV-B leads to coloration of bronze which later converted into chlorotic and necrotic surfaces followed by leaf fall. Sometimes long-term exposure leads to the curling or cupping of leaves. A change in various morphological parameters is described in Table 17.1.

Koti et al. (2004) recorded the negative impact on floral morphology, such as reduction in petal length and staminal length either alone (UV-B) or interaction with temperature and CO_2. Higher dose of UV-B induces reduction in flower length (28%) and pollen production or the pollen number in different genotypes of soybean. At the dose of 15 $kJ\ m^{-2}\ d^{-1}$ pollens were not developed any aperture while the control plants are triporate (Koti et al. 2004). As documented by Koti et al. (2004), floral length and the number of pollen number/anther were significantly reduced under sUV-B exposure in *Glycine max*. A reduction of 45.5% in leaf growth was observed while the number of leaves was found to be increased. A reduced leaf area and increased leaf thickness are a well-known morphological responses reported by Jansen (2002), Furness et al. (2005), Hectors et al. (2007), Yang et al. (2008), Wargent et al. (2009), Klem et al. (2012), and Robson and Aphalo (2012). Tripathi et al. (2019) observed reductions in all the studied floral parameters in two cultivars of sunflower (DRSF 108 and Sungold) under UV-B exposure as compared to control. Stomatal number and density were also found to be increased under the UV-B exposure with higher under DRSF 108. UV-B reduced the stem elongation whereas it promotes leaf elongation, leaf thickness, and axillary branching (Potters et al. 2007). Increased tillering, axillary branching, and reduced stem elongation are well-known distinguished features produced by UV-B (Jansen 2002; Furness et al. 2005). As revealed by Kumari and Agrawal (2010) in an experiment of two doses, higher dose-induced reduction (45%) in leaf growth at the later stages whereas specific leaf weight and the number of leaves were increased. Most of the studies on UV-B showed that higher dose of UV-B has several detrimental effects on plant morphology, which may affect the reproductive capability of plants.

Table 17.1 Morphological responses of plants against UV-B stress

Plants	Dose	Parameters	Effects (%)	References
Morus alba	Ambient+3.78 kJ $m^{-2}d^{-1}$	Plant height	Decreased	Chen et al. (2016)
		Leaf area	Decreased	
		Petiole length	Decreased	
		No. of leaves	Decreased	
Heteropogon contortus	Ambient+7.2 k J $m^{-2}d^{-1}$	Plant height	Decreased	Hamid et al. (2018)
		Root height	Decreased	
		No. of leaves	Decreased	
		No. of tillers	Decreased	
		Leaf area	Decreased	
		Biomass	Decreased	
Gossypium hirsutum	Ambient+16 k J $m^{-2}d^{-1}$	Plant height	Decreased	Kakani et al. (2003a, b)
		Branch number	Increased/not changes	
		Branch length	Increased/not changes	
		Leaf area	Decreased	
Glycine max	9.8 kJ $m^{-2}d^{-1}$	Petal length	Decreased	Koti et al. (2004)
		Staminal column length	Decreased	
		Flower length	Decreased	
		Pollen number	Decreased	
		Pollen germination rate	Decreased	
		Pollen tube length	Decreased	
Cymbopogon citratus	1.8 kJ $m^{-2}d^{-1}$	Biomass (lower dose)	Not change	Kumari and Agrawal (2010)
	3.6 kJ $m^{-2}d^{-1}$	Biomass (higher dose)	Decreased	
		Leaf area	Decreased	
		No. of leaves	Increased	
Acorus calamus	1.8 kJ $m^{-2}d^{-1}$ 3.6 kJ $m^{-2}d^{-1}$	Plant height	Decreased	Kumari et al. (2009a, b)
		Leaf area	Decreased	
		Leaf number	Increased	
		Branch number	Increased	
Coleus forskohlii	3.6 kJ $m^{-2}d^{-1}$	Plant height	Decreased	Agrawal (2015b)
		Leaf number	Decreased	
		Leaf area	Decreased	

17.2.2 Physiological Changes

Physiological processes are key mechanisms in the plant upon which the whole plant life is dependent. As sunlight is the fundamental need of the plant for conducting physiological processes, and UV-B is the fraction of sunlight, so, it can not be removed by any kind of secondary management practices. Excess UV-B works as an oxidative stress for plant and disturbs the plant physiology, which ultimately affects the growth and metabolism. Photosynthetic processes were also targeted as disruption of photosynthetic pigments by UV-B. Some previously reported targeted processes of photosynthesis are (1) reduced C-fixation and oxygen evolution, (2) impairment and unbalancing between PS I (photo system) and PS II, (3) reduced Rubisco activity, (4) ATP (adenosine triphosphate) synthesis, (5) photosynthetic storage, and (6) impairment of electron pool between Q_A (quinone) to Q_B.

Kataria et al. (2014) reported that sUV-B has various negative impacts on photosynthesis linked to damaging PS II, thylakoid membrane integrity, Rubisco activity and stomatal conductance (g_s). In *Arabidopsis thaliana* (Colombia), photosynthetic rate was unaltered while transpiration rate (T_r) and g_s increased under UV-B treatment (Lake et al. 2009). Alteration in carbon and nitrogen metabolism occurs due to a decrease in photosynthesis and growth. UV radiation also involves in degradation of D_1 and D_2 proteins of reaction center and it can be degraded by a fluence rate of 1 μmol m^{-2} s^{-1} of UV radiation. Photosynthetic activity reduced in rice due to a decrease in Rubisco content (Fedina et al. 2010; Zlatev et al. 2012). Reduced photosynthetic rate and g_s were recorded in *Coleus forskohlii* at all the stages with maximum at 90 (31%) and 60 (30.9%) DAT (days after treatment) (Takshak and Agrawal 2015b). As documented by Kumari and Agrawal (2010), photosynthetic rate has changed non-significantly in *Cymbopogon citratus* exposed against sUV-B whereas g_s and T_r were reduced at both low and high doses of UV-B. Contrary to this, water use efficiency (WUE) was found to be increased. Exposure of sUV-B on different cultivars of *G. max* also showed reduction in photosynthetic rate in cultivar JS-335 (62%) followed by PK-416 (55%), JS 97–52 (47%) and minimum in PS-1042 (39%) at the later stages of growth. Stomatal conductance and WUE showed the similar trend with a maximum decrease in JS-335 and a minimum decrease in PS-1042 (Choudhary and Agrawal 2015). Hofmann et al. (2003) revealed that leaf water potential was found to be increased in *Trifolium repens*. Different doses of sUV-B lead to cause changes in several physiological parameters of plant (Table 17.2).

Photosynthetic efficiency of *C. citratus* was found to be reduced by 14% at the higher dose of UV-B (Kumari and Agrawal 2010). Quantum yield of *C. forskohlii* declined under sUV-B exposure at all the stages with maximum at later stages of growth. As reported by Yao et al. (2005), quantum yield of PS II was reduced significantly under UV-B in *Cucumis sativus*. Ghisi et al. (2002) reported that starch content was found to be increased by 18% in barley exposed to UV-B while the sucrose content was reduced by 36%. Here, chlorophyll content and photosynthetic oxygen evolution were not significantly influenced. In most of the study, it was

Table 17.2 Physiological responses of plants against sUV-B stress

Plants	Dose	Parameter	Effects	References
Trifolium repens L.	13.3 kJ m^{-2}d^{-1}	Leaf water potential	Increased	Hofmann et al. (2003)
		Quantum yield	Not change	
Arabidopsis thaliana	9.96 kJ m^{-2}d^{-1}	Photosynthetic rate	Not change	Lake et al. (2009)
		Transpiration	Increased	
		Stomatal conductance	Increased	
		Quantum yield	Decreased	Schultze and Bilger (2019)
Cucumis sativus	3.5 kJ m^{-2}	Photosynthetic efficiency	Decreased	Yao et al. (2005)
C. citratus	1.8 kJ m^{-2}d^{-1} 3.6 kJ m^{-2}d^{-1}	Photosynthetic rate	Not changed	Kumari and Agrawal (2010)
		Stomatal conductance	Decreased	
		Transpiration rate	Decreased	
		Water use efficiency	Decreased	
		Photosynthetic efficiency	Decreased	
Glycine max	7.2 kJ m^{-2}d^{-1}	Photosynthetic rate	Decreased	Choudhary and Agrawal (2015)
		Stomatal conductance	Decreased	
		Transpiration rate	Decreased	
		Water use efficiency	Decreased	
		Photosynthetic efficiency	Decreased	
Vigna radiata	7.2 kJ m^{-2}d^{-1}	Photosynthetic rate	Decreased	Choudhary and Agrawal (2014)
		Stomatal conductance	Decreased	
		Water use efficiency	Decreased	
C. Forskohlii	3.6 kJ m^{-2}d^{-1}	Photosynthetic rate	Decreased	Agrawal (2015b)
		Stomatal conductance	Decreased	
		Water use efficiency	Decreased	
		Photosynthetic efficiency	Decreased	

found that photosynthesis, stomatal conductance, and quantum yield of the plants were reduced under UV-B and it may vary upon treatment and growth stages.

17.2.3 Biochemical Changes

Alteration in metabolism and biochemistry is a key regulatory process that takes place in plants in response to stress which makes plants system capable to overcome the stress. There are several pronounced effects of UV-B that take place in plants: decreased photosynthetic pigments, increased UV-B screening compounds such as flavonoids and anthocyanin, changes in enzymatic and non-enzymatic antioxidants and protein contents (Table 17.3). In most of the work, it was found that photosynthetic pigments were decreased such as in *alfalfa*, barley, *mustard*, cowpea, green gram, pea, rice, rye, soybean, and wheat and these reductions ranged from 10 to 70% with maximum in dicot species than monocot (Kakani et al. 2003a, b). Chlorophyll content was found to be reduced by 15 and 20% in sunflower cotyledon irradiated with 15 and 30 kJ m^{-2} sUV-B. Photosynthetic pigments in the leaves of *C. forskohlii* exposed to sUV-B were reduced significantly at all the stages (Takshak and Agrawal 2015b). Afreen et al. (2006) reported that melatonin concentration in *Glycyrrhiza uralensis* was found to be increased by 160% in presence of sUV-B as compared to white light control. Among three dose experiments of sUV-B, chlorophyll a and b content of the plant quinoa was reduced as the UV-B dose increased and maximum reduction was noticed under the dose 3 (Hilal et al. 2004). Epidermal flavonoid concentration was found to be increased in rye during developmental stages due to both ontogenic responses and sUV-B exposure (Burchard et al. 2000).

Exposure to sUV-B induces ROS generation, which may cause peroxidation of membrane lipids, measured in form of malondialdehyde (MDA) content. sUV-B exposure increased the MDA content in *C. forskohlii* (Agrawal 2015b). Ma et al. (2019) reported the increase of MDA with an increasing dose of UV-B and maximum after 12 h of exposure. Lipid peroxidation was increased with growth stages in two cultivars of *Vigna radiata* with higher in cultivar HUM 1 than HUM 12 exposed to sUV-B (ambient +7.2 kJ m^{-2} d^{-1}). An exposure of 25 kJ m^{-2} dose of sUV-B increased vitamin D_2 in several parts of shitake mushroom by 36.7, 68.6, and 106.4 μg/g for pileus, middle, and gill parts, respectively. In the gill part of mushroom, concentration of vitamin D_2 was increased from 2.77 (unexposed) to 13.8, 40.7, and 61.9 μg g^{-1} after exposures of 25, 50, and 75 kJm^{-2}, respectively, at 35 °C, which denoted the increasing dose of UV-B increased concentration of vitamin D_2 and it may be due to the conversion of ergosterol in to vitamin D_2 by UV-B (Ko et al. 2008).

Total protein content of plant was also affected by UV-B radiation. Santos et al. (2004) found a reduction of protein by 8.4% in leaves of potato exposed to biological effective UV-B radiation (7.83 kJ m^{-2} d^{-1}). Protein content was reduced by 32.2 and 44.2% in *Raphanus sativus* exposed to sUV-B, at both 20 DAG (days after germination) and 40 DAG, respectively (Singh et al. 2010). Reduction in protein

Table 17.3 Biochemical responses of plants against UV-B stress

Plants	Dose	Parameter	Effects	References
Helianthus annuus	15 kJ m^{-2}d^{-1} 30 kJ m^{-2}d^{-1}	Chlorophyll	Decreased	Costa et al. (2002)
		Ascorbic acid	Increased	
		Dehydroascorbate	Increased	
Chenopodium quinoa	7.5 W m^{-2}	Chlorophyll	Decreased	Hilal et al. (2004)
		Phenols	Increased	
Solanum tuberosum	7.83 kJ m^{-2}d^{-1}	Pigment	Decreased	Santos et al. (2004)
		Protein	Decreased	
Taxus chinensis	10.8 μw cm^{-2} nm^{-1}	Chlorophyll	Decreased	Zu et al. (2010)
		Flavonoids	Increased	
Raphanus sativus	7.2 kJ m^{-2}d^{-1}	Chlorophyll	Decreased	Singh et al. (2010)
		Ascorbic acid	Increased	
		Protein	Decreased	
Triticum aestivum L.	7.1 kJ m^{-2}	Chlorophyll	Decreased	Agrawal and Rathore (2007)
		Ascorbic acid	Decreased	
		Thiol	Increased	
Vigna radiata	7.1 kJ m^{-2}d^{-1}	Chlorophyll	Decreased	Agrawal and Rathore (2007)
		Ascorbic acid	Decreased	
		Thiol	Increased	
Vigna radiata L.	7.2 kJ m^{-2}d^{-1}	Chlorophyll	Decreased	Choudhary and Agrawal (2014)
		MDA	Increased	
		Flavonoids	Increased	
		Phenol	Increased	
		Protein	Decreased	
Acorus calamus	1.8 kJ m^{-2}d^{-1} 3.6 kJ m^{-2}d^{-1}	Chlorophyll	Decreased	Kumari et al. (2009a, 2009b)
		Phenol	Increased	
C. citratus	3.6 kJ m^{-2}d^{-1}	Chlorophyll	Decreased	Kumari and Agrawal (2010)
		Ascorbic acid	Decreased/ increased	
		MDA	Increased	
		Phenol	Increased	
C. forskohlii	3.6 kJ m^{-2}d^{-1}	Chlorophyll	Decreased	Takshak and Agrawal (2015b)
		Protein	Decreased	
		Thiol	Increased	
		Proline Phenol	Increased Increased	

content was also recorded in mung bean by sUV-B exposure (Choudhary and Agrawal 2014).

High UV-B reduced the carbohydrate content by 22% in white clover (*T. repens*). Nitrogen content was also increased but more at higher UV-B dose (Lindroth et al. 2000). As reported by Quaggiotti et al. (2004), nitrate reductase (NR) activity in the second leaf of *Zea mays* was found to be reduced 41% at the 12th day of UV-B exposure while the nitrate content of the second leaf was also decreased in both control and UV-B-treated plants but finally at 12th day a 24% reduction in nitrate content was reported. Photosynthetic oxygen evolution rate was reduced by 10% under sUV-B exposure at the 12th day of treatment. As reported by Ubi et al. (2006), anthocyanin content in four early ripening cultivars of apple was increased under UV-B. Taxol content in *Taxus* was increased by 31% while the flavonoid content was increased by 36% under UV-B exposure. In a recent study, Hamid et al. (2018) showed that elevated UV-B reduced the amount of reducing sugar whereas total sugar, starch, and sucrose were increased at the later stages of growth. The data from most of the studies showed that UV-B imposed on plants negatively impact the biochemistry of plants.

17.2.4 Molecular Changes

UV-B radiation perceived by the plants and respond to it which may vary upon nature of the UV-B treatment, the extent of adaptation and acclimation to UV-B, and its interaction with other environmental factors. Response of UV-B was mediated by two signaling pathways: specific signaling (photomorphogenic responses) and non-specific signaling (Fig. 17.2). Photomorphogenic responses initiated by activation of UVR8, combined with CONSTITUTIVE PHOTOMORPHOGENESIS1 (COP1), involve activation of transcription factors of ELONGATED HYPOCOTYL5 (HY5), which through various signaling mechanisms lead to the activation of enzymes involved in secondary metabolism pathway and stomatal functioning. Non-specific signaling involves generation of ROS, DNA damage, and wound/defense signaling molecules (Jenkins 2009). UV-B exposure reduced RNA transcripts of Chl *a/b* binding proteins (cab) to low or even undetectable levels in third leaf and younger leaf bud tissue in *Pisum sativum* L (Jordan et al. 1994). sUV-B radiation also induced the photo damage of D_1 and D_2 proteins in reaction center PS II in *Dunaliella salina* (Masi and Melis 1997).

In *Leucaena leucocephala*, mimosine accumulation increased due to several stress including UV. The induction of mimosine takes place at the molecular level by stimulating multiple cysteine synthases, one or more involved in mimosine biosynthesis (da Silva Rodrigues-Corrêa et al. 2019). A study by Gupta et al. (2018) on *Z. mays* denoted the role of differentially expressed genes (DEGs) in UV-B signaling pathways and other molecular functions responsible for leaf cell death.

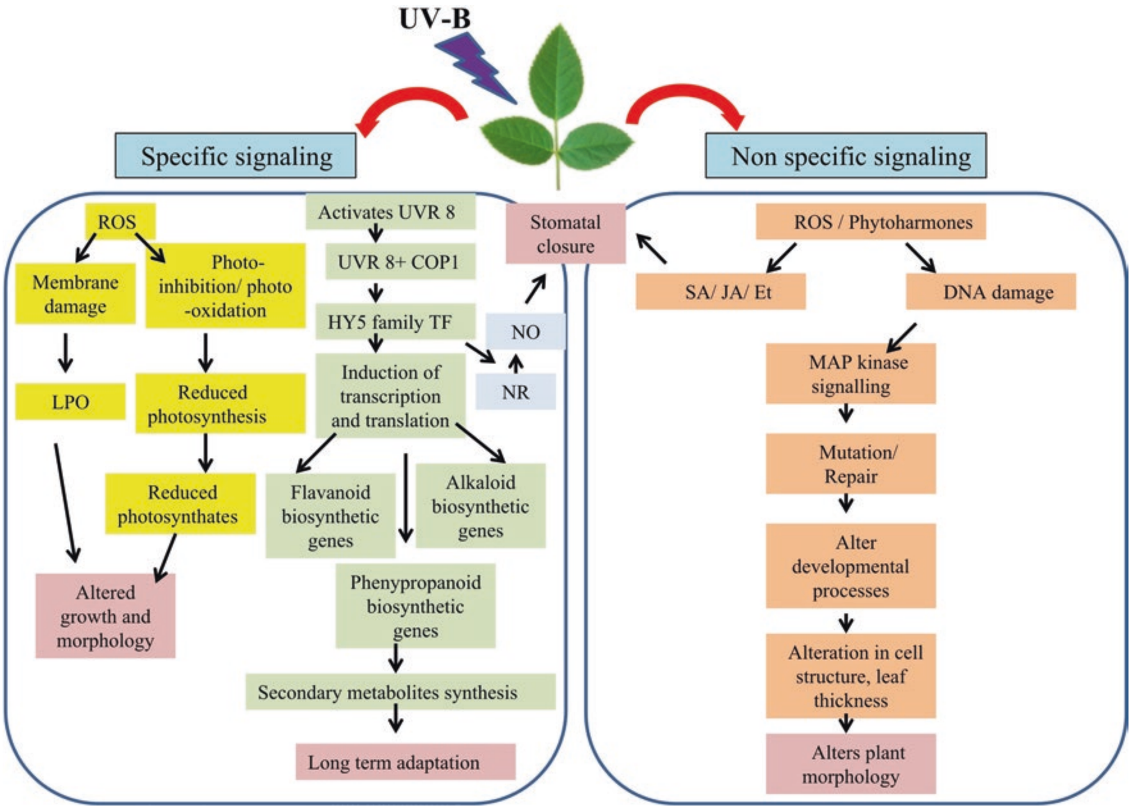

Fig. 17.2 UV-B-induced specific and non-specific signaling in plants involved in plant adaptation (Tossi et al. 2014; Müller-Xing et al. 2014; Matsuura et al. 2013; Gupta et al. 2018; Fan et al. 2018).

A proteomic analysis of linseed leaf reported a total of 17 bands (from 28 to 278.06 kDa) in control plants, among which 7 protein bands were affected by treatments (sUV-B, tropospheric O_3, sUV-B + O_3). It was observed that the three protein bands (222.24, 90.58, and 60.38 kDa) were sensitive against the UV-B exposure, among which 222.24 and 90.58 kDa proteins were absent whereas a reduced amount of 60.38 kDa proteins was observed under the sUV-B exposure. RAPD (Rapid amplification of polymorphic DNA) analysis for the detection of DNA damage which is induced by stress showed a variation in appearance and disappearance of new bands in all the treatments. The unique band index (UBI) showed changes in RAPD profiles and was 39.4, 45.3, and 56.6% for sUV-B, O_3, and sUV-B + O_3 samples, respectively (Tripathi et al. 2011). It is clear from several studies that regulatory/damaging effect of UV-B at molecular level may induce developmental changes and secondary metabolic pathway in plants.

17.3 Adaptation Under UV-B Stress

17.3.1 Morphological and Anatomical Adaptations

Plants avoid the harmful UV-B using two mechanisms: (1) molecular mechanism which includes DNA damage and repair and (2) morphological adaptations such as increasing leaf hair, cuticular wax, and leaf thickness through changes in epidermal reflectance and transmittance. In natural system, both the mechanisms are important. As epidermis is the first layer of protection and it has potential to alter the incident light, there are several modifications that occur to counter the stress, for example, in several cases, epidermis is ornamented with hairs and trichomes which contain UV-absorbing compounds (Skaltsa et al. 1994). Sometimes there is deposition of epicuticular waxes on leaf surfaces which is also responsible for UV-B reflectance as reported by Tevini and Steinmüller (1987). Deposition of wax on adaxial surface of leaf was found under sUV-B (Kumari and Agrawal 2010). Wax deposition was also observed by Takshak and Agrawal (2017) in *Withania somnifera* exposed to sUV-B.

In *Chenopodium quinoa*, leaf mesophyll cells were substituted by a layer of palisade parenchyma with elongated cells under +UV-B treatment which is not present in –UV-B plants where the mesophyll tissues were non-distinguishable without differences in cells, a homogeneous spongy parenchyma. This thicker epidermal wall may lead to protection against UV-B. To avoid the UV-B stress in plants, some common changes which occur in plants are increasing leaf thickness with a decrease in leaf area and stomatal frequencies (Barnes et al. 1990). As analyzed by Hollósy (2002), the ultra-structural observation of mesophyll cells (UV-A-exposed) of *Lysimachia nummularia* L. plant showed a lesser amount of starch grains as compared to control plants, besides there is an accumulation of electron dense precipitates in vacuoles bordering the tonoplast membrane. Chloroplasts lost its structural integrity linked by the loss of orderly pattern of grana and thylakoid in UV-B-exposed cells. Hamid et al. (2018) observed an increase in mesophyll, spongy, and palisade cells of *H. contortus* under UV-B exposure as compared to control ones.

As reported by Brandle et al. (1977), various ultrastructural modifications were found in *P. sativum* leaf cells, that is, rupture of chloroplast outer membrane, swelling of chloroplast, swollen cisternae, and vesiculation of plasmalemma. Under enhanced UV-B radiation, shortened chloroplasts with swollen and distorted thylakoids were observed in *Morus alba*. Besides, osmiophilic granules were also increased in females than in males (Chen et al. 2016). According to Hilal et al. (2004), a fivefold increase in wall thickness was due to lignin deposition in cotyledons of *Quinoa* due to UV-B radiation. In contrast to this, leaf thickness was decreased on the adaxial surface of blueberry leaves as compared to control plants. Among the two varieties, the reduction was greater in Brigitta (5.6-fold) than in Bluegold (2.4-fold). The intercellular cavities were found to be increased, 58% in Bluegold and 46% in Brigitta as compared to control ones (Inostroza-Blancheteau et al. 2014). A tanniferous deposition on stomatal guard cells and epidermal cell lumen of Scots pine needles while, in loblolly pines tannins accumulated on the central vacuole of mesophyll cells (Laakso et al. 2000). The cross-sectional area was also reduced significantly in treated plants. In spite of this, needle length was also found to be reduced in both 9- and 12-day-old plants. In 61-day-old plants, both the abaxial and adaxial surfaces were thicker in UV-B-treated plants. The increased thickness of cutin layer was also found in Scots pines. UV-B also increased the thickness of secondary walls of outer epidermal layer as compared to control plants. UV-B exposure induced stomatal closure in cucumber seedling, bean, and oilseed rape leaves (Allen et al. 1997; Teramura 1983; Nogués and Baker 2000). It showed that the various modifications take place in leaf structure both at epidermal anatomy and internally to reduce the stress on plants.

17.3.2 Antioxidative Defense Mechanisms

Plants respond to stress by scavenging free radicals or by generation and increment of antioxidative defense compounds which include enzymatic and non-enzymatic antioxidants. Carotenoids work as a potential UV screening compound in plants and are found to be increased under UV-B exposure. A variable increase in these antioxidants was found in plants exposed to the radiation. Plants exposed to mineral nutrient amendment with sUV-B showed more carotenoid contents in comparison to control. A two-dose experiment on sunflower cotyledons showed that GSH (non-oxidized sulfhydryl form of glutathione) content has increased by sixfold under UV-B treatment and GSH/GSSG (oxidized form of glutathione) ratio was also enhanced. Ascorbate-deficient mutants of *A. thaliana* showed lower antioxidative defense, measured in form of total glutathione, CAT activity, and APX activity as compared to wild ones under sUV-B exposure (Gao and Zhang 2008). After 3 days' exposure of cucumber first leaves to UV-B, it showed a large increase (4.5-fold) in SOD and APX activity, while non-significant effect on GR activity (Kondo and Kawashima 2000). Costa et al. (2002) reported that lower dose of UV-B induced more antioxidant system as compared to high dose of UV-B in sunflower cotyledons, such as GSSG and ratio of GSH and GSSG was also increased in both the doses but it was higher (150%) in lower dose as compared to higher dose (75%). Ascorbic acid and dehydroascorbate were also increased and it was maximum under lower dose, that is, 53 and 54% as compared to control. CAT and GPX activity increased under UV-B whereas SOD activity reduced under both the doses with maximum reduction under lower dose (Costa et al. 2002).

A short-term exposure of UV-B on *Achyranthes bidentata* showed a significant increase in scavenging activity in form of enzymatic activities (SOD, POD, and CAT activity) that was found to be increased significantly but the activity may vary upon time (Li et al. 2019). Antioxidant enzymes SOD, CAT, and POD were expressed and increased to protect cells when oxidative stresses such as H_2O_2 (hydrogen peroxide) concentration increases in cell. The same results also recorded in germinating soybeans to counter the negative effect of H_2O_2 (Ma et al. 2019). As reported by Singh et al. (2010), antioxidant activity in *R. sativus* varied with age and treatment. CAT activities were found to be reduced at both (20 and 40 DAG) the stages while the POX, SOD, and GR activity was increased at both the stages. APX activity was reduced initially, but a large and significant increase at the later stage of growth was recorded. Ascorbic acid content was also increased at both the stages with maximum at initial stage. Two doses (15 and 30 kJ m^{-2} d^{-1}) of sUV-B effects on sunflower cotyledons showed an increase in CAT and GPX activities while reduction in APX activity as compared to control ones (Yannarelli et al. 2006). Ascorbic acid content of leaves was reduced under UV-B exposure in both mung bean and wheat. sUV-B exposure increased the thiol content in both the cultivars (Agrawal and Rathore 2007). Total phenol and flavonoid were increased with increasing doses of UV-B with maximum under three doses of UV-B while betalains were maximum under dose 1 and lowest under dose 3.

17.3.3 Secondary Metabolites Production

17.3.3.1 Phenolics

Shikimic acid pathway involves production of various phenolic compounds and the common precursors for the phenolics are aromatic amino acids, phenylalanine and tyrosine. The key enzymes, PAL (phenylalanine ammonia lyase), and TAL (tyrosine ammonia lyase), were involved in the formation of cinnamic acid and *p*-coumaric acid. Cinnamic acid leads to stilbenes and styrylpyrones, while the *p*-coumaric acid leads to lignins, coumarins, furanocoumarins, hydrolysable tannins, condensed tannins, and flavonoids. Tannins from *Betula pendula* and *Laurus nobilis* were increased, while *Phlomis fruticosa, Ceratonia siliqua, Vaccinium* spp., *Caluma vulgaris, Rubus* *chamaemorus*, showed no significant changes under UV-B radiation. Coumarins and furanocoumarins in *Pastinacea sativa* were increased while these were decreased in *Quercus robur*. Hydroxycinnamates content in *B. pendula, B. resinifera*, and *Hordeum vulgare* was increased under UV-B exposure. Most of the species showing an increase in flavonoids content under UV-B exposure (Bassman 2004). Whole and sliced strawberry showed an increase in total soluble phenolic (TSP) content under UV-B exposure with maximum TSP at lower dose of UV-B (Du et al. 2014). High blush blueberries treated with UV-B showed an increase in total phenolic content with maximum under high dose and 2 h of adaptation time (Eichholz et al. 2011). Here, the dominant phenolic fractions are flavonoids (40%) and phenolic acids (49%). As we know that flavonoids work as UV-B screening compound and involve in defense as antioxidant molecules. Postharvest irradiation of visible + UV-B on apple fruit (*Malus domestica*), increased the sum of flavonoids, sum of phenols, and sum of total phenols significantly. Quercetin glycosides showed a significant increase under Vis treatment alone, while a sixfold higher increase in presence of Vis + UV-B treatment was noted. Anthocyanin content was also increased by 20–25% under Vis + UV-B treatment (Hagen et al. 2007). The results showed that UV-B treatment increased the phenolic compounds as due to the induction of PAL. Total phenolic content in the peel of harvested lemons was increased highly in flavedo (outer colored layer of mesocarp of citrus) after 2 min of UV-B treatment (Interdonato et al. 2011). As reported previously by Schreiner et al. (2009), among four different treatments (1 h dose of 0.075 W h m^{-2} with 2 h (T-1) and 22 h (T-2) adaptation time and 2 h dose of 0.150 W h m-2 with 2 h (T-3) and 22 h (T-4) adaptation time) on *Tropaeolum majus*, T-1 showed a maximum increase of phenolics in inflorescence, while in leaves and seeds T-4 showed a maximum increase in phenolic content. Phenolic compounds were found to be increased in the second summer under long-term exposure of *B. pendula* (Tegelberg and Julkunen-Tiitto 2001). Zagoskina et al. (2003) also proved that phenolic compounds were increased by sUV-B radiation in tea plant callus culture.

17.3.3.2 N-Containing Compounds/Alkaloids

Among N-containing compounds, alkaloids contribute in a major form. Alkaloids are low-molecular-weight nitrogen-containing heterocyclic organic compounds and present in 20% of all plant species. The numbers of identified structures of alkaloids have been 12,000 or more than 16,000 (Zhang and Björn 2009). The plant species that contain desired alkaloids showed variation in growth and alkaloid contents (Schläger and Dräger 2016). As reported by Ramani and Chelliah (2007), catharanthine (alkaloid) concentration in cell suspension cultures of *Catharanthus roseus* was found to be induced by UV-B through receptor activation, medium alkalinization (Ca^{2+} influx and Cl^{-} efflux), ROS production and MAP kinase pathway activation, which finally led to transcription of two genes encoding tryptophan decarboxylase (*Tdc*) and strictosidine synthase (*Str*). Another report by Ramani and Jayabaskaran (2008) showed that alkaloids (catharanthine and vindoline) from cell suspension cultures of leaves of *C. roseus* were found to be increased by sUV-B and it was highest at 48–72 h of irradiation. Terpenoid indole alkaloids (TIAs) absorb UV-B radiation and involve protection against UV-B radiation. In a study, Binder et al. (2009) showed the effect of UV-B radiation on six different terpenoid indole alkaloids of *C. roseus*. The results showed that among all six alkaloids (serpentine, catharanthine, ajmalicine, horhammericine, lochnericine, and tabersonine), lochnericine concentration was found to be increased highly after 20 min of exposure and the lowest increase of catharanthine content after 10 min of exposure. Besides, serpentine after 10 min, ajmalicine after 20 min, and tabersonine after 15 min of exposure while horhammericine concentration was highest initially before exposure and reduced continuously after exposure. Another study by Gregianini et al. (2003) showed that TIA of *Psychotria brachyceras* that is brachycerine was also influenced by UV radiation. Synthesis of TIA needs three compartments—plastid, cytosol, and vacuole—while, for vindoline, endoplastic reticulum is also required. This study showed that the brachycerine concentration was found to be increased tenfold by UV-C radiation 16 h daily on rootless cutting cultures. Daily exposure of UV-B for 16 h increased the concentration of alkaloid by twofold. A brachycerine absorbance maximum is 226 and 280 nm, showing its UV protecting or filters properties. In *Aquilegia caerulea*, alkaloid content was reduced by UV-B exposure as the control fraction was high as compared to UV-B-treated plants. This may occur due to destruction of ultraviolet radiation. A study of acetylsalicylic acid and UV-B on hairy root cultures of *Anisodus luridus* showed that UV-B induced and upregulated the gene expression level of four structural genes, including *PMT*, *TRI*, *CYP80F1,* and *H6H,* of tropane biosynthetic pathway and accumulation of tropane alkaloids, which finally led to higher production of end-product scopolamine (Qin et al. 2014). As studied by Rai et al. (2011), artemisinin concentration in *Artemisia annua* L. was increased by 10.5% upon short-term (14 days) pre-treatment of UV-B (4.2 kJ m^{-2} d^{-1}) on seedling. Gao et al. (2016) reported that post-treatment of high level of UV-B followed by dark caused sevenfold increase in indole alkaloid (6-hydroxyl-1H-indol-3-yl) carboxylic acid methyl ester. The binary stress upregulates the genes involved in the metabolic pathway converting shikimate to L-tryptophan and the frameworks of indole biosynthesis anthranilate, indole, and L-tryptophan, which increased 2-, 441-, and 1-fold, respectively.

17.3.3.3 Terpenes/Essential Oil

Essential oils are a kind of natural oils obtained from medicinal plants with the help of extraction and distillation technique. They are a mixture of volatile and non-volatile compounds and mostly soluble in ethanol (Trujillo et al. 2015). The constituent of plant essential oil comes under two entirely distinct chemical classes, terpenoids and phenylpropanoids (Sangwan et al. 2001). Terpenes represent the major components, occurring much more frequently and abundantly, while phenylpropanoids provide essential and significant flavor and odor to the oil (Sangwan et al. 2001).

An indoor plant *Picea abies* exposed to UV-B radiation for 4 h led to an epigenetic change, which includes DNA methylation and in a defensive way the plant responds by emitting volatile terpenes; the monoterpene hydrocarbons myrcene, limonene, borneol, and the monoterpene ester bornyl acetate (Ohlsson et al. 2013). In a study of Chang et al. (2009), enhanced UV-B radiation alters the growth of *Ocimum basilicum* L. and induces the synthesis of volatile oils among which the three major compounds (cineole, linalool, and eugenol) were found to be increased significantly as compared to control. Dolzhenko et al. (2010) reported that UV-B induces the expression of genes involved in terpenoid biosynthesis. Dolzhenko and co-workers studied by exposing field grown and growth chamber grown peppermint plants to UV-B radiation which showed that in both the experiments genes involved in terpenes biosynthesis was upregulated but the content of essential oil was higher in growth chamber grown plants with lower phenol content and vice versa in field plants. In *Cuminum cyminum* L. genes involved in secondary metabolites, biosynthesis was found to be increased under UV-B stress (Ghasemi et al. 2019). Two UV-B treatments (A-1 h, B-2 h) were applied on the plants and it was found that in both the treatments, terpenes concentration was increased up to 6 h but after that a decrease was analyzed. After 6 h, treatment A showed an increase of 2.5 mg 100–1 of extract while in treatment B 4.5 mg 100–1 was reported as compared to control plants. Here, we can say that UV-B treatment of 2 h has more inducing effect on terpenes biosynthetic enzymes. Gil et al. (2012) reported that sUV-B (low, 16 h at 8.25 μW cm^{-2}, and high 4 h at 33 μW cm^{-2}) dose increases the terpenes content in in vitro-cultured plants of *Vitis vinifera*. At low UV-B dose, membrane-related sterols (regulate membrane fluidity under stress) were increased in young leaves, which led to accumulation of grapevine, while at high UV-B dose antioxidant diterpenes and stress-related hormone abscisic acid was increased in mature leaves that showed defense response of plants against UV-B stress. In a previous study, Hikosaka et al. (2010) documented that UV-B radiation increased the essential oil content and total antioxidant capacity of Japanese mint after 7 days of exposure. It may occur due to the increasing number of unfolded leaves, which led to higher biomass accumulation and higher essential oil content per plant. In sweet basil (*O. basilicum*), sUV-B exposure increased secondary metabolites content with the highest increase in eugenol content at five leaf stage (Johnson et al. 1999). Among all the compounds, most of them increased at five leaf stages (b-pinene, 1, 8-cineole, linalool, and eugenol) while two of them (trans-b-ocimene and methyl eugenol) were increased at three leaf stages. Supplemental UV-B exposure (1.4 kJ m^{-2} d^{-1}) on *O. sanctum* L. increased the essential oil content by 42% (Kumari and Agrawal 2011). Major compound eugenol showed non-significant reduction under sUV-B while the other major compound β-caryophyllene was increased by 18.6%.Electron microscopic observations of basil plant showed that plants exposed to sUV-B induced more production of oil which might led to smooth surface oil sacs, whereas control plants have partially filled wrikled oil sacs. In a recent study of Li et al. (2019), total oleanolic acid (OA) content (terpene) in leaves showed the highest increase by 201% after 3 h exposure (among 1 h, 2 h, 3 h and 4 h) of sUV-B than control plants of *A. bidentata*. In roots, OA was also increased up to 3 h (highest) while non-significant changes between control and 4 h treatment. Secondary metabolites increase refers to the adaptation of plants against sUV-B stress. In *Mentha piperita*, essential oil content was increased under UV-B treatment with a decrease in menthol content. Besides, menthol reduction in other compounds such as menthone, menthofuran, and menthyl acetate synthesis was increased (Maffei and Scannerini 2000). Another study on sweet basil showed that the number of oil glands was increased in both mature and developing leaves exposed to UV-B as compared to controls, which ultimately led to higher production of oil in UV-B-exposed plants (Ioannidis et al. 2002). As studied by Kumari and Agrawal (2010), sUV-B exposure on *C. citratus* (D.C.) Staph increased the essential oil content by 25% as compared to control. Another study made by Takshak and Agrawal (2018) showed that essential oil content in *C. forskohlii* was decreased by 8.6% under sUV-B exposure.

17.4 Heavy Metal Stress

17.4.1 Physiological Responses of Plants Under Heavy Metal Stress

HMs affect various physiological processes in plants directly or indirectly (Clijsters et al. 1999), in fact the majority of responses in plants in relation to HMs are linked with growth, differentiation and physiological processes. HMs affect the photosynthetic efficiency in several plants (Krupa and Baszynski 1995). The HMs Cu, Cd, and Pb in excess directly inhibit photosynthetic electron transport and activity of Calvin Benson cycle enzymes (Myśliwa-Kurdziel et al. 2004). In addition, HMs can also affect photosynthetic activity indirectly by decreasing the content of photosynthetic pigments or by damaging the photosynthetic apparatus and structure of chloroplast (Molas 2002). Zhou et al. (2017) reported that chloroplast ultrastructure of *Robinia pseudoacacia* disturbed as thylakoid lamellae gradually disordered and loosely packed under Pb stress. Van Assche and Clijsters (1986) revealed that excess of Zn supplied in nutrient medium displaces Mg from the water-splitting site in oxygen-evolving complex of photosystem II (PS II), thereby inhibiting electron transport chain in *Phaseolus vulgaris*. Excess of Cd caused reduction in net photosynthetic rate (P_n) and chlorophyll fluorescence parameters such as maximal photochemical efficiency of PS II (F_v/F_m), effective quantum yield of PS II (ϕPS II), photochemical quenching (qP) in rice and tomato seedlings, respectively (He et al. 2008; López-Millán et al. 2009). In fact, maximal photochemical efficiency of photosystem II ($\mathrm{F_v/F_m}$) used as an indicator of stress in plants (He et al. 2008). In *Triticum aestivum* Cr (VI) significantly reduced F_v/F_m, qP (Tripathi et al. 2015). Li et al. (2015) also found decreased F_v/F_m, qP, ϕPS II, and electron transport rate (ETR) under higher level of Cd in *Elsholtzia argyi*, a Cd-accumulating plant. Contrary to these results, mild effect of excess HMs on PS II efficiency was observed in *Triticum durum* by Ciscato et al. (1997) and in *C. sativus* by Burzyński and Kłobus

(2004). So the disturbance in PS II efficiency under HMs stress depends on plant species, time of exposure to metals and their content in leaf tissues (Burzyński and Kłobus 2004). Todeschini et al. (2011) observed that excess Zn negatively affected the activity of PS II by decreasing the expression of D1 and D2 reaction center proteins.

Kosobrukhov et al. (2004) reported the photosynthetic activity of plants also determined by stomatal regulation of photosynthesis as well as transpiration, and suggested that lower T_r under Pb stress is due to a decrease in the number, size and conductance of stomata, which in turn leads to decreased internal CO_2 (C_i) and net photosynthesis rate (P_n) in *Plantago major*. Similarly, inhibition in P_n due to the reduction of g_s and photosynthetic pigment contents in *Arachis hypogaea* was reported under Cd and Zn stress (Shi and Cai 2008, 2009). Gill et al. (2012) also suggested that a decrease in P_n under Cd stress in *Lepidium sativum* could be partially due to decreased g_s and C_i; likewise, Emamverdian et al. (2018) reported decreased photosynthetic parameters such as P_n, C_i, g_s, T_r under high concentration of Cu, Pb, and Zn in *Indocalamus latifolius*.

HMs also affect two distinct physiological processes, that is, water relation and mineral nutrition in plants which are essential for both photosynthesis and growth of plants (Burzyński and Kłobus 2004). In general, HMs are known to alter the water relation of plants (Barceló and Poschenrieder 1990). HMs caused perturbation in water balance and thus a reduction in WUE was observed under Cd stress in *P. sativum* and *E. argyi* (Januškaitienė 2012; Li et al. 2015). In *Brassica oleracea*, leaf water potential and transpiration rate was reduced accompanied with increased leaf diffusive resistance, which showed development of water stress under excess of Cd^{2+}, Co^{2+}, and Ni^{2+} (Pandey and Sharma 2002). Suppression of the gene expression of dehydration-related transcription factors and aquaporin isoforms showed that water stress is a potential constituent of Cd-induced obstruction in *Solanum torvum* (Yamaguchi et al. 2009).

HMs compete with nutrients for their absorption and uptake by plants which consequently affect utilization and function of these nutrients in plants (Krupa et al. 2002). Membrane transporters are involved in the uptake of bioavailable metal ions by plants; in addition, non-nutrient HMs that shared similar chemical properties can also enter inside plants through these transporters (DalCorso et al. 2013). Arsenate competes with major plant nutrients phosphorus in the form of phosphate for the same transporter in root cell membrane (Vetterlein et al. 2007). Likewise, selenate (SeO_4^{2-}) and sulfate (SO_4^{2-}) are chemically similar; therefore, selenate competes with sulfate for the translocation across membrane, by sulfate transporter (Schiavon et al. 2012). HMs also affect the nutrient contents in plants as Gonçalves et al. (2009) revealed that Cd^{2+} decreased the macronutrients and micronutrients content in the root and shoot of in vitro-cultured *Solanum tuberosum* cultivars. Zouari et al. 2016 also reported *Olea europaea* plant treated with 30 mg $CdCl_2$ kg^{-1} soil showed a decrease in Ca, Mg, and K contents, in both above and below ground plant parts. Addition of Cr (VI) to nutrient medium decreased the nutrients element Na, K, Ca, and Mg in wheat (Tripathi et al. 2015). Similarly, Ni toxicity decreased N, P, and K concentrations in rice (Nazir et al. 2016). Ni toxicity also decreased Cu and Mn concentrations in wheat (Wang et al. 2015). It was found that application of excess Zn caused elevated concentration of Cu and Fe whereas lowered concentration of Mn in the root of *Brassica juncea* and *Brassica napus* (Feigl et al. 2014). Excess of Zn also induced the expression of the ferric-chelate reductase gene (*FRO2*) that contributed to high uptake of Fe in *A. thaliana* (van de Mortel et al. 2006). Table 17.4 summarizes the physiological responses of plants under HMs stress.

17.4.2 Biochemical and Molecular Responses of Plants

One of the primary responses of plants when exposed to excess of HMs, are the generation of ROS, which leads to oxidative stress in plants (Kohli et al. 2017). Several redox active metals (Cr, Cu, Mn, and Fe) can directly generate oxidative stress via formation of ROS through Haber-Weiss and Fenton reaction whereas non-redox active metals (Cd, Ni, Zn, Hg) lead to oxidative stress via multiple mechanisms such as inhibition of the activity of antioxidant enzymes and depletion of glutathione, binding to sulfhydryl group of proteins (Emamverdian et al. 2015). These ROS are very toxic and lead to alteration of various biochemical processes and induce damage to biomolecules such as peroxidation of membrane lipids, alteration of proteins and enzymes functions, DNA breakage, damage to pigments, and disruption of some metabolic pathway (Kohli et al. 2017). Therefore, plants have developed several defense mechanisms such as enzymatic and non-enzymatic antioxidant defense systems to combat the stress generated by HMs. Plant damage occurs when the equilibrium between ROS production and scavenging perturb and the amount of ROS exceeds the capacity of antioxidant defense systems (Kisa et al. 2016). Table 17.5 summarizes the various biochemical responses of plants under HMs stress.

17.4.2.1 Lipid Peroxidation

Plasma membranes of cells are the primary target of HMs toxicity in plants. HMs cause lipid peroxidation via production of ROS (Shahid et al. 2014). Measurement of the level of thiobarbituric acid reactive substance (TBARS) such as MDA in tissues is widely used as an indicator of lipid peroxidation in plants (Yusuf et al. 2012; Rai et al. 2014).

Singh et al. (2016a) suggested that increased content of MDA in the root and shoot of *T. aestivum* must be due to increased formation of ROS under excess of Cd and Cu. In the root of *Astragalus neo-mobayenii,* MDA level increased with increasing concentration of Cu (Karimi et al. 2012). Rai et al. (2014) also reported that when Cr applied in excess, MDA content significantly increased in the leaves of *C. roseus*.

Table 17.4 Physiological responses of plants under HMs stress

Plants	Heavy metals	Parameters	Effect	References
Phragmites australis (Cav.) Trin. Ex. Steudel	Pb, Zn	Photosynthetic rate	Decreased	Bernardini et al. (2016)
		Stomatal conductance	Decreased	
		Internal CO_2	Decreased	
		Mesophyll conductance	Decreased	
Robinia pseudoacacia	Pb	Photosynthetic rate	Decreased	Zhou et al. (2017)
		Stomatal conductance	Decreased	
		Internal CO_2	Decreased	
		Fv/Fm	Decreased	
		ϕPS II	Decreased	
Bana (*Pennisetum americanum* × *P. purpureum*) and vetiver (*Vetiveria zizanioides*) grass	Cd	Fe concentration	Decreased in both plant	Zhang et al. (2014)
		Water content and transpiration rate	Decreased in bana grass whereas not affected in vetiver	
Zea mays L. var. Super 20–20	Cr and Pb	Ca, Mg, Na and K concentration	Decreased	Singh et al. (2015)
Cucumis sativus L. var. Jinyan 4.	Cd	Photosynthetic rate	Decreased	Sun et al. (2016)
		Stomatal conductance	Decreased	
		Transpiration rate	Decreased	
		Internal CO_2	Increased	
Zea mays L. genotype EV-77 and EV-1098	Pb	Stomatal conductance	Decreased	Ahmad et al. (2011)
		Internal CO_2	Decreased	
		Transpiration rate	Increased	
		Water use efficiency	Decreased	
		K^+ and Cu^{2+} ions	Decreased	
Amaranthus paniculatus L.	Ni	Fv/Fm	Decreased	Pietrini et al. (2015)
		ϕPS II	Decreased	
		qP	Decreased	

17.4.2.2 Protein Damages

HMs induce changes in the quantity and quality of protein through various mechanisms as they cause structural modification in proteins and render them inactive via binding with –COOH, $–NH_2$ –SH functional groups, modify genes expression, displace essential metal ions from metal-dependent proteins and increase ribonuclease activity (Shahid et al. 2014). Proteomic analysis in cucumber under Cd stress indicated that relative abundance of several proteins that are involved in response to

Table 17.5 Biochemical responses of plants under HMs stress

Plants	Heavy metals	Parameters	Effect	References
Brassica juncea L. Czern and Coss.) cv, Pusa Jai Kisan and SS2	Cd	H_2O_2 content	Increased	Iqbal et al. (2010)
		MDA content	Increased	
		Ascorbate content	Decreased	
		GSH content	Increased	
		CAT, APX, GR, SOD activity	Increased	
Avena sativa,Pennisetum glaucum, and *Eleusine coracana*	Ni	Total chlorophyll content	Decreased	Gupta et al. (2017)
		MDA content	Decreased	
		Proline content	Increased	
		SOD activity	Increased	
		CAT activity	Decreased	
Brassica juncea L. var. Pusa Jaikisan	Ni, Cr, Pb, Cd, Hg	Total chlorophyll content	Decreased	Sheetal et al. (2016)
		Proline content	Increased	
		SOD and POX activity	Increased	
Amaranthus paniculatus L.	Ni	Total chlorophyll content	Decreased	Pietrini et al. (2015)
		MDA content	Increased	
		SOD and GPX activity	Increased	
		APX and CAT activity	Not affected	
Catharanthus roseus (L.) G. Don., *rosea* and *alba*	Cr	Total chlorophyll content	Decreased	Rai et al. (2014)
		Carotenoid content	Increased	
		Protein content	Decreased	
		MDA content	Increased	
		Proline content	Increased	
		APX, CAT, GPX activity	Increased	

stress, metabolism, photosynthesis, and storage were repressed due to Cd treatment (Sun et al. 2016). Duquesnoy et al. (2009) revealed that *Agrostis tenuis* leaf proteome such as oxygen-evolving enhancer protein, RubisCO small and large subunit, ATP synthase differentially expressed under As stress. Beltagi (2005) reported that Pb caused qualitative and quantitative changes in protein of *Vicia faba* root nodule. Cr treatment significantly reduced protein content in *C. roseus* leaves (Rai et al. 2014). Similarly, maize (*Z. mays*) seedling treated with different concentration of Pb and Cr revealed that increasing concentration of Pb and Cr decreased protein content in the root and shoot of maize (Singh et al. 2015).

17.4.2.3 DNA Damages

HMs-induced DNA damage has been widely reported in several plants species (Aina et al. 2004; Gichner et al. 2006; Pourrut et al. 2011). Metal ions may bind to four different potential sites of DNA such as the base ring nitrogen, the negatively charged phosphate oxygen atoms, the hydroxyl group of ribose and the exocyclic base keto groups (Oliveira et al. 2008). Oliveira et al. (2008) also reported that Pb, Cd, and Ni bind to dsDNA and lead to different modifications in the structure of dsDNA such as destabilization of double-helix, conformational changes. Ou et al. (2012) suggested that DNA methylation patterns were modified in the leaf tissue of *Oryza sativa* treated with Cu^{2+} Cd^{2+} Cr^{2+} Hg^{2+} and these modifications were exclusively confined to CHG (Cytosine and guanine rich site where H represents A,T or C) hypomethylation. Genome expression analysis in *Z. mays* inbred line 178 revealed that genes related to cellular processes, signaling, and metabolic functions were more than five times up- or downregulated compared to control under Pb stress (Shen et al. 2013). Pourrut et al. (2011) demonstrated a cross link between Pb-induced oxidative stresses, DNA strand breakage and chromosomal aberrations in *V. faba* roots.

17.4.2.4 Photosynthetic Pigments

Combination of heavy metals such as Cd, Zn, Cr, and Cu leads to decreased content of chlorophyll and carotenoids in all poplar hybrids except for the Eco28 hybrid (Chandra and Kang 2016). Pb and Cr at higher concentration significantly decreased total chlorophyll and carotenoids content in maize seedlings (*Z. mays*) (Singh et al. 2015). Tripathi et al. (2015) reported that due to toxicity of Cr (VI) total chlorophyll content decreased by 19% compared to control in wheat. Xue et al. (2013) also revealed that Cd decreased the total chlorophyll content and chl a/b ratio in soybean seedlings (*G. max*). δ-Aminolevulinic acid (ALA) synthetic ability and δ-aminolevulinic acid dehydratase (ALAD) play a key role in the biosynthesis of chlorophyll (Cenkci et al. 2010). Cenkci et al. (2010) reported that higher concentration of Pb increased ALA level, which is the substrate for ALAD activity and inhibited the activity of ALAD, resulting in decreased formation of porphobilinogen, which is required for synthesis of chlorophyll and thus content of chlorophyll a and chlorophyll b decreased in *Brassica rapa*. Prasad and Prasad (1987) showed that by binding with –SH group of ALAD, Pb and Hg inhibit the activity of ALAD enzyme leading to decreased chlorophyll content in *Pennisetum typhoideum*.

17.5 Adaptation and/or Tolerance Mechanism Under Heavy Metal Stress

Plants have numerous interrelated networks of defense mechanisms to avoid or tolerate HMs toxicity. In the environment, different types of plants species may have evolved different strategies to tolerate and/or avoid HMs toxicity (Meharg 1994). Some of the mechanisms adopted by plants species, when they come into contact with HMs, include (1) immobilization or chelation of HMs and (2) exclusion and restriction of HMs uptake. Once heavy metals overcome these barriers and enter inside the cell, a variety of potential defense mechanisms exist there to attenuate the effect of HMs such as compartmentation of HMs within vacuoles, chelation or sequestration of HMs by organic acids, amino acids, peptides (phytochelatins and metallothioneins [MTs]), synthesis of stress proteins, and activation of enzymatic and non-enzymatic antioxidant systems (Hall 2002; Zhu et al. 2011; Hossain et al. 2012). Figure 17.3 depicts the HMs toxicity and detoxification mechanism in plants.

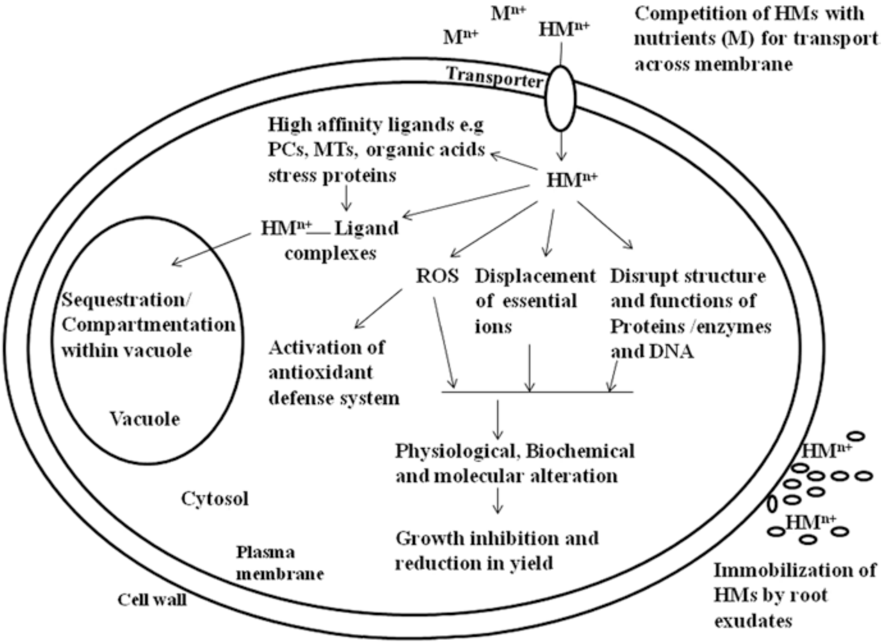

Fig. 17.3 Possible mechanisms of HMs toxicity and detoxification in plants (Hossain et al. 2012; DalCorso et al. 2013; Emamverdian et al. 2015).

17.5.1 Extracellular Defense Mechanisms

Root exudates of plants play an important role in chelation of metals and prevent intracellular accumulation of HMs; for example, plants exude histidine and citrate, which chelates Ni and leads to reduced uptake of Ni by plants (Salt et al. 1999). Pinto et al. (2008) reported that organic acids such as malate and citrate released by roots of sorghum and maize may play an important role in tolerance of these species under Cd stress. Organic acids released by root apex of maize also play a prominent role in Al tolerance (Pellet et al. 1995). Zhu et al. (2011) reported that root apex of tomato plant secrete oxalate which helps to exclude Cd from entering tomato roots, thereby contributes to Cd resistance in the Cd-resistant tomato cultivar. Several plants species also reduce the uptake of metals by restricting heavy metal ions to apoplast (Tice et al. 1992). *Silene vulgaris* ssp. *Humilis*, a heavy metal-tolerant plant, accumulated several HMs in the epidermal cell wall either by binding to a protein or as silicates (Bringezu et al. 1999).

17.5.2 Intracellular Defense Mechanisms

17.5.2.1 Compartmentation or Sequestration of Heavy Metals

One of the strategies adopted by plants to divert heavy metal ions from the cytosol or other cellular compartments is the sequestration of HMs into the vacuoles, for example, preferential storage of Cd in the vacuoles reduced the Cd toxicity to plants which may be responsible for the long-term growth of *B. napus* on Cd-contaminated soil (Carrier et al. 2003). Wang et al. (1991, 1992), on the basis of computer simulation studies, suggested that sequestration of Cd and Zn in the vacuoles via chloride/phosphate and citrate may be a possible mechanism in the accumulation of Cd and Zn, respectively, in *Nicotiana tabacum*. From *A. thaliana*, a gene (*ZAT*) was isolated, which is closely related to animal *ZnT* (Zn transporter) gene, under high level of Zn, overexpression of *ZAT* gene in transgenic plants led to accumulation of Zn in the roots (Van der zaal et al. 1999). Persans et al. (2001) suggested that high-level expression of *TgMPT1* gene that encodes vacuolar metal ion transport protein accounts for the enhanced ability of *Thlaspi goesingense* to accumulate metal ions in shoot vacuoles. In addition to vacuolar sequestration, plants also have some morphological features such as trichomes that are involved in sequestration of HMs. Choi et al. (2001) reported that head cell of the trichomes of *N. tabacum* actively exclude Cd by forming and excreting Cd/Ca-containing crystals.

17.5.2.2 Chelation by Phytochelatins

Chelation of heavy metals by the high-affinity peptide ligands such as phytochelatins (PCs) and metallothioneins (MTs) constitutes the potential detoxification and tolerance mechanism in the cells under HMs stress. PCs are synthesized from glutathione (GSH) by the enzyme phytochelatin synthase and have the general structure $(\gamma\text{-Glu-Cys})_n\text{-X}$, where X is Gly, γ-Ala, Ser, Gln, or Glu and $n = 2$ to 11, depending on the organism; however, the most common forms have 2–4 peptides (Yang et al. 2005). The biosynthesis of PCs is induced by several HMs such as Cd, Hg, Ag, Cu, Ni, Pb, As, and Zn; however, Cd is the strongest inducer (Zenk 1996). PCs are synthesized in the cytosol as the product of enzymatically synthesized peptides (Verkleij et al. 2003) and interact with metals to form complexes which are actively transported from cytosol to vacuoles as their final destination (Song et al. 2014). The cysteine residue of PCs interacts with HMs via their thiol (−SH) group; Di Toppi and Gabbrielli (1999) reported that the thiol group of PCs forms complex with Cd, which are sequestered in the vacuoles and thus prevent the free circulation of Cd^{2+} ion inside the cytosol. The HMs–PCs complex is transported from the cytosol to vacuoles by metal/H^+ antiporter or ABC transporter of tonoplast (Song et al. 2014). Nouairi et al. (2009) reported that PCs content increased significantly under Cd stress in *B. juncea* and play an important role in metal detoxification. In *Solanum nigrum,* production of PCs was increased at 200 μmol L^{-1} Cu concentration, which resulted in immobilization of excess Cu in root (Fidalgo et al. 2013).

17.5.2.3 Chelation by Metallothioneins

Plant metallothioneins (MTs) are the low-molecular-weight, cysteine-rich, metal-binding polypeptides that also play an important role in metal detoxification and homeostasis (Guo et al. 2013). MTs show high affinity with several metals such as Cu, Cd, Zn, and As. MTs are the product of mRNA translation (Verkleij et al. 2003). Plants possess multiple types of MTs and on the basis of arrangement of cysteine residue divided into four distinct subgroups (Ferraz et al. 2012). Guo et al. (2013) identified a metallothionein gene designated as *ScMT2–1-3* from sugarcane and reported that Cu^{2+} stress upregulated the expression of *ScMT2–1-3* and this gene is significantly involved in the detoxification of Cu and storage in the cells. Zhigang et al. (2006) reported that at seedling stage ectopic expression of *BjMT2,* a metallothionein type 2 gene from *B. juncea*, increased copper and cadmium tolerance in *A. thaliana*. Overexpression of *Elsholtzia haichowensis* metallothionein type 1 (*EhMT1*) in transgenic tobacco plant also increased the tolerance of tobacco plant to Cu toxicity (Xia et al. 2012).

17.5.2.4 Chelation by Organic Acids and Amino Acids

Organic and amino acids (citrate, malate, oxalate, histidine, and nicotinamine) are involved in the both extracellular and intracellular detoxification systems of plants. Intracellularly organic acids may chelate with HMs and transformed into non-toxic forms (Hall 2002). Lee et al. (1978) reported that Ni bound to citrate and strong correlation found in level of Ni and citrate in Ni hyperaccumulating plants. Oven et al. (2002) reported that cells of *Crotalaria cobalticola*, a Co hyperaccumulator and non-accumulators *Rauvolfia serpentina* and *Silene cucubalus* when exposed to excess of Co^{2+} ions, resulted in increased concentration of citrate and cysteine which may denote their involvement in HMs detoxification.

In addition, root exudates of plants also accumulate non-toxic forms of metals, under Al stress *Fagopyrum esculentum* secrete oxalic acid, which chelate Al ions and allow the accumulation of a non-toxic Al–oxalate complex in the leaves (Ma et al. 2001). Nicotinamine (NA) is a non-proteinogenic amino acid and possesses high affinity to many HMs such as Zn, Cu, Mn, Ni, and Cd (Lin and Aarts 2012). The Zn–NA complexes also have been detected in root cells of *A. thaliana* (Deinlein et al. 2012).

17.5.2.5 Enzymatic and Non-enzymatic Antioxidants

A number of enzymatic antioxidants such as SOD, APX, POX, CAT, and GR and non-enzymatic antioxidants such as ascorbic acid, glutathione, cysteine, amino acids, phenolic compounds, proline, and carotenoids perform potential detoxification role against stress induced by HMs. Enzymatic antioxidants are a potent regulator of oxidative stress caused by HMs in plants. Zouari et al. (2016) showed that SOD, GPX, and CAT activities increased significantly whereas APX activity decreased in Cd-treated *O. europaea* plant. Ni toxicity increased the activity of SOD, CAT, and POX in *B. juncea* (Yusuf et al. 2012). Similarly, SOD, CAT, and POX activities significantly increased in leaves and roots of *Astragalus neo-mobayenii* with increasing concentration of Cu (Karimi et al. 2012). Rai et al. (2014) observed that Cr toxicity resulted in increased activity of APX, CAT, and GPX activity in *C. roseus*.

Proline is an amino acid and believed to provide tolerance against HMs in plants (Singh et al. 2012). *Vigna mungo* seedlings grown with excess of Pb and Ni showed rapid accumulation of proline in their tissues (Singh et al. 2012). Zouari et al. (2016) also reported increased proline content in leaves and roots of Cd-treated *O. europaea* plant. The proline content also increased significantly with increasing Cu concentration in *Astragalus neo-mobayenii* (Karimi et al. 2012).

Glutathione is a low-molecular-weight tripeptide (γGlu-Cys-Gly) involved in a wide range of metabolic processes and also a major transport and storage form of sulfur in plants; furthermore, it is one of the main potential antioxidant and redox buffers in plants (Yadav 2010). GSSG is converted to GSH with the help of enzyme GR and also the ratio of GSH/GSSG is an indicative of cellular redox balance in plants (Yadav 2010). It involves the control of H_2O_2 level in cells through AsA-GSH cycle (Foyer and Noctor 2005). Kumar et al. (2012) suggested that Pb stress indirectly caused oxidative stress in *Talinum triangulare,* which is indicated by the decrease in the ratio of GSH/GSSG with increased dose of Pb treatment.

Phenolic compounds are the plants' secondary metabolites and have high tendency to chelate metals. Kısa et al. (2016) reported that total phenolics content increased in *Z. mays* under Cd, Cu, and Pb treatment. At higher Ni concentration, total phenolics and flavonoids content increased in *Matricaria chamomilla* due to increased PAL and shikimate dehydrogenase (SKDH) activity which are the main enzymes involved in biosynthesis of phenolics (Kováčik et al. 2009). Elguera et al. (2013) reported that Cd decreased the content of phenolic acids such as chlorogenic acid, ferulic acid, and caffeic acid in the leaves of *L. sativum*. In a medicinal plant *Gynura procumbens* total phenolics and flavonoids content was found to be reduced under Cd and Cu treatments, which might be due to reduced PAL enzyme activity (Ibrahim et al. 2017).

17.6 Interactive Effects of UV-B and Heavy Metals on Plants

Excess of both HMs and UV-B individually has detrimental effects on plant life. Effects of UV-B on growth, physiology, and biochemistry are modified by several other abiotic factors such as drought, fertilizer, ozone, and HMs. As HMs are an important component of soil system and required by plants while excess may cause toxic effects in plant system. In literature, there are limited studies on the interactive effect of sUV-B and HMs stress on plants. An experiment with sUV-B (0.4 W m^{-2}) and Ni (0.01, 0.10, and 1.00 mM) on young soybean seedling showed that higher reduction in growth (plant height, leaf area, fresh mass, and dry mass) and chlorophyll content was found in combination of sUV-B with higher dose of Ni (1.00 mM) than Ni and control (Prasad et al. 2005). Lipid peroxidation and ROS production were also maximum under higher Ni dose with UV-B radiation. As previously reported by Valkama et al. (2003), high selenium (Se) concentration in soil increased the sensitivity of strawberry plants to sUV-B radiation. High Se dose (1 mg kg^{-1}) with UV-B decreased the leaf growth by 15% in strawberry. The combined treatment of UV-B and Cd induces the oxidative stress in wheat (Gondor et al. 2014). Cd-treated wheat induces the salicylic acid accumulation, which was not enhanced by sUV-B but increased oxidative stress with antioxidant enzyme activation and polyamine synthesis (Kovács et al. 2014). In *Spinacia oleracea* L., chlorophyll (25.4%) and carotenoid (27.4%) contents were decreased maximum under combination of sUV and Cd at 15 days after sowing (DAS) than individual treatment and control while the anthocyanin and flavonoids showed non-significant changes. Peroxidation of lipid was maximum under sUV-B + Cd followed by sUV-B + Ni, sUV-B, Ni, and Cd. Ascorbic acid content was maximum sUV-B + Cd at 15

DAS. Proline content was found to be higher under combination as compared to individual ones and control (Shweta and Agrawal 2006). In short, we can say that interactive effects of heavy meats and sUV-B cause an additive detrimental effect as compared to their individual ones.

17.7 Conclusion

Based on current evidences, it becomes clear that both stresses affect various physiological and biochemical processes, which ultimately lead to reduction in growth and productivity of plants. Plants perform different strategies to tolerate these stresses which include morphological and anatomical adaptation, induction of antioxidant systems, secondary metabolite production, and extracellular and intracellular defense mechanisms. Interactive effects of UV-B and HMs cause higher reduction in plant performance as compared to their individual effects. Although lots of works have been done in the area of these stresses individually but limited studies reported their interactive effects. It can be suggested that more studies will be conducted in near future to evaluate their interactive effects and also the possible mechanism to combat these stresses.

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References

Afreen F, Zobayed SM, Kozai T (2006) Melatonin in *Glycyrrhiza uralensis*: response of plant roots to spectral quality of light and UV-B radiation. J Pineal Res 41:108–115

Agrawal SB, Rathore D (2007) Changes in oxidative stress defense system in wheat (*Triticum aestivum* L.) and mung bean (*Vigna radiata* L.) cultivars grown with and without mineral nutrients and irradiated by supplemental ultraviolet-B. Environ Exp Bot 59:21–33

Ahmad MSA, Ashraf M, Tabassam Q, Hussain M, Firdous H (2011) Lead (Pb)-induced regulation of growth, photosynthesis, and mineral nutrition in maize (*Zea mays* L.) plants at early growth stages. Biol Trace Elem Res 144:1229–1239

Aina R, Sgorbati S, Santagostino A, Labra M, Ghiani A, Citterio S (2004) Specific hypomethylation of DNA is induced by heavy metals in white clover and industrial hemp. Physiol Plant 12:472–480

Allen DJ, McKee IF, Farage PK, Baker NR (1997) Analysis of limitations to CO_2 assimilation on exposure of leaves of two *Brassica napus* cultivars to UV-B. Plant Cell Environ 20:633–640

Barceló JUAN, Poschenrieder C (1990) Plant water relations as affected by heavy metal stress: a review. J Plant Nutr 13:1–37

Barnes PW, Flint SD, Caldwell MM (1990) Morphological responses of crop and weed species of different growth forms to ultraviolet-B radiation. Am J Bot 77:1354–1360

Bassman JH (2004) Ecosystem consequences of enhanced solar ultraviolet radiation: secondary plant metabolites as mediators of multiple trophic interactions in terrestrial plant communities. Photochem Photobiol 79:382–398

Bassman JH, Edwards GE, Robberecht R (2003) Photosynthesis and growth in seedlings of five forest tree species with contrasting leaf anatomy subjected to supplemental UV-B radiation. For Sci 49:176–187

Beltagi MS (2005) Phytotoxicity of lead (Pb) to SDS-PAGE protein profile in root nodules of faba bean (*Vicia faba* L.) plants. Pak J Biol Sci 8:687–690

Bernardini A, Salvatori E, Guerrini V, Fusaro L, Canepari S, Manes F (2016) Effects of high Zn and Pb concentrations on *Phragmites australis* (Cav.) Trin. Ex. Steudel: photosynthetic performance and metal accumulation capacity under controlled conditions. Int J Phytoremediation 18:16–24

Binder BY, Peebles CA, Shanks JV, San KY (2009) The effects of UV-B stress on the production of terpenoid indole alkaloids in *Catharanthus roseus* hairy roots. Biotechnol Prog 25:861–865

Brandle JR, Campbell WF, Sisson WB, Caldwell MM (1977) Net photosynthesis, electron transport capacity, and ultrastructure of *Pisum sativum* L. exposed to ultraviolet-B radiation. Plant Physiol 60:165–169

Bringezu K, Lichtenberger O, Leopold I, Neumann D (1999) Heavy metal tolerance of *Silene vulgaris*. J Plant Physiol 154:536–546

Brown BA, Cloix C, Jiang GH, Kaiserli E, Herzyk P, Kliebenstein DJ, Jenkins GI (2005) A UV-B-specific signaling component orchestrates plant UV protection. PNAS 102:18225–18230

Burchard P, Bilger W, Weissenböck G (2000) Contribution of hydroxycinnamates and flavonoids to epidermal shielding of UV-A and UV-B radiation in developing rye primary leaves as assessed by ultraviolet-induced chlorophyll fluorescence measurements. Plant Cell Environ 23:1373–1380

Burzyński M, Kłobus G (2004) Changes of photosynthetic parameters in cucumber leaves under Cu, Cd and Pb stress. Photosynthetica 42:505–510

Carrier P, Baryla A, Havaux M (2003) Cadmium distribution and microlocalization in oilseed rape (*Brassica napus*) after long-term growth on cadmium-contaminated soil. Planta 216:939–950

Cenkci S, Ciğerci İH, Yıldız M, Özay C, Bozdağ A, Terzi H (2010) Lead contamination reduces chlorophyll biosynthesis and genomic template stability in *Brassica rapa* L. Environ Exp Bot 67:467–473

Chandra R, Kang H (2016) Mixed heavy metal stress on photosynthesis, transpiration rate and chlorophyll content in poplar hybrids. For Sci Technol 12:55–61

Chang X, Alderson PG, Wright CJ (2009) Enhanced UV-B radiation alters basil (*Ocimum basilicum* L.) growth and stimulates the synthesis of volatile oils. J Hortic For 1:27–31

Chen M, Huang Y, Liu G, Qin F, Yang S, Xu X (2016) Effects of enhanced UV-B radiation on morphology, physiology, biomass, leaf anatomy and ultrastructure in male and female mulberry (*Morus alba*) saplings. Environ Exp Bot 129:85–93

Choi YE, Harada E, Wada M, Tsuboi H, Morita Y, Kusano T, Sano H (2001) Detoxification of cadmium in tobacco plants: formation and active excretion of crystals containing cadmium and calcium through trichomes. Planta 213:45–50

Choudhary KK, Agrawal SB (2014) Cultivar specificity of tropical mung bean (*Vigna radiata* L.) to elevated ultraviolet-B: changes in antioxidative defense system, nitrogen metabolism and accumulation of jasmonic and salicylic acids. Environ Exp Bot 99:122–132

Choudhary KK, Agrawal SB (2015) Effect of elevated ultraviolet-B on four tropical soybean cultivars: quantitative and qualitative aspects with special emphasis on gas exchange, chlorophyll fluorescence, biomass and yield. Acta Physiol Plant 37:31

Ciscato M, Valcke R, Van Loven K, Clijsters H, NavariIzzo F (1997) Effects of in vivo copper treatment on the photosynthetic apparatus of two *Triticum durum* cultivars with different stress sensitivity. Physiol Plant 100:901–908

Clijsters H, Cuypers A, Vangronsveld J (1999) Physiological responses to heavy metals in higher plants; defence against oxidative stress. Z Naturforsch C 54:730–734

Cooley NM, Holmes MG, Attridge TH (2000) Growth and stomatal responses of temperate meadow species to enhanced levels of UV-A and UV-B+ A radiation in the natural environment. J Photochem Photobiol B Biol 57:179–185

Costa H, Gallego SM, Tomaro ML (2002) Effect of UV-B radiation on antioxidant defense system in sunflower cotyledons. Plant Sci 162:939–945

da Silva Rodrigues-Corrêa KC, Honda MD, Borthakur D, Fett-Neto AG (2019) Mimosine accumulation in *Leucaena leucocephala* in response to stress signaling molecules and acute UV exposure. Plant Physiol Biochem 135:432–440

DalCorso G, Manara A, Furini A (2013) An overview of heavy metal challenge in plants: from roots to shoots. Metallomics 5:1117–1132

Deinlein U, Weber M, Schmidt H, Rensch S, Trampczynska A, Hansen TH, Husted S, Schjoerring JK, Talke IN, Kramer U (2012) Elevated nicotianamine levels in *Arabidopsis halleri* roots play a key role in zinc hyperaccumulation. Plant Cell 24:708–723

Di Toppi LS, Gabbrielli R (1999) Response to cadmium in higher plants. Environ Exp Bot 41:105–130

Dolzhenko Y, Bertea CM, Occhipinti A, Bossi S, Maffei ME (2010) UV-B modulates the interplay between terpenoids and flavonoids in peppermint (*Mentha*× *piperita* L.). J Photochem Photobiol B Biol 100:67–75

Du WX, Avena-Bustillos RJ, Breksa AP III, McHugh TH (2014) UV-B light as a factor affecting total soluble phenolic contents of various whole and fresh-cut specialty crops. Postharvest Biol Technol 93:72–82

Duquesnoy I, Goupil P, Nadaud I, Branlard G, Piquet-Pissaloux A, Ledoigt G (2009) Identification of *Agrostis tenuis* leaf proteins in response to As (V) and As (III) induced stress using a proteomics approach. Plant Sci 176:206–213

Eapen S, D'souza SF (2005) Prospects of genetic engineering of plants for phytoremediation of toxic metals. Biotechnol Adv 23:97–114

Eichholz I, Huyskens-Keil S, Keller A, Ulrich D, Kroh LW, Rohn S (2011) UV-B-induced changes of volatile metabolites and phenolic compounds in blueberries (*Vaccinium corymbosum* L.). Food Chem 126:60–64

Elguera JCT, Barrientos E, Wrobel K, Wrobel K (2013) Effect of cadmium (Cd (II)), selenium (Se (IV)) and their mixtures on phenolic compounds and antioxidant capacity in *Lepidium sativum*. Acta Physiol Plant 35:431–441

Emamverdian A, Ding Y, Mokhberdoran F, Xie Y (2015) Heavy metal stress and some mechanisms of plant defense response. Sci World J 2015:756120

Emamverdian A, Ding Y, Mokhberdoran F, Xie Y (2018) Growth responses and photosynthetic indices of bamboo plant (*Indocalamus latifolius*) under heavy metal stress. Sci World J 2018:1219364

Fan FY, Li CL, Luo Z, Tang GZ (2018) UV-B radiation-induced changes in tea metabolites and related gene expression. In: Han WY, Li X, Ahammed G (eds) Stress physiology of tea in the face of climate change. Springer, Singapore, pp 111–133

Fedina I, Hidema J, Velitchkova M, Georgieva K, Nedeva D (2010) UV-B induced stress responses in three rice cultivars. Biol Plant 54:571–574

Feigl G, Lehotai N, Molnár Á, Ördög A, Rodríguez-Ruiz M, Palma JM, Corpas FJ, Erdei L, Kolbert Z (2014) Zinc induces distinct changes in the metabolism of reactive oxygen and nitrogen species (ROS and RNS) in the roots of two *Brassica* species with different sensitivity to zinc stress. Ann Bot 116:613–625

Ferraz P, Fidalgo F, Almeida A, Teixeira J (2012) Phytostabilization of nickel by the zinc and cadmium hyperaccumulator *Solanum nigrum* L. Are metallothioneins involved? Plant Physiol Biochem 57:254–260

Fidalgo F, Azenha M, Silva AF, de Sousa A, Santiago A, Ferraz P, Teixeira J (2013) Copper induced stress in *Solanum nigrum* L. and antioxidant defense system responses. Food Energy Secur 2:70–80

Foyer CH, Noctor G (2005) Redox homeostasis and antioxidant signaling: a metabolic interface between stress perception and physiological responses. Plant Cell 17:1866–1875

Fraser DP, Sharma A, Fletcher T, Budge S, Moncrieff C, Dodd AN, Franklin KA (2017) UV-B antagonises shade avoidance and increases levels of the flavonoid quercetin in coriander (*Coriandrum sativum*). Sci Rep 7:17758

Furness NH, Jolliffe PA, Upadhyaya MK (2005) Competitive interactions in mixtures of broccoli and *Chenopodium album* grown at two UV-B radiation levels under glasshouse conditions. Weed Res 45:449–459

Gao Q, Zhang L (2008) Ultraviolet-B-induced oxidative stress and antioxidant defense system responses in ascorbate-deficient vtc1 mutants of *Arabidopsis thaliana*. J Plant Physiol 165:138–148

Gao C, Yang B, Zhang D, Chen M, Tian J (2016) Enhanced metabolic process to indole alkaloids in *Clematis terniflora* DC. After exposure to high level of UV-B irradiation followed by the dark. BMC Plant Biol 16:231

Ghasemi S, Kumleh HH, Kordrostami M (2019) Changes in the expression of some genes involved in the biosynthesis of secondary metabolites in *Cuminum cyminum* L. under UV stress. Protoplasma 256:279–290

Ghisi R, Trentin AR, Masi A, Ferretti M (2002) Carbon and nitrogen metabolism in barley plants exposed to UV-B radiation. Physiol Plant 116:200–205

Gichner T, Patková Z, Száková J, Demnerová K (2006) Toxicity and DNA damage in tobacco and potato plants growing on soil polluted with heavy metals. Ecotoxicol Environ Saf 65:420–426

Gil M, Pontin M, Berli F, Bottini R, Piccoli P (2012) Metabolism of terpenes in the response of grape (*Vitis vinifera* L.) leaf tissues to UV-B radiation. Phytochemistry 77:89–98

Gill SS, Khan NA, Tuteja N (2012) Cadmium at high dose perturbs growth, photosynthesis and nitrogen metabolism while at low dose it up regulates sulfur assimilation and antioxidant machinery in garden cress (*Lepidium sativum* L.). Plant Sci 182:112–120

Gonçalves JF, Antes FG, Maldaner J, Pereira LB, Tabaldi LA, Rauber R, Rossato LV, Bisognin DA, Dressler VL, de Moraes Flores EM, Nicoloso FT (2009) Cadmium and mineral nutrient accumulation in potato plantlets grown under cadmium stress in two different experimental culture conditions. Plant Physiol Biochem 47:814–821

Gondor OK, Szalai G, Kovács V, Janda T, Pál M (2014) Impact of UV-B on drought-or cadmium-induced changes in the fatty acid composition of membrane lipid fractions in wheat. Ecotoxicol Environ Saf 108:129–134

Gregianini TS, da Silveira VC, Porto DD, Kerber VA, Henriques AT, Fett-Neto AG (2003) The alkaloid Brachycerine is induced by ultraviolet radiation and is a singlet oxygen quencher. Photochem Photobiol 78:470–474

Guo J, Xu L, Su Y, Wang H, Gao S, Xu J, Que Y (2013) *ScMT2-1-3*, a metallothionein gene of sugarcane, plays an important role in the regulation of heavy metal tolerance/accumulation. Biomed Res Int 2013:904769

Gupta V, Jatav PK, Verma R, Kothari SL, Kachhwaha S (2017) Nickel accumulation and its effect on growth, physiological and biochemical parameters in millets and oats. Environ Sci Pollut Res 24:23915–23925

Gupta S, Gupta V, Singh V, Varadwaj PK (2018) Extrapolation of significant genes and transcriptional regulatory networks involved in *Zea mays* in response in UV-B stress. Genes Genomics 40:973–990

Hagen SF, Borge GIA, Bengtsson GB, Bilger W, Berge A, Haffner K, Solhaug KA (2007) Phenolic contents and other health and sensory related properties of apple fruit (*Malus domestica* Borkh., cv. Aroma): effect of postharvest UV-B irradiation. Postharvest Biol Technol 45:1–10

Hall JL (2002) Cellular mechanisms for heavy metal detoxification and tolerance. J Exp Bot 53:1–11

Hamid A, Singh S, Agrawal M, Agrawal SB (2018) *Heteropogon contortus* BL-1 (Pilli grass) and elevated UV-B radiation: the role of growth, physiological, and biochemical traits in determining forage productivity and quality. Photochem Photobiol 95(2):572–580

He JY, Ren YF, Zhu C, Yan YP, Jiang DA (2008) Effect of Cd on growth, photosynthetic gas exchange, and chlorophyll fluorescence of wild and Cd-sensitive mutant rice. Photosynthetica 46:466–470

Hectors K, Prinsen E, De Coen W, Jansen MA, Guisez Y (2007) *Arabidopsis thaliana* plants acclimated to low dose rates of ultraviolet B radiation show specific changes in morphology and gene expression in the absence of stress symptoms. New Phytol 175:255–270

Hikosaka S, Ito K, Goto E (2010) Effects of ultraviolet light on growth, essential oil concentration, and total antioxidant capacity of Japanese mint. Environ Control Biol 48:185–190

Hilal M, Parrado MF, Rosa M, Gallardo M, Orce L, Massa EM, Prado FE et al (2004) Epidermal lignin deposition in *Quinoa* cotyledons in response to UV-B radiation. Photochem Photobiol 79:205–210

Hofmann RW, Campbell BD, Bloor SJ, Swinny EE, Markham KR, Ryan KG, Fountain DW (2003) Responses to UV-B radiation in *Trifolium repens* L.–physiological links to plant productivity and water availability. Plant Cell Environ 26:603–612

Hollósy F (2002) Effects of ultraviolet radiation on plant cells. Micron 33:179–197

Hossain MA, Piyatida P, da Silva JAT, Fujita M (2012) Molecular mechanism of heavy metal toxicity and tolerance in plants: central role of glutathione in detoxification of reactive oxygen species and methylglyoxal and in heavy metal chelation. J Bot 2012:872875

Ibrahim M, Chee Kong Y, Mohd Zain N (2017) Effect of cadmium and copper exposure on growth, secondary metabolites and antioxidant activity in the medicinal plant Sambung Nyawa (*Gynura procumbens* (Lour.) Merr). Molecules 22:1623

Inostroza-Blancheteau C, Reyes-Díaz M, Arellano A, Latsague M, Acevedo P, Loyola R, Alberdi M et al (2014) Effects of UV-B radiation on anatomical characteristics, phenolic compounds and gene expression of the phenylpropanoid pathway in highbush blueberry leaves. Plant Physiol Biochem 85:85–95

Interdonato R, Rosa M, Nieva CB, González JA, Hilal M, Prado FE (2011) Effects of low UV-B doses on the accumulation of UV-B absorbing compounds and total phenolics and carbohydrate metabolism in the peel of harvested lemons. Environ Exp Bot 70:204–211

Ioannidis D, Bonner L, Johnson CB (2002) UV-B is required for normal development of oil glands in *Ocimum basilicum* L. (Sweet Basil). Ann Bot 90:453–460

Iqbal N, Masood A, Nazar R, Syeed S, Khan NA (2010) Photosynthesis, growth and antioxidant metabolism in mustard (*Brassica juncea* L.) cultivars differing in cadmium tolerance. Agric Sci China 9:519–527

Jansen MA (2002) Ultraviolet-B radiation effects on plants: induction of morphogenic responses. Physiol Plant 116:423–429

Jansen MA, Gaba V, Greenberg BM (1998) Higher plants and UV-B radiation: balancing damage, repair and acclimation. Trends Plant Sci 3:131–135

Januškaitienė I (2012) The effect of cadmium on several photosynthetic parameters of pea (*Pisum sativum* L.) at two growth stages. Zemdirbystė 99:73–85

Jenkins GI (2009) Signal transduction in responses to UV-B radiation. Annu Rev Plant Biol 60:407–431

Johnson CB, Kirby J, Naxakis G, Pearson S (1999) Substantial UV-B-mediated induction of essential oils in sweet basil (*Ocimum basilicum* L.). Phytochemistry 51:507–510

Jordan BR, James PE, Strid Å, Anthony RG (1994) The effect of ultraviolet-B radiation on gene expression and pigment composition in etiolated and green pea leaf tissue: UV-B-induced changes are gene-specific and dependent upon the developmental stage. Plant Cell Environ 17:45–54

Kakani VG, Reddy KR, Zhao D, Mohammed AR (2003a) Effects of ultraviolet-B radiation on cotton (*Gossypium hirsutum* L.) morphology and anatomy. Ann Bot 91:817–826

Kakani VG, Reddy KR, Zhao D, Sailaja K (2003b) Field crop responses to ultraviolet-B radiation: a review. Agric For Meteorol 120:191–218

Karimi P, Khavari-Nejad RA, Niknam V, Ghahremaninejad F, Najafi F (2012) The effects of excess copper on antioxidative enzymes, lipid peroxidation, proline, chlorophyll, and concentration of Mn, Fe, and Cu in *Astragalus neo-mobayenii*. Sci World J 2012:615670

Kataria S, Jajoo A, Guruprasad KN (2014) Impact of increasing Ultraviolet-B (UV-B) radiation on photosynthetic processes. J Photochem Photobiol B Biol 137:55–66

Kısa D, Elmastaş M, Öztürk L, Kayır Ö (2016) Responses of the phenolic compounds of *Zea mays* under heavy metal stress. Appl Biol Chem 59:813–820

Klem K, Ač A, Holub P, Kováč D, Špunda V, Robson TM, Urban O (2012) Interactive effects of PAR and UV radiation on the physiology, morphology and leaf optical properties of two barley varieties. Environ Exp Bot 75:52–64

Ko JA, Lee BH, Lee JS, Park HJ (2008) Effect of UV-B exposure on the concentration of vitamin D_2 in sliced shiitake mushroom (*Lentinus edodes*) and white button mushroom (*Agaricus bisporus*). J Agric Food Chem 56:3671–3674

Kohli SK, Handa N, Gautam V, Bali S, Sharma A, Khanna K, Arora S, Thukral AK, Ohri P, Karpets YV, Kolupaev YE (2017) ROS signaling in plants under heavy metal stress. In: Khan M, Khan N (eds) Reactive oxygen species and antioxidant system in plants: role and regulation under abiotic stress. Springer, Singapore, pp 185–214

Kondo N, Kawashima M (2000) Enhancement of the tolerance to oxidative stress in cucumber (*Cucumis sativus* L.) seedlings by UV-B irradiation: possible involvement of phenolic compounds and antioxidative enzymes. J Plant Res 113:311–317

Kosobrukhov A, Knyazeva I, Mudrik V (2004) *Plantago major* plants responses to increase content of lead in soil: growth and photosynthesis. Plant Growth Regul 42:145–151

Koti S, Reddy KR, Kakani VG, Zhao D, Reddy VR (2004) Soybean (*Glycine max*) pollen germination characteristics, flower and pollen morphology in response to enhanced ultraviolet-B radiation. Ann Bot 94:855–864

Kováčik J, Klejdus B, Bačkor M (2009) Phenolic metabolism of *Matricaria chamomilla* plants exposed to nickel. J Plant Physiol 166:1460–1464

Kovács V, Gondor OK, Szalai G, Majláth I, Janda T, Pál M (2014) UV-B radiation modifies the acclimation processes to drought or cadmium in wheat. Environ Exp Bot 100:122–131

Krupa Z, Baszynski T (1995) Some aspects of heavy metals toxicity towards photosynthetic apparatus-direct and indirect effects on light and dark reactions. Acta Physiol Plant 2:177–190

Krupa Z, Siedlecka A, Skórzynska-Polit E, Maksymiec W (2002) Heavy metal interactions with plant nutrients. In: Prasad MNV, Strzałka K (eds) Physiology and biochemistry of metal toxicity and tolerance in plants. Springer, Dordrecht, pp 287–301

Kumar A, Prasad MNV, Sytar O (2012) Lead toxicity, defense strategies and associated indicative biomarkers in *Talinum triangulare* grown hydroponically. Chemosphere 89:1056–1065

Kumari R, Agrawal SB (2010) Supplemental UV-B induced changes in leaf morphology, physiology and secondary metabolites of an Indian aromatic plant *Cymbopogon citratus* (DC) Staph under natural field conditions. Int J Environ Stud 67:655–675

Kumari R, Agrawal SB (2011) Comparative analysis of essential oil composition and oil containing glands in *Ocimum sanctum* L.(Holy basil) under ambient and supplemental level of UV-B through gas chromatography–mass spectrometry and scanning electron microscopy. Acta Physiol Plant 33:1093–1101

Kumari R, Agrawal SB, Singh S, Dubey NK (2009a) Supplemental ultraviolet-B induced changes in essential oil composition and total phenolics of *Acorus calamus* L. (sweet flag). Ecotoxicol Environ Saf 72:2013–2019

Kumari R, Singh S, Agrawal SB (2009b) Effects of supplemental ultraviolet-B radiation on growth and physiology of *Acorus calamus* L. (sweet flag). Acta Biol Cracov Bot 51:19–27

Kumari R, Singh S, Agrawal SB (2010) Response of ultraviolet-B induced antioxidant defense system in a medicinal plant, *Acorus calamus*. J Environ Biol 31:907–911

Laakso K, Sullivan JH, Huttunen S (2000) The effects of UV-B radiation on epidermal anatomy in loblolly pine (*Pinus taeda* L.) and Scots pine (*Pinus sylvestris* L.). Plant Cell Environ 23:461–472

Lake JA, Field KJ, Davey MP, Beerling DJ, Lomax BH (2009) Metabolomic and physiological responses reveal multi-phasic acclimation of *Arabidopsis thaliana* to chronic UV radiation. Plant Cell Environ 32:1377–1389

Lee J, Reeves RD, Brooks RR, Jaffré T (1978) The relation between nickel and citric acid in some nickel-accumulating plants. Phytochemistry 17:1033–1035

Li S, Yang W, Yang T, Chen Y, Ni W (2015) Effects of cadmium stress on leaf chlorophyll fluorescence and photosynthesis of *Elsholtzia argyi*—a cadmium accumulating plant. Int J Phytoremediation 17:85–92

Li J, Han X, Wang C, Tang L, Zhang W, Qi W (2019) The response of *Achyranthes bidentata* Blume to short-term UV-B exposure. Russ J Plant Physiol 66:160–170

Lin YF, Aarts MGM (2012) The molecular mechanism of zinc and cadmium stress response in plants. Cell Mol Life Sci 69:3187–3206

Lindroth RL, Hofman RW, Campbell BD, McNabb WC, Hunt DY (2000) Population differences in *Trifolium repens* L. response to ultraviolet-B radiation: foliar chemistry and consequences for two lepidopteran herbivores. Oecologia 122:20–28

López-Millán AF, Sagardoy R, Solanas M, Abadía A, Abadía J (2009) Cadmium toxicity in tomato (*Lycopersicon esculentum*) plants grown in hydroponics. Environ Exp Bot 65:76–385

Ma JF, Ryan PR, Delhaize E (2001) Aluminium tolerance in plants and the complexing role of organic acids. Trends Plant Sci 6:273–278

Ma M, Wang P, Yang R, Zhou T, Gu Z (2019) UV-B mediates isoflavone accumulation and oxidative-antioxidant system responses in germinating soybean. Food Chem 275:628–636

Maffei M, Scannerini S (2000) UV-B effect on photomorphogenesis and essential oil composition in peppermint (*Mentha piperita* L.). J Essent Oil Res 12:523–529

Masi A, Melis A (1997) Morphological and molecular changes in the unicellular green alga Dunaliella salina grown under supplemental UV-B radiation: cell characteristics and photosystem II damage and repair properties. Biochim Biophys Acta Bioenerg 1321:183–193

Matsuura HN, de Costa F, Yendo ACA, Fett-Neto AG (2013) Photoelicitation of bioactive secondary metabolites by ultraviolet radiation: mechanisms, strategies, and applications. In: Chandra S, LATA H, Varma A (eds) Biotechnology for medicinal plants. Springer, Berlin, pp 170–190

Meharg AA (1994) Integrated tolerance mechanisms: constitutive and adaptive plant responses to elevated metal concentrations in the environment. Plant Cell Environ 17:989–993

Molas J (2002) Changes of chloroplast ultrastructure and total chlorophyll concentration in cabbage leaves caused by excess of organic Ni (II) complexes. Environ Exp Bot 47:115–126

Müller-Xing R, Xing Q, Goodrich J (2014) Footprints of the sun: memory of UV and light stress in plants. Front Plant Sci 5:474

Myśliwa-Kurdziel B, Prasad MNV, Strzałtka K (2004) Photosynthesis in heavy metal stressed plants. In: Prasad MNV (ed) Heavy metal stress in plants. Springer, Berlin, pp 146–181

Nazir H, Asghar HN, Zahir ZA, Akhtar MJ, Saleem M (2016) Judicious use of kinetin to improve growth and yield of rice in nickel contaminated soil. Int J Phytoremediation 18:651–655

Nogués S, Baker NR (2000) Effects of drought on photosynthesis in Mediterranean plants grown under enhanced UV-B radiation. J Exp Bot 51:1309–1317

Nouairi I, Ammar WB, Youssef NB, Miled DDB, Ghorbal MH, Zarrouk M (2009) Antioxidant defense system in leaves of Indian mustard (*Brassica juncea*) and rape (*Brassica napus*) under cadmium stress. Acta Physiol Plant 31:237–247

Ohlsson AB, Segerfeldt P, Lindström A, Borg-Karlson AK, Berglund T (2013) UV-B exposure of indoor-grown Picea abies seedlings causes an epigenetic effect and selective emission of terpenes. Z Naturforsch C 68:139–147

Oliveira SCB, Corduneanu O, Oliveira-Brett AM (2008) In situ evaluation of heavy metal–DNA interactions using an electrochemical DNA biosensor. Bioelectrochemistry 72:53–58

Ou X, Zhang Y, Xu C, Lin X, Zang Q, Zhuang T, Jiang L, von Wettstein D, Liu B (2012) Transgenerational inheritance of modified DNA methylation patterns and enhanced tolerance induced by heavy metal stress in rice (*Oryza sativa* L.). PLoS One 7:e41143

Oven M, Grill E, Golan-Goldhirsh A, Kutchan TM, Zenk MH (2002) Increase of free cysteine and citric acid in plant cells exposed to cobalt ions. Phytochemistry 60:467–474

Pandey N, Sharma CP (2002) Effect of heavy metals Co^{2+}, Ni^{2+} and Cd^{2+} on growth and metabolism of cabbage. Plant Sci 163:753–758

Pellet DM, Grunes DL, Kochian LV (1995) Organic acid exudation as an aluminum-tolerance mechanism in maize (*Zea mays* L.). Planta 196:788–795

Persans MW, Nieman K, Salt DE (2001) Functional activity and role of cation-efflux family members in Ni hyperaccumulation in *Thlaspi goesingense*. Proc Natl Acad Sci 98:9995–10000

Pietrini F, Iori V, Cheremisina A, Shevyakova NI, Radyukina N, Kuznetsov VV, Zacchini M (2015) Evaluation of nickel tolerance in *Amaranthus paniculatus* L. plants by measuring photosynthesis, oxidative status, antioxidative response and metal-binding molecule content. Environ Sci Pollut Res 22:482–494

Pinto AP, Simoes I, Mota AM (2008) Cadmium impact on root exudates of sorghum and maize plants: a speciation study. J Plant Nutr 31:1746–1755

Potters G, Pasternak TP, Guisez Y, Palme KJ, Jansen MA (2007) Stress-induced morphogenic responses: growing out of trouble? Trends Plant Sci 12(3):98–105

Pourrut B, Jean S, Silvestre J, Pinelli E (2011) Lead-induced DNA damage in *Vicia faba* root cells: potential involvement of oxidative stress. Mutat Res Genet Toxicol Environ Mutagen 726:123–128

Prasad DDK, Prasad ARK (1987) Altered δ-aminolevulinic acid metabolism by lead and mercury in germinating seedlings of Bajra (*Pennisetum typhoideum*). J Plant Physiol 127:241–249

Prasad SM, Dwivedi R, Zeeshan M (2005) Growth, photosynthetic electron transport, and antioxidant responses of young soybean seedlings to simultaneous exposure of nickel and UV-B stress. Photosynthetica 43:177–185

Qin B, Ma L, Wang Y, Chen M, Lan X, Wu N, Liao Z (2014) Effects of acetylsalicylic acid and UV-B on gene expression and tropane alkaloid biosynthesis in hairy root cultures of *Anisodus luridus*. Plant Cell Tiss Org Cult 117:483–490

Quaggiotti S, Trentin AR, Dalla Vecchia F, Ghisi R (2004) Response of maize (*Zea mays* L.) nitrate reductase to UV-B radiation. Plant Sci 167:107–116

Rai R, Meena RP, Smita SS, Shukla A, Rai SK, Pandey-Rai S (2011) UV-B and UV-C pretreatments induce physiological changes and artemisinin biosynthesis in *Artemisia annua* L.—an antimalarial plant. J Photochem Photobiol B Biol 105:216–225

Rai V, Tandon PK, Khatoon S (2014) Effect of chromium on antioxidant potential of *Catharanthus roseus* varieties and production of their anticancer alkaloids: vincristine and vinblastine. Biomed Res Int 2014:934182

Ramani S, Chelliah J (2007) UV-B-induced signaling events leading to enhanced-production of catharanthine in *Catharanthus roseus* cell suspension cultures. BMC Plant Biol 7:61

Ramani S, Jayabaskaran C (2008) Enhanced catharanthine and vindoline production in suspension cultures of by ultraviolet-B light. J Mol Signal 3:9

Robson TM, Aphalo PJ (2012) Species-specific effect of UV-B radiation on the temporal pattern of leaf growth. Physiol Plant 144:146–160

Rozema J, van de Staaij J, Björn LO, Caldwell M (1997) UV-B as an environmental factor in plant life: stress and regulation. Trends Ecol Evol 12:22–28

Salt DE, Kato N, Krämer U, Smith RD, Raskin I (1999) The role of root exudates in nickel hyperaccumulation and tolerance in accumulator and non-accumulator species of *Thlaspi*. In: Banuelos G (ed) Phytoremediation of contaminated soil and water. CRC, Boca Raton, FL, pp 191–202

Sangwan NS, Farooqi AHA, Shabih F, Sangwan RS (2001) Regulation of essential oil production in plants. Plant Growth Regul 34:3–21

Santos I, Fidalgo F, Almeida JM, Salema R (2004) Biochemical and ultrastructural changes in leaves of potato plants grown under supplementary UV-B radiation. Plant Sci 167:925–935

Schiavon M, Pittarello M, Pilon-Smits EAH, Wirtz M, Hell R, Malagoli M (2012) Selenate and molybdate alter sulfate transport and assimilation in *Brassica juncea* L. Czern implications for phytoremediation. Environ Exp Bot 75:41–51

Schläger S, Dräger B (2016) Exploiting plant alkaloids. Curr Opin Biotechnol 37:155–164

Schreiner M, Krumbein A, Mewis I, Ulrichs C, Huyskens-Keil S (2009) Short-term and moderate UV-B radiation effects on secondary plant metabolism in different organs of nasturtium (*Tropaeolum majus* L.). Innov Food Sci Emerg Technol 10:93–96

Schultze M, Bilger M (2019) Acclimation of *Arabidopsis thaliana* to low temperature protects against damage of photosystem II caused by exposure to UV-B radiation at 9 °C. Plant Physiol Biochem 134:73–80

Shahid M, Pourrut B, Dumat C, Nadeem M, Aslam M, Pinelli E (2014) Heavy-metal-induced reactive oxygen species: phytotoxicity and physicochemical changes in plants. In: Whitacre D (ed) Reviews of environmental contamination and toxicology, vol 232. Springer, Cham, pp 1–44

Sheetal KR, Singh SD, Anand A, Prasad S (2016) Heavy metal accumulation and effects on growth, biomass and physiological processes in mustard. Indian J Plant Physiol 21:219–223

Shen Y, Zhang Y, Chen J, Lin H, Zhao M, Peng H, Liu L, Yuan G, Zhang S, Zhang Z, Pan G (2013) Genome expression profile analysis reveals important transcripts in maize roots responding to the stress of heavy metal Pb. Physiol Plant 147:270–282

Shi GR, Cai QS (2008) Photosynthetic and anatomic responses of peanut leaves to cadmium stress. Photosynthetica 46:627–630

Shi GR, Cai QS (2009) Photosynthetic and anatomic responses of peanut leaves to zinc stress. Biol Plant 53:391–394

Shweta M, Agrawal SB (2006) Interactive effects between supplemental ultraviolet-B radiation and heavy metals on the growth and biochemical characteristics of *Spinacia oleracea* L. Braz J Plant Physiol 18:307–314

Singh A, Sarkar A, Singh S, Agrawal SB (2010) Investigation of supplemental ultraviolet-B-induced changes in antioxidative defense system and leaf proteome in radish (*Raphanus sativus* L. cv truthful): an insight to plant response under high oxidative stress. Protoplasma 245:75–83

Singh G, Agnihotri RK, Reshma RS, Ahmad M (2012) Effect of lead and nickel toxicity on chlorophyll and proline content of Urd (*Vigna mungo* L.) seedlings. Int J Plant Physiol Biochem 4:136–141

Singh S, Srivastava PK, Kumar D, Tripathi DK, Chauhan DK, Prasad SM (2015) Morpho-anatomical and biochemical adapting strategies of maize (*Zea mays* L.) seedlings against lead and chromium stresses. Biocatal Agric Biotechnol 4:286–295

Singh V, Tripathi BN, Sharma V (2016a) Interaction of Mg with heavy metals (Cu, Cd) in *T. aestivum* with special reference to oxidative and proline metabolism. J Plant Res 129:487–497

Singh S, Parihar P, Singh R, Singh VP, Prasad SM (2016b) Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics, and ionomics. Front Plant Sci 6:1143

Skaltsa H, Verykokidou E, Harvala C, Karabourniotis G, Manetasi Y (1994) UV-B protective potential and flavonoid content of leaf hairs of *Quercus ilex*. Phytochemistry 37:987–990

Song WY, Mendozacozatll DG, Lee Y, Schroeder JI, Ahn SN, Lee HS, Wicker T, Martinoia E (2014) Phytochelatin–metal (loid) transport into vacuoles shows different substrate preferences in barley and *Arabidopsis*. Plant Cell Environ 37:1192–1201

Sullivan JH, Gitz DC, Peek MS, McElrone AJ (2003) Response of three eastern tree species to supplemental UV-B radiation: leaf chemistry and gas exchange. Agric For Meteorol 120:219–228

Sun H, Dai H, Wang X, Wang G (2016) Physiological and proteomic analysis of selenium-mediated tolerance to Cd stress in cucumber (*Cucumis sativus* L.). Ecotoxicol Environ Saf 133:114–126

Surabhi GK, Reddy KR, Singh SK (2009) Photosynthesis, fluorescence, shoot biomass and seed weight responses of three cowpea (*Vigna unguiculata* (L.) Walp.) cultivars with contrasting sensitivity to UV-B radiation. Environ Exp Bot 66:160–171

Takshak S, Agrawal SB (2014) Effect of ultraviolet-B radiation on biomass production, lipid peroxidation, reactive oxygen species, and antioxidants in *Withania somnifera*. Biol Plant 58:328–334

Takshak S, Agrawal SB (2015a) Alterations in metabolite profile and free radical scavenging activities of *Withania somnifera* leaf and root extracts under supplemental ultraviolet-B radiation. Acta Physiol Plant 37:260

Takshak S, Agrawal SB (2015b) Defence strategies adopted by the medicinal plant *Coleus forskohlii* against supplemental ultraviolet-B radiation: augmentation of secondary metabolites and antioxidants. Plant Physiol Biochem 97:124–138

Takshak S, Agrawal SB (2017) Anatomical changes linked performance of two indigenous medicinal plants, *Withania Somnifera* Dunal and Coleus Forskohlii Briq. Exposed to Supplemental Ultraviolet-B Radiation

Takshak S, Agrawal SB (2018) Interactive effects of supplemental ultraviolet-B radiation and indole-3-acetic acid on *Coleus forskohlii* Briq.: alterations in morphological-, physiological, and biochemical characteristics and essential oil content. Ecotoxicol Environ Saf 147:313–326

Takshak S, Agrawal SB (2019) Defense potential of secondary metabolites in medicinal plants under UV-B stress. J Photochem Photobiol B 193:51–88

Tegelberg R, Julkunen-Tiitto R (2001) Quantitative changes in secondary metabolites of dark-leaved willow (*Salix myrsinifolia*) exposed to enhanced ultraviolet-B radiation. Physiol Plant 113:541–547

Teramura AH (1983) Effects of ultraviolet-B radiation on the growth and yield of crop plants. Physiol Plant 58:415–427

Teramura AH, Sullivan JH (1994) Effects of UV-B radiation on photosynthesis and growth of terrestrial plants. Photosynth Res 39:463–473

Tevini M, Steinmüller D (1987) Influence of light, UV-B radiation, and herbicides on wax biosynthesis of cucumber seedling. J Plant Physiol 131:111–121

Tice KR, Parker DR, DeMason DA (1992) Operationally defined apoplastic and symplastic aluminum fractions in root tips of aluminum-intoxicated wheat. Plant Physiol 100:309–318

Todeschini V, Lingua G, D'agostino G, Carniato F, Roccotiello E, Berta G (2011) Effects of high zinc concentration on poplar leaves: a morphological and biochemical study. Environ Exp Bot 71:50–56

Tossi V, Lamattina L, Jenkins GI, Cassia RO (2014) Ultraviolet-B-induced stomatal closure in Arabidopsis is regulated by the *UV RESISTANCE LOCUS8* photoreceptor in a nitric oxide-dependent mechanism. Plant Physiol 164:2220–2230

Tripathi R, Sarkar A, Pandey Rai S, Agrawal SB (2011) Supplemental ultraviolet-B and ozone: impact on antioxidants, proteome and genome of linseed (*Linum usitatissimum* L. cv. Padmini). Plant Biol 13:93–104

Tripathi DK, Singh VP, Prasad SM, Chauhan DK, Dubey NK, Rai AK (2015) Silicon-mediated alleviation of Cr (VI) toxicity in wheat seedlings as evidenced by chlorophyll florescence, laser induced breakdown spectroscopy and anatomical changes. Ecotoxicol Environ Saf 113:133–144

Tripathi R, Rai K, Singh S, Agrawal M, Agrawal SB (2019) Role of supplemental UV-B in changing the level of ozone toxicity in two cultivars of sunflower: growth, seed yield and oil quality. Ecotoxicology 28(3):277–293

Trujillo LS, Graü AJ, Fortuny RS, Belloso OM (2015) Physicochemical characterization and antimicrobial activity of foodgrade emulsions and nano emulsions incorporating essential oils. Food Hydrocoll 43:547–556

Ubi BE, Honda C, Bessho H, Kondo S, Wada M, Kobayashi S, Moriguchi T (2006) Expression analysis of anthocyanin biosynthetic genes in apple skin: effect of UV-B and temperature. Plant Sci 170:571–578

Valkama E, Kivimäenpää M, Hartikainen H, Wulff A (2003) The combined effects of enhanced UV-B radiation and selenium on growth, chlorophyll fluorescence and ultrastructure in strawberry (*Fragaria*× *ananassa*) and barley (*Hordeum vulgare*) treated in the field. Agric For Meteorol 120:267–278

Van Assche F, Clijsters H (1986) Inhibition of photosynthesis in *Phaseolus vulgaris* by treatment with toxic concentrations of zinc: effects on electron transport and photophosphorylation. Physiol Plant 66:717–721

van de Mortel JE, Villanueva LA, Schat H, Kwekkeboom J, Coughlan S, Moerland PD, van Themaat EVL, Koornneef M, Aarts MG (2006) Large expression differences in genes for iron and zinc homeostasis, stress response, and lignin biosynthesis distinguish roots of *Arabidopsis thaliana* and the related metal hyperaccumulator *Thlaspi caerulescens*. Plant Physiol 142:1127–1147

van der Zaal BJ, Neuteboom LW, Pinas JE, Chardonnens AN, Schat H, Verkleij JA, Hooykaas PJ (1999) Overexpression of a novel *Arabidopsis* gene related to putative zinc-transporter genes from animals can lead to enhanced zinc resistance and accumulation. Plant Physiol 119:1047–1056

Verkleij JAC, Sneller FEC, Schat H (2003) Metallothioneins and phytochelatins: ecophysiological aspects. In: Abrol YP, Ahmad A (eds) Sulphur in plants. Springer, Dordrecht, pp 163–176

Vetterlein D, Szegedi K, Ackermann J, Mattusch J, Neue HU, Tanneberg H, Jahn R (2007) Competitive mobilization of phosphate and arsenate associated with goethite by root activity. J Environ Qual 36:1811–1820

Wang J, Evangelou BP, Nielsen MT, Wagner GJ (1991) Computer-simulated evaluation of possible mechanisms for quenching heavy metal ion activity in plant vacuoles: I. Cadmium. Plant Physiol 97:1154–1160

Wang J, Evangelou BP, Nielsen MT, Wagner GJ (1992) Computer simulated evaluation of possible mechanisms for sequestering metal ion activity in plant vacuoles: II. Zinc. Plant Physiol 99:621–626

Wang Y, Wang S, Nan Z, Ma J, Zang F, Chen Y, Li Y, Zhang Q (2015) Effects of Ni stress on the uptake and translocation of Ni and other mineral nutrition elements in mature wheat grown in sierozems from northwest of China. Environ Sci Pollut Res 22:19756–19763

Wargent JJ, Gegas VC, Jenkins GI, Doonan JH, Paul ND (2009) UVR8 in *Arabidopsis thaliana* regulates multiple aspects of cellular differentiation during leaf development in response to ultraviolet B radiation. New Phytol 183:315–326

Xia Y, Qi Y, Yuan Y, Wang G, Cui J, Chen Y, Zhang H, Shen Z (2012) Overexpression of *Elsholtzia haichowensis* metallothionein 1 (*EhMT1*) in tobacco plants enhances copper tolerance and accumulation in root cytoplasm and decreases hydrogen peroxide production. J Hazard Mater 233:65–71

Xue ZC, Gao HY, Zhang LT (2013) Effects of cadmium on growth, photosynthetic rate and chlorophyll content in leaves of soybean seedlings. Biol Plant 57:587–590

Yadav SK (2010) Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. S Afr J Bot 76:167–179

Yamaguchi H, Fukuoka H, Arao T, Ohyama A, Nunome T, Miyatake K, Negoro S (2009) Gene expression analysis in cadmium-stressed roots of a low cadmium-accumulating solanaceous plant, *Solanum torvum*. J Exp Bot 61:423–437

Yang XE, Jin XF, Feng Y, Islam E (2005) Molecular mechanisms and genetic basis of heavy metal tolerance/hyperaccumulation in plants. J Integr Plant Biol 47:1025–1035

Yang Y, Yao Y, He H (2008) Influence of ambient and enhanced ultraviolet-B radiation on the plant growth and physiological properties in two contrasting populations of *Hippophae rhamnoides*. J Plant Res 121:377

Yannarelli GG, Gallego SM, Tomaro ML (2006) Effect of UV-B radiation on the activity and isoforms of enzymes with peroxidase activity in sunflower cotyledons. Environ Exp Bot 56:174–181

Yao Y, Li Y, Yang Y, Li C (2005) Effect of seed pretreatment by magnetic field on the sensitivity of cucumber (*Cucumis sativus*) seedlings to ultraviolet-B radiation. Environ Exp Bot 54:286–294

Yu GH, Li W, Yuan ZY, Cui HY, Lv CG, Gao ZP, Chen GX et al (2013) The effects of enhanced UV-B radiation on photosynthetic and biochemical activities in super-high-yield hybrid rice *Liangyoupeijiu* at the reproductive stage. Photosynthetica 51:33–44

Yusuf M, Fariduddin Q, Varshney P, Ahmad A (2012) Salicylic acid minimizes nickel and/or salinity-induced toxicity in Indian mustard (*Brassica juncea*) through an improved antioxidant system. Environ Sci Pollut Res 19:8–18

Zagoskina NV, Dubravina GA, Alyavina AK, Goncharuk EA (2003) Effect of ultraviolet (UV-B) radiation on the formation and localization of phenolic compounds in tea plant callus cultures. Russ J Plant Physiol 50:270–275

Zenk MH (1996) Heavy metal detoxification in higher plants-a review. Gene 179:21–30

Zhang WJ, Björn LO (2009) The effect of ultraviolet radiation on the accumulation of medicinal compounds in plants. Fitoterapia 80:207–218

Zhang X, Gao B, Xia H (2014) Effect of cadmium on growth, photosynthesis, mineral nutrition and metal accumulation of bana grass and vetiver grass. Ecotoxicol Environ Saf 106:102–108

Zhigang A, Cuijie L, Yuangang Z, Yejie D, Wachter A, Gromes R, Rausch T (2006) Expression of *BjMT2*, a metallothionein 2 from *Brassica juncea*, increases copper and cadmium tolerance in *Escherichia coli* and *Arabidopsis thaliana*, but inhibits root elongation in *Arabidopsis thaliana* seedlings. J Exp Bot 57:3575–3582

Zhou J, Jiang Z, Ma J, Yang L, Wei Y (2017) The effects of lead stress on photosynthetic function and chloroplast ultrastructure of *Robinia pseudoacacia* seedlings. Environ Sci Pollut Res 24:10718–10726

Zhu XF, Zheng C, Hu YT, Jiang TAO, Liu YU, Dong NY, Yang JL, Zheng SJ (2011) Cadmium induced oxalate secretion from root apex is associated with cadmium exclusion and resistance in *Lycopersicon esulentum*. Plant Cell Environ 34:1055–1064

Zlatev ZS, Lidon FJ, Kaimakanova M (2012) Plant physiological responses to UV-B radiation. Emir J Food Agr 24:481–501

Zouari M, Ahmed CB, Elloumi N, Bellassoued K, Delmail D, Labrousse P, Abdallah FB, Rouina BB (2016) Impact of proline application on cadmium accumulation, mineral nutrition and enzymatic antioxidant defense system of *Olea europaea* L. cv Chemlali exposed to cadmium stress. Ecotoxicol Environ Saf 128:195–205

Zu YG, Pang HH, Yu JH, Li DW, Wei XX, Gao YX, Tong L (2010) Responses in the morphology, physiology and biochemistry of *Taxus chinensis* var. mairei grown under supplementary UV-B radiation. J Photochem Photobiol 98(2):152–158

Chapter 18
Impact of UV Radiation on Photosynthetic Apparatus: Adaptive and Damaging Mechanisms

Anatoly Kosobryukhov, Alexandra Khudyakova, and Vladimir Kreslavski

Contents

Abstract Thickness reduction of stratospheric ozone layer is one of the environmental threats that leads to shared increase of UV-B radiation reaching the Earth's surface. Mechanisms of adaptation and damage of the photosynthetic apparatus (PA) in higher plants are considered in this review. Mn-containing water-oxidizing complex, D1 and D2 proteins, quinone molecules, disruption of thylakoid membrane integrity, and a number of Calvin cycle enzymes, first of all Rubisco, are the first targets of UV radiation. This review examines various mechanisms that can protect the PA against UV radiation. A shift of pro-/antioxidant balance towards antioxidants, synthesis of UV-absorbing pigments, and a number of other mechanisms are considered in this review. Reactive oxygen species, UVR8 protein, and photoreceptors such as phytochrome and cryptochrome are included in the UV-transduction chain. UV-induced inhibition of photosynthesis and growth

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processes together with the positive effects of UV manifesting in an enhancement of the biosynthesis of different pigments such as flavonoids and carotenoids and increasing stress resistance of the PA are also discussed.

Keywords UV radiation · Photosynthesis · Oxidative stress · Photosystem II · Pigments · Protection

Abbreviations

CPD	Cyclobutane pyrimidine dimers
DNA	Deoxyribonucleic acid
FRL	Far-red light
LHCII	Light-harvesting complex II
PA	Photosynthetic apparatus
PAR	Photosynthetically active radiation
PFR	Phytochrome active form
phyB	Phytochrome B
POL	Lipid peroxide oxidation
PSI	Photosystem I
PSII	Photosystem II
RL	Red light
ROS	Reactive oxygen species
UAPs	UV-absorbing pigments
WT	Wild type

18.1 Introduction

The wavelengths of UV radiation are in the range from 10 to 400 nm. However, solar radiation incident on the Earth contains only two wavelength ranges: UV-A (320–400 nm) and UV-B [280–320 (or 315) nm] (Strid et al. 1994). The shorter-wavelength UV quanta are absorbed by the ozone layer localized in the stratosphere and partly by atmospheric aerosols. As a result, UV irradiation reaching the Earth's surface begins from the wavelengths of 290–300 nm depending on the region, and the proportion of UV radiation composes approximately 7% from the total solar irradiation, reaching the Earth's surface (Caldwell 1981), but this value varies with ozone layer thickness (Qing et al. 2004). Herein approximately 95% of the UV radiation incident on the plants belongs to the UV-A region and only 5% refers to UV-B (White and Jahnke 2002).

It is known that for many plants, UV radiation in the range of 280–320 nm is a stress factor that can act nonlinearly. Even with a small decrease in the stratospheric ozone layer, it can be expected that a relatively strong biological effect of UV radiation will appear, which can lead to a change in species diversity, plant productivity, and metabolic orientation in the process of plant development. What do we have in reality? The surface level of UV-B radiation was really elevated during the period from 1979 to 2008 (Ballaré et al. 2011). Although it is hard to predict ozone variations in the future due to many factors affecting this process, currently, in some areas of the Earth, an enhancement of UV-B radiation is expected due to the ozone layer depletion and other atmospheric changes (Bais et al. 2015). Hence, predicted increase in UV-B irradiation can induce additional decline of photosynthetic activity and the productivity of higher plants, and it is necessary to study the effect of ultraviolet radiation on plant organisms, especially its interaction with other stress factors. However, there is also an opinion that most of the experiments that study the effect of UV radiation were carried out under conditions far from the actual doses and spectral composition of the light actually acting on the plants, so it is hard to expect that even a slight increase in the proportion of UV-B can actually noticeably increase the negative effect of UV-B on plants (Fiscus and Booker 1995).

Ecological and physiological studies are often conducted in order to determine how the typical and elevated intensity of UV radiation, and solar UV-B in particular, inhibits growth, development, biomass accumulation, and photosynthesis in plants (Mark and Tevini 1996) and to estimate how clipping UV radiation affects these parameters using UV-absorbing filters (Kadur et al. 2007; Klem et al. 2012; Kataria et al. 2013, 2014; Dehariya et al. 2011).

Solar UV radiation primarily affects the photomorphogenetic regulation system, and its exclusion leads to enhanced leaf growth and plant biomass and an increase in the plant photosynthesis rate, but little effect on the electron transport speed and activity of the photosystem II (PSII) (Kadur et al. 2007; Dehariya et al. 2011; Kataria et al. 2013, 2014). However, with the combined effect of other stress factors and the expected increase in UV-B dose (Bais et al. 2015), a noticeable effect of solar UV radiation on the primary photosynthesis processes is also possible (Kataria et al. 2014). With regard to carbon exchange, it can be assumed that the presence of UV radiation retards carbon sequestration in plants (Kadur et al. 2007). In many plant species, reduced photosynthesis rate and productivity are especially effective under the action of UV-B radiation (290–320 nm) (Teramura and Ziska 1996). UV-B radiation also induces different changes in plant metabolism (Schreiner et al. 2012), including the production of secondary metabolites, such as alkaloids and flavonoids, mostly involved in the plant defense system (Zhang and Björn 2009; Schreiner et al. 2012).

Along with a decrease in the activity of ribulose-1,5-bisphophate-carboxylase/oxygenase (Rubisco), a decrease may be due to a decrease in availability of CO_2, PSII activity, stomatal conductivity, reduction of photosynthetic and accessory pigments, and the expression of photosynthetic genes which are vulnerable to UV radiation (Teramura and Ziska 1996; Klem et al. 2012; Kataria et al. 2014; Kosobryukhov et al. 2015). The effect of UV radiation on various physiological parameters is described in detail in a number of papers (Teramura and Sullivan 1994; Jordan 1996; Teramura and Ziska 1996; Hollosy 2002; Dehariya et al. 2011; Klem et al. 2012; Schreiner et al. 2012; Kataria et al. 2013, 2014; Kosobryukhov et al. 2015).

All these effects are due to either the direct action of UV on the photosynthetic apparatus (PA), including a number of amino acids, proteins, enzymes, nucleic acids, unsaturated lipids, and others, or indirect effect by the generation of reactive oxygen species. For example, the action of UV radiation can change the activity of any enzymes themselves, as well as changes on the cell metabolism that affect the pattern and intensity of PA responses to stress (Lyubimov 2010). Investigation of UV radiation effect in model systems in the absence of light in the visible region is undoubtedly useful for studying targets of exposure to UV radiation. However, it should, if possible, be compared with the action of UV radiation under natural conditions, when visible light is present in different spectral ranges (Vass et al. 2005), which plays a protective role against the inhibitory action of UV radiation. The spectral ranges of red and blue radiation play a particularly important role in the adaptation to UV radiation and UV resistance of PA (Kreslavski et al. 2018a, b; Hoffmann et al. 2015).

The interaction of photosynthetically active radiation (PAR) (and its spectral ranges) with UV under different conditions is discussed in detail in a number of recent papers (Klem et al. 2012; Hoffmann et al. 2015; Kreslavski et al. 2018a, b). Here, the ability of one or another wavelength to restore the reduced activity of PSII as a result of the resynthesis of photosynthetic proteins, first the D1 protein, plays an important role (Vass et al. 2005; Zsiros et al. 2006).

However, note that authors of the majority of works investigated the impact of UV radiation on the PA activity for a long period of time, or plants were briefly irradiated but the irradiation was repeated for many days (Joshi et al. 1991; Lingakumar and Kulandaivelu 1993a, b; Biswal et al. 2003). These approaches are legitimate, and it is necessary to take into account the changes in plant characteristics during long-term variations in growth conditions into account. However, to dissect the mechanisms and pathways of plant adaptation to UV radiation, it is also of great importance to study the nature of plant responses to UV radiation for a short time, for example, a few hours or a few minutes (Kreslavski et al. 2013a, b; Khudyakova et al. 2017).

18.2 Effects of UV Radiation on Photosynthetic Processes

18.2.1 Impact of UV Radiation on Photosynthesis

There are several direct effects of UV-B on photosynthesis in sensitive plants (Kataria et al. 2014). They are: decline in Rubisco activity, damage of PSII, decrease in carbon dioxide fixation, and photosynthetic pigment degradation. Changes in leaf

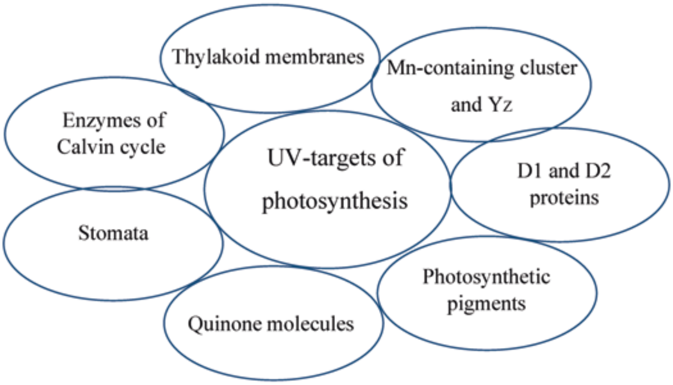

Fig. 18.1 Main targets in photosynthetic apparatus under UV radiation

thickness, stomatal closure, leaf anatomy, canopy morphology, and chloroplast arrangement can indirectly affect photosynthetic processes (Bornman and Vogelman 1991; Vass et al. 2005). Figure 18.1 illustrates the possible sites of UV radiation damaging effects.

Decrease in CO_2 assimilation rate plays an important role in stress-induced responses of photosynthetic apparatus lowering light-harvesting antenna size, disrupting thylakoid membrane integrity, and inactivating Calvin cycle enzymes, first Rubisco (Takeuchi et al. 2002). A number of works have also demonstrated that lowered CO_2 assimilation rate can cause changes in stomatal conductance under UV (Urban et al. 2006; Dennis et al. 2013). So, Dennis et al. (2013) studied the effect of solar ambient UV-B on stomatal density, conductance, and isotope discrimination in four field-grown soybean [*Glycine max* (L.) Merr.] isolines. It was shown that UV-B decreased stomatal density and conductance in isolines expressing a unique branched kaempferol triglycoside. Authors suggested that lowered stomatal density was linked to elevated season-long water-use efficiency and reduction of internal CO_2 concentration in leaves.

In the work (Schumaker et al. 1997), the authors examined the physiological and morphological reactions of rooted cuttings of *Populus trichocarpa* Torr. & Grey and *P. trichocarpa* × *P. deltoides* Bartr. ex Marsh., grown either in the presence of UV-B, the intensity of which was close to the intensity of solar UV-B (cellulose diacetate film, $I = 120.6$ mJ m^{-2} s^{-1}), or low UV-B radiation (polyester film, $I = 1.6$ mJ m^{-2} s^{-1}) during one growing season. The study demonstrated higher net photosynthesis, transpiration rate, and stomatal conductance in mature leaves exposed to low UV-B radiation level than in mature leaves exposed to UV-B radiation like the sun. However, changes in chlorophyll content and PSII activity were not observed. The authors concluded that the increase in net photosynthesis in response to the sub-ambient UV-B radiation treatment was partly a result of enhanced photosynthetic efficiency due to elevated amounts of palisade parenchyma cells in leaves.

Note that changes of photosynthesis depend on the strength of stress and on the parameter to which the data are related (Mark and Tevini 1996). Sunflower and maize plants were grown in climate-controlled growth chambers under solar radiation. Using UV-transmitting filters as covers, authors simulated a decrease in stratospheric ozone of about 12% based on ambient ozone levels in Lisbon. The photosynthetic rates of sunflower and maize plants based on leaf area showed higher or similar photosynthetic rates under enhanced UV-B radiation in comparison to the plants under normal UV-B radiation. However, photosynthetic rates on a plant basis were significantly decreased under enhanced UV-B radiation. The difference in the effect of enhanced UV radiation on photosynthetic rates calculated on various bases can be related to different leaf structures.

18.2.2 Impact of UV Radiation on Photosystem II

Between many cellular systems under environmental stress conditions, photosystem II is the most sensitive cellular element (Berry and Bjorkman 1980; Barber and Andersson 1992; Allakhverdiev et al. 2008). Especially, it is known that even moderate UV radiation can decrease PSII activity (Melis et al. 1992; Vass et al. 2005; Tyystjarvi 2008). PSII, stronger than photosystem I (PSI), is considered to be the most sensitive target of UV-B (Tyystjärvi and Vass 2000; Tyystjarvi 2008). PSII acceptor side components such as Q_A and Q_B, as well as D1 and D2 proteins, light harvesting complex II, the Mn_4CaO cluster, Y_Z, cyt *f*, and enzymes of the Calvin cycle, first of all Rubisco, seem to be the most susceptible to photodamage due to UV irradiation (Vass et al. 1996; Kolli et al. 1998; Rodrigues et al. 2006; Zsiros et al. 2006; Tyystjarvi 2008; Lidon et al. 2012; Hou and Hou 2013; Kataria et al. 2014). Especially, the Mn cluster of the water oxidation complex seems to be the most sensitive to UV radiation, and among all the components, it is the initial target of UV (Kataria et al. 2014). As a result, PA activities such as photosynthetic rate (P_n) and PSII quantum yields Y(II) and F_V/F_M are declined. However, the integrity of the thylakoid membrane and chloroplast structure seems to be more sensitive compared to the photosynthetic parameters (Lidon et al. 2012).

In the UV-B region, the quanta of light have high energy and can easily damage the target molecules. There is a number of papers that analyze the UV absorption spectra of the PSII components and intermediate products in the process of electron transport (Bensasson and Land 1973; Vass et al. 2005). The significant selective absorption of plastosemiquinones was found in the UV-B range (Vass et al. 2005). The maximum of the plastosemiquinone-9 anion minus plastoquinone-9 difference spectra in methanol solution was approximately 320 nm (Bensasson and Land 1973). However, probably it is necessary to discuss the modification of the Q_B-binding protein niche as it was also indicated by the lowered affinity of atrazine and DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea) to occupy the Q_B site in UV-irradiated thylakoids and cyanobacterial cells (Vass et al. 2005). The damaging effects of UV-B radiation on the redox function of Tyr-Z and Tyr-D are also indicated (Vass et al. 1996).

The Mn cluster is extremely sensitive to UV-B (Szilárd et al. 2007). However, the Mn cluster in higher S-states has relatively good UV-B absorption; UV-B-induced damage may result in UV-B-induced photolysis of peroxidic intermediates to highly damaging hydroxyl radicals produced within the Mn cluster. The following mechanism of UV-B damaging effect is suggested (Szilárd et al. 2007). Damage to the Mn cluster is sensitized by the S-state-dependent UV-B absorption. As a result, UV-B disrupts the Mn cluster structure and/or induces ROS production, in particular hydroxyl radicals and hydrogen peroxides.

Karpinski et al. (1997) reported that the inhibition of photosynthesis by UV-B radiation was accompanied with elevated H_2O_2 content and was linked to the damage and degradation of D1 and D2 proteins of the PSII reaction center.

It is suggested (Vass et al. 2005) that there is a following sequence of PSII events induced by UV radiation: the primary event of UV radiation effects is the impairment of the Mn cluster of the water-oxidizing complex. Then electron acceptors such as quinone and tyrosine donors are damaged. Eventually, D1 and D2 subunits of the reaction center are destroyed together with inhibition of photosynthesis and increase in elevated H_2O_2 (Karpinski et al. 1997). Note that the action spectrum of the degradation of D1 protein and the absorption spectrum of plastosemiquinones are similar (Jansen et al. 1996). Not only plastosemiquinones but also the Mn cluster and Y_Z in the PSII reaction center can be considered as possible UV-active chromophores, which are able to degrade D1 and D2 proteins (Babu et al. 1999; Vass et al. 2005).

Thus, PSII D1 and D2 proteins are the most vulnerable under UV-B; their degradation can occur when the UV-B intensity is equal to 1 μE m^{-2} s^{-1} (Jansen et al. 1996). However, the presence of visible light can decrease significantly the degradation of these proteins in vivo, since in intact cells and plants, the PSII damage is simultaneously repaired by de novo synthesis of the damaged components, first of all D1 and D2 proteins (Nishiyama et al. 2011). Here, D1 protein is quickly synthesized, and its turnover time is 30 min (Wilson and Greenberg 1993).

It is also suggested that inhibition of light-harvesting complex II (LHCII) at UV-B radiation (Lidon et al. 2012) is linked to a decrease of content of LHCII chlorophyll *a*/*b*-binding proteins, due to declining expression of the cab genes, coding the proteins. Obviously, the decrease of content of the proteins leads to the disconnection of LHCII main components from PSII (Jordan et al. 1994).

Note that the inhibition action of UV radiation on PSII is mainly demonstrated by irradiation of intact leaves and isolated chloroplasts or on plants using UV-B under conditions different from sunlight conditions, but it is suggested that UV-B-induced inhibition of PSII activity is not a spread primary effect on photosynthetic processes in native plants under field conditions (Nogues et al. 1998). However, under conditions other than physiological, for example, with multiple stress and/or with an increase in UV-B dose caused by a decrease in thickness of the ozone layer (McKenzie et al. 2011), the impact of solar UV-B on PSII activity can be noticeably manifested (Ziska et al. 1993). So, in cassava (*Manihot escuientum* Crantz) which were grown at field, a significant reduction in maximal quantum PSII yield ($F_V/F_{M)}$ and a subsequent enhancement of photoinhibition under elevated UV-B radiation were indicated if temperature or PAR was higher than 35 °C or 1800 μmol quanta m^{-2} s^{-1}, respectively (Ziska et al. 1993). Here, plants were grown at ambient solar radiation and ambient radiation plus an added UV-B radiation (5.5 kJ m^{-2} s^{-1}) for 95 days. The supplemental UV-B fluence, which was used in this experiment, simulated 15% depletion in stratospheric ozone at the region of the equator.

18.3 Protection Mechanisms of Photosynthetic Apparatus Under UV Radiation

The energy of light quanta related to the UV-B region of 280–315 nm is the highest in comparison with the emission quanta of other parts of the light spectrum incident on plants. UV-B easily damages most organic molecules, including proteins, lipids, chlorophyll, deoxyribonucleic acid (DNA), and others; in particular, it damages cell membranes through processes of lipid peroxide oxidation (POL) (Strid et al. 1994; Foyer and Noctor 2005; Schmitt et al. 2014). In phototrophic organisms, oxidative stress damages first of all chloroplasts and induces POL processes (Foyer et al. 1994; Schmitt et al. 2014) resulting in disruption of cellular processes (Nawkar et al. 2013). Therefore, to protect against UV stress, plants have formed a number of adaptation and regulatory mechanisms, including morphological changes, alterations in pigment composition, and photosynthesis (Strid et al. 1994; Schumaker et al. 1997; Sicora et al. 2003; Vass et al. 2005; Klem et al. 2012; Kataria et al. 2014; Kosobryukhov et al. 2015).

Note that plant responses to high intensity of UV-B radiation are mediated by various signal molecules, first of all H_2O_2 and products of POL (Hung et al. 2005; Schmitt et al. 2014), without involvement of specific photoreceptors (Frohnmeyer and Staiger 2003). After this, a specific signal chain induces expression of various genes leading to switching of adaptive reactions, including genes encoding antioxidant enzymes and photosynthetic proteins (Schmitt et al. 2014).

PA is one of the most sensitive to ultraviolet radiation cellular systems (Kataria et al. 2014; Kosobryukhov et al. 2015). Thermal dissipation of excess of absorbed light energy, alternative electron transport pathways, induction of chloroplast antioxidant systems, and repair of damaged PSII, taking place mainly by resynthesis of D1 and D2 proteins, are key protection mechanisms against oxidative stress (Niyogi 1999; Asada 2006; Kreslavski et al. 2007; Kataria et al. 2014).

Adaptation to UV radiation is also manifested through thermal dissipation of excess energy of absorbed light. In principle, such dissipation into heat is found in the reaction center of PSI and PSII and in the antennae (Kreslavski et al. 2007). Dissipation of excess light energy occurs via the proton gradient on the thylakoid membrane. This gradient is formed by cyclic electron flux in PSI, photorespiration, and O_2 reduction to the anion radicals that are disproportionated with the formation of H_2O_2.

The recovery of damaged PSII and nuclear and chloroplast DNA from UV-B-induced dysfunction of proteins and enzymes is also an important adaptive mechanism under UV stress. The resynthesis of D1 protein and the reassembly of repaired PSII centers are required for PSII recovery from a damage (Aro et al. 1993). Bergo et al. (2003) studied the role of visible light in the recovery of PSII from UV-B-induced stress. It was demonstrated that PSII recovery takes place only in white light and it is absent if the protein synthesis is blocked. Photoreceptors such as cryptochromes, phytochromes, and UVR8 can play a significant role in PA repair processes. We consider in detail the possible participation of the various light and photoreceptors in protection against UV radiation.

In addition, data available in literature lead to a conclusion that plant protection mechanisms are enough for PA adaptation to solar UV radiation. However, the impact of UV-B on PA can be significant under a majority of stress factors and is predicted to increase the UV-B fraction in the total solar radiation (Bais et al. 2015).

18.4 Visible Light Protection from UV Radiation: Role of Different Photoreceptors

Understanding the mechanisms of UV damage of molecular targets in plant cells, as well as the mechanisms of inhibition and poststress recovery of PA activity is required to clarify the ecophysiological role of UV radiation as an integral part of solar radiation (Strid et al. 1994; Vass et al. 2005; Lidon et al. 2012; Hideg and Strid 2017).

There is general agreement that PAR can alleviate some of the negative effects of enhanced UV-B radiation on plants (Sicora et al. 2003; Vass et al. 2005; Klem et al. 2012). It was found that high ratios of PAR to UV-B often decline UV-B damage in plants. Studies conducted under artificial conditions at low PAR, low UV-A, and high UV-B often show enhanced UV-B damage (Krizek 2004; Hoffmann et al. 2015). Therefore, spectral balance of PAR, UV-A, and UV-B plays an important role in UV plant sensitivity. In model experiments, it is also important to know if PAR affects the plants before irradiation (photoprotection), or PAR is switched after UV treatment (reactivation) (Han et al. 2001), or UV treatment is applied simultaneously with PAR.

It is shown that spectral balance between PAR, UV-A, and UV-B is an important factor for plant UV sensitivity in field studies (Krizek 2004). Given this dependence, they should be studied taking into account the action of each of these factors interacting with each other primarily through the corresponding photoreceptors (UVR8, phototropins, cryptochromes, and phytochromes) and the corresponding signaling systems (Kreslavski et al. 2009; Mishra and Khurana 2017). It is also necessary to take into account that a high level of UV radiation is usually combined with a high light intensity in the visible region, as well as with water deficiency or other adverse factors that can modify the negative effect of stress on photosynthetic activity (Caldwell et al. 2007).

18.4.1 Role of UVR8 Photoreceptor

It is known that the UVR8 protein is a photoreceptor absorbing UV-B radiation (Christie et al. 2012; Tilbrook et al. 2013). A role of UVR8 as a UV-B photoreceptor was evidenced and studied in detail by Jenkins (2014). Low levels of UV-B exposure induce signaling involving UVR8 and induce some UV-light-dependent genes participating in the protection against UV-induced stress (Brown and Jenkins 2008*;* Christie et al. 2012; Tilbrook et al. 2013), while higher dosages damage plants and their PA (Nawkar et al. 2013). In plant responses to UV-B, this photoreceptor interacts with the multifunctional RING E3 ubiquitin ligase COP1, which is an essential component of UV-B signaling (Favory et al. 2009). It participates in the degradation of the ubiquitin-proteasome system (Lau and Deng 2012) and ultimately affects gene expression, metabolism, and morphology (Hideg and Strid 2017). Hereby, overexpression of *UVR8* leads to increased UV-B photomorphogenesis, adaptation, and resistance to UV-B and, conversely, insufficient expression of *UVR8* and *COP1* increases sensitivity to UV-B. Apparently, the induction of UV-B-specific photoregulatory path is important for the survival of plants in sunlight.

18.4.2 Effects of UV Radiation and Blue Light: Role of Cryptochromes

The induction of a protection system can be induced not only by UV radiation, mainly, UV-A (Jenkins 2009), but also by visible light (Sicora et al. 2003; Bergo et al. 2003) in the blue (Häder et al. 2003; Hoffmann et al. 2015) and red (Khudyakova et al. 2017) spectral regions.

Blue light region is known to regulate many processes such as phototropism, photomorphogenesis, stomatal opening, and leaf photosynthesis (Banerjee and Batschauer 2005). Besides, it improves stress acclimation of plants (Hoffmann et al. 2015) and alleviates repair of DNA damage (Bergo et al. 2003).

It is known that DNA damage mainly occurs due to the formation of cyclobutane pyrimidine dimers (CPD) produced by dimerization of adjacent pyrimidines, and CPD can represent 75% of total DNA damage (Hollosy 2002). Blue light stimulates the production of photolyases involved in the repair of UV-B-induced CPD of DNA formed under UV-B (Bergo et al. 2003; Ballaré et al. 2011).

High-intensity blue light alleviates acclimation and promotes photosynthetic recovery in pepper plants exposed to UV radiation (Hoffmann et al. 2015). Thus, it was shown that a high dose of blue light induces biochemical and physiological processes linked to stress protection which improves plant acclimation and alleviates the recovery of PA in response to UV stress. The research demonstrated that UV-irradiated pepper plants grown either at light of high intensity (PAR = 300 μE m^{-2} s^{-1}) or at blue light of high intensity (62%) showed elevated photosynthetic rate P_n, higher maximal photochemical PSII yield, and lowered non-photochemical quenching than UV-stressed plants cultivated under light at lesser white (PAR = 100 μE m^{-2} s^{-1}) or blue (30%) light intensity.

In the last years, some studies concerning the role of cryptochromes in regulating abiotic plant stress responses appeared (Ohgishi et al. 2004; Mishra and Khurana 2017). Blue light conditions transform cryptochromes in active state and they can activate a number of blue-light-inducible photosynthetic genes regulated by cryptochromes, especially genes encoding enzymes of the Calvin cycle and D2 protein (gene *psbD*) (Ohgishi et al. 2004).

18.4.3 Impact of UV Radiation and Red Light: Role of Phytochromes

There are many data on the protective action of RL irradiation in PA responses to UV radiation (Joshi et al. 1991; Lingakumar and Kulandaivelu 1993a, b; Biswal et al. 1997; Khudyakova et al. 2017; Kreslavski et al. 2004, 2016, 2018a). The studies suggest that RL-induced production of phytochrome active form (P_{FR}) and elevated content of phytochrome B (PhyB) are involved in the stress-protective action of RL (Kreslavski et al. 2018a). Activation of Phy induces various protective mechanisms, which lead to diminishing of the UV-induced oxidative stress and, consequently, mitigate chlorophyll degradation, the decline of PSII activity, and the distortion of thylakoid membrane integrity (Biswal et al. 2003; Khudyakova et al. 2017; Kreslavski et al. 2018a, b).

RL can be used in different combinations with UV irradiation and photoperiod. For instance, Lingakumar and Kulandaivelu (1993a) examined the effects of UV-B on PSII activity in cotyledon leaves of the *Vigna sinensis* irradiated at the middle of the photoperiod and indicated that short-term RL (λ_m = 612 nm) protected the PSII activity likely due to induction of formation of PhyB active form due to RL irradiation.

Preillumination of the *A. thaliana* plants with RL (λ_m = 664 nm) promoting the formation of P_{FR} decreased the inhibitory action of UV-A radiation on photosynthesis (Fig. 18.2) and PSII activity (Kreslavski et al. 2013b) and declined H_2O_2 content, but elevated the peroxidase activity in *A. thaliana* leaves compared with irradiation of plants with UV radiation only (Kreslavski et al. 2012, 2013a, 2016). Preillumination of leaves with RL (max = 620–660 nm) after dark period alleviated the UV-A inhibitory action on PSII activity and reduced the pigment losses but increased the peroxidase activity in leaves and thylakoid membrane preparations, as compared to the respective effects of UV-A light applied without preillumination

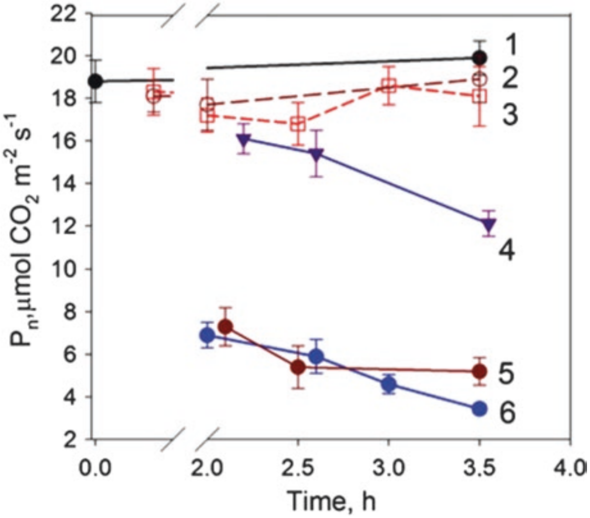

Fig. 18.2 Impact of various light illumination schemes: red light (RL) (3), far-red light (FRL) (2), UV-A (6), and short-time preillumination with red light (4) or RL/FRL (5) on the photosynthetic rate (P_n) in *A. thaliana* plants, placed in the dark after they were irradiated for 0, 0.5, and 1.5 h (1). The far-red light (λ_{max}—730 nm, 2 W m^{-2} s^{-1}). UV irradiation (365 nm, 8 W m^{-2}), $n = 3$. From Kreslavski et al. (2013a) with modifications

(Kreslavskii et al. 2012). The formation of P_{FR} also leads to less chlorophyll and carotenoid degradation and contributes to the maintenance of the chloroplast structure and activity in the process of leaf aging (Joshi et al. 1991; Biswal et al. 2003). Partial or complete reversibility of observed effects of RL with the following illumination of plants with far-red light (FRL) was shown, suggesting the participation of PhyB in these processes (Kreslavski et al. 2018a).

In a number of studies, the effects of short-term RL leading to activation of the phytochrome system on oxidant-antioxidant balance were investigated. For example, Sharma et al. (1976) demonstrated phytochrome-regulated peroxidase activity in maize. In leaves of *A. thaliana*, phytochrome regulation of the content of UV-absorbing pigments (UAPs) was indicated (Kreslavski et al. 2013b). In lettuce leaves, RL preillumination increased the total peroxidase activity (Kreslavskii et al. 2012) and the content of UAPs.

In other series of works, the role of phytochromes in the protection of PA from UV-induced damage was studied using phytochrome mutants and superproducers of PhyB (Kreslavski et al. 2013a, 2015, 2018a; Khudyakova et al. 2017).

The impact of elevated PhyB content on the resistance of photosynthesis to UV-B was studied by superproducers of PhyB—transgenic potato plants (Dara-12 and Dara-5) (Kreslavski et al. 2015). These transgenic plants showed the elevated resistance of photosynthesis in response to UV-B (Fig. 18.3). Conversely, deficit of phytochromes led to declined UV-B resistance of PSII (Figs. 18.4 and 18.5). Thus, in *phyAphyB A. thaliana* mutants grown under white light, the inhibition effect of PSII activity was slightly bigger than in wild type (WT) (Fig. 18.4). Growing *A. thaliana* mutants under RL led to significant vulnerability to UV-B (Fig. 18.5). It is suggested that this effect is associated with the absence of cryptochrome activity in such plants (Khudyakova et al. 2017).

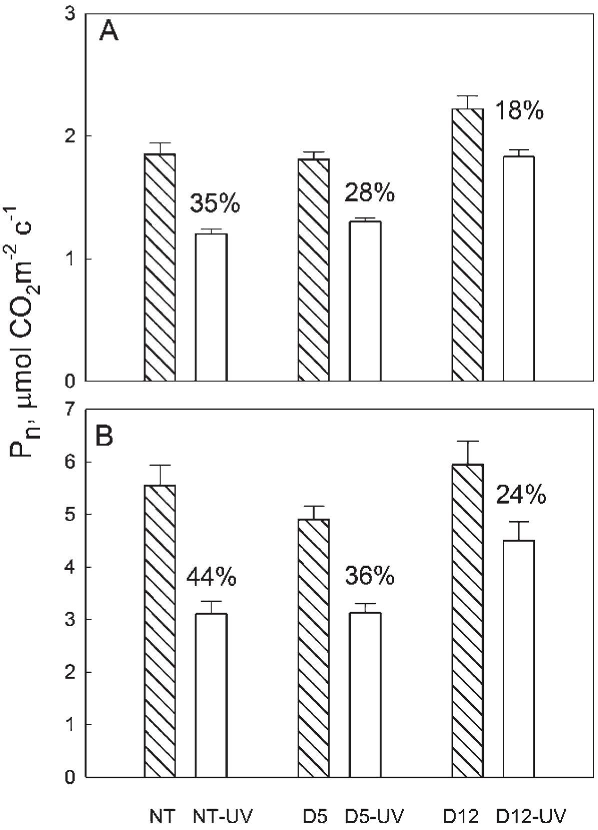

Fig. 18.3 The impact of UV-B irradiation (45 min) on the photosynthetic rate in transgenic potato plants—superproducers of phytochrome B (D-5 and D-12) and non-transformed plants (NT). A, plants for analysis were taken immediately after growing on an agar medium; B, after 55 days of growing plants in the greenhouse. Above the bars, the percentage of photosynthesis rate (ΔPn) after UV-B irradiation is reflected. The difference between the options is significant when $p < 0.05$ ($n = 3$). From Kreslavski et al. (2015), with modifications

In our opinion, elevated resistance of the PA to UV-A radiation was formed with the involvement of P_{FR} production and the antioxidant system, especially the content of UV-absorbing pigments (UAPs) induced by oxidative stress after preillumination of plants with RL (Kreslavski et al. 2018a). Elevated content of P_{FR} alleviates the UV-induced oxidative stress and, consequently, declines a damage of PSII, the distortion in thylakoid membrane integrity, and decrease in Rubisco activity (Takeuchi et al. 2002; Biswal et al. 2003; Kreslavskii et al. 2012, 2018a). However, such mechanism can work under conditions when the content of P_{FR} is initially relatively low.

Induction of an antioxidant system by UV radiation can be implemented by the activation of antioxidant enzymes and formation of low-molecular-weight antioxidants, which can also act as UV-absorbing filter and antioxidants, simultaneously (Niyogi 1999; Asada 2006; Kreslavski et al. 2012, 2018a). In PA protection against

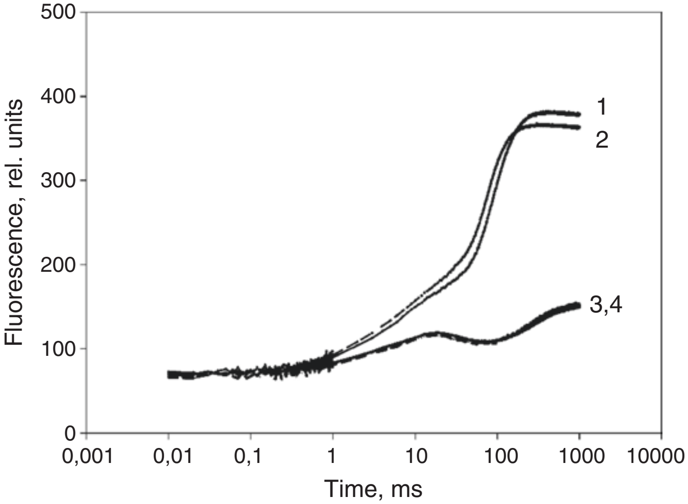

Fig. 18.4 Chl *a* fluorescence induction curves of *A. thaliana* wild type (1,2) and phyA phyB double mutant (3,4) before (1,3) and after (2,4) irradiation with UV-B. Typical curves are shown ($n = 7$). From Khudyakova et al. (2017) with modification

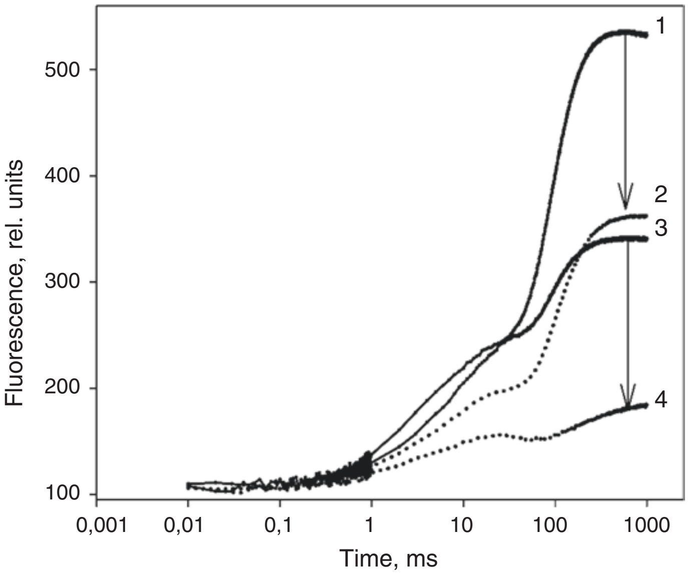

Fig. 18.5 Chl *a* fluorescence induction curves of *A. thaliana* wild type (1,2) and phyA phyB double mutant (3,4) before (1,3) and after (2,4) exposure of plants to UV-B. Arrows show decline of fluorescence in WT and mutant. Plants were grown at the red light. From Khudyakova et al. (2017) with modification

UV, such effects were found for flavonoids, carotenoids, alkaloids, and some other pigments (Klem et al. 2012; Solovchenko and Merzlyak 2008). Note that some of the UV-shielding compounds absorb both in the UV and visible regions (Krins et al. 2010). Consequently, they can be generated by PAR and reduce a damage of the PA as a result of the UV-induced stress. Among such compounds, hydroxycinnamic acid esters and flavonoids have high absorbance in the UV range and, besides, they are localized mainly in the epidermal layers; therefore, they play an important role in the protection from UV radiation (Bharti and Khurana 1997).

18.4.4 Role of UV-Protective Substances, Phenolic Compounds, and Carotenoids in Protection Against UV

In higher plants, epidermal tissues contain phenolic compounds and chloroplasts comprise carotenoids. This optical filter is one of the most important defense mechanisms (Solovchenko and Merzlyak 2008; Götz et al. 2010; Klem et al. 2012; Schreiner et al. 2012; Saewan and Jimtaisong 2013). These and other compounds, for example, alkaloids, are usually induced under UV radiation and act as a sunscreen, decreasing the penetration of UV-B into the leaf volume (Solovchenko and Schmitz-Eiberger 2003; Solovchenko and Merzlyak 2008; Klem et al. 2012; Barnes et al. 2016).

Just the epidermal layer of leaves, where the main content of flavonoids is located, can play an especially protective role from UV radiation (Tevini et al. 1991). Thus, *A. thaliana* mutants having defects in the general phenylpropanoid pathway and therefore lowered UAP content in the epidermis showed higher sensitivity to UV-B compared with the wild type (Bharti and Khurana 1997; Chapple et al. 1992; Li et al. 1993).

Moreover, some flavonoids function as antioxidants (Husain et al. 1987; Li et al. 1993) which can repair or protect PA from UV-B damage. Murali and Teramura (1986) reported that a different sensitivity to UV-B in cucumber seedlings is due to quantitative and qualitative difference in flavonoid content. It is suggested that UV radiation affects the content of flavonoids by activating the main enzymes of the phenylpropanoid pathway, most importantly, phenylalanine ammonia-lyase (*PAL* gene) and chalcone synthase (*CHS* gene) (Bharti and Khurana 1997; Solovchenko and Merzlyak 2008). Here, it is indicated that a network of photoreceptor phototransduction pathways including phytochromes, cryptochromes, and UV-B photoreceptor participates in the control of chalcone synthase gene expression (Wade et al. 2001).

The presence of PAR usually has a positive influence on the accumulation of UAPs in leaves. So, PAR supplementary treatment induced photoprotective mechanisms, which partially alleviate the negative effect of UV on the photochemical activity and carbon assimilation in plant acclimation to UV radiation in two barley varieties (Barke, Bonus) grown at field conditions (Klem et al. 2012). It was also shown that the PAR treatment triggered the flavonol accumulation, preferably in young leaves. It is shown that in some plants, like parsley and mustard, phytochrome is likely involved in the induction of flavonoid genes (56–58). RL acting through PhyB can regulate the content of UAPs (Kreslavski et al. 2018a). For example, short-term RL irradiation increased the content of UAPs in lettuce leaves (Kreslavski et al. 2013b). Gerhardt et al. (2008) demonstrated that an increase in the spectrum of far-red light led to a suppression of UV-B-mediated induction of flavonoids in far-red light pre-irradiated *B. napus* plants. These authors also reported on higher contents of kaempferol glycosides and lowered levels of quercetin glucosides in the presence of supplemental UV-B and moderate intensities of far-red light. With a low PAR, a protective effect of UV-A against UV-B was also detected (Jenkins 2009).

Carotenoids are included in the antioxidant protection against high-intensity light and UV-B irradiation (Solovchenko and Merzlyak 2008). In particular, carotenoids protect PA from excess blue light and UV-A, for example, by shielding light-harvesting complexes due to absorption of wavelengths up to 500 nm (Shaish et al. 1993; White and Jahnke 2002).

18.5 The Interaction of UV-B and Other Stress Factors

In addition, the impact of UV radiation depends significantly on the presence of other environmental factors, primarily environmental stressors (Ballaré et al. 2011), which can enhance a damage likely by inhibition of the recovery of the photosynthetic apparatus in case of UV-B stress (Vass et al. 2005). On the other hand, the negative effects of UV-B can be weakened under the joint action of UV radiation and other stress factors (Teklemariam and Blake 2004; Vass et al. 2005; Caldwell et al. 2007). The alleviation might be explained by antioxidant enzyme system enhancement, synthesis of low-molecular-weight antioxidants like phenolic compounds and carotenoids which serve also as UV-B-absorbing filter (Solovchenko and Merzlyak 2008; Barnes et al. 2016). In addition, changes in protein composition, leaf geometry, and stomatal resistance induced with another stress can decrease PA damage under UV irradiation.

For example, tropical legumes, *Vigna unguiculata*, were irradiated with elevated UV-B doses only or combined with stress induced by UV-B and higher temperatures. Damage was less if the plants were exposed to both stress factors. Heat stress ameliorating effect was explained with the heat-induced biosynthesis of “heat shock” proteins (Nedunchezhian and Kulandaivelu 1996). Freezing tolerance of jack pine was studied in growth chambers with and without low, ambient levels of UV-B radiation (Teklemariam and Blake 2004). It was shown that freezing tolerance increased by UV-B radiation and this increase was linked to induction of phenolics in plant tissues. Drought was demonstrated to ameliorate the PA damage likely by induction of antioxidant enzyme systems (Hideg et al. 2003).

18.6 Conclusion

Further research will be required to understand enough complex interaction of UV radiation and other stressful factors, such as elevated and lowered temperature and drought, as well as the interaction of UV with visible light, which influences the protection and recovery systems under conditions of predicted UV-B levels and other stressors. It is also important to find out a link between UV signaling system involved in the transduction of UV signal to cells and photosynthetic response. In addition, it is important to determine a system of genes sensitive to UV radiation and at the same time participating in photosynthetic regulation.

References

Allakhverdiev SI, Kreslavski VD, Klimov VV, Los DA, Carpentier R, Mohanty P (2008) Heat stress: an overview of molecular responses in photosynthesis. Photosynth Res 98:541–550

Aro E-M, Virgin I, Andersson B (1993) Photoinhibition of photosystem II: inactivation, protein damage and turnover. Biochim Biophys Acta Bioenerg 1143:113–134

Asada K (2006) Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol 141(2):391–396

Babu TS, Jansen MAK, Greenberg BM, Gaba V, Malkin S, Mattoo AK, Edelman M (1999) Amplified degradation of photosystem II D1 and D2 proteins under a mixture of photosynthetically active radiation and UV-B radiation: dependence on redox status of photosystem II. Photochem Photobiol 69:553–559

Bais AF, McKenzie RL, Bernhard G, Aucamp PJ, Ilyas M, Madronich S, Tourpali K (2015) Ozone depletion and climate change: impacts on UV-radiation. Photochem Photobiol Sci 14:19–52

Ballaré CL, Caldwell MM, Flint SD, Robinson A, Bornman JF (2011) Effects of solar ultraviolet radiation on terrestrial ecosystems. Patterns, mechanisms, and interactions with climate change. Photochem Photobiol Sci 10:226–241

Banerjee R, Batschauer A (2005) Plant blue-light receptors. Planta 220:498–502

Barber J, Andersson B (1992) Too much of a good thing: light can be bad for photosynthesis. Trends Biochem Sci 17(2):61–66

Barnes PW, Tobler MA, Keefover-Ring K, Flint SD, Barkley AE, Ryel RJ, Lindroth RL (2016) Rapid modulation of ultraviolet shielding in plants is influenced by solar ultraviolet radiation and linked to alterations in flavonoids. Plant Cell Environ 39:222–230

Bensasson R, Land EJ (1973) Optical and kinetic properties of semireduced plastoquinone and ubiquinone: electron acceptors in photosynthesis. Biochim Biophys Acta Bioenerg 325:175–181

Bergo E, Segalla A, Giacometti GM, Tarantino D, Soave C, Andreucci F, Barbato R (2003) Role of visible light in the recovery of photosystem II structure and function from ultraviolet-B stress in higher plants. J Exp Bot 54(388):1665–1673

Berry JA, Bjorkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. Annu Rev Plant Physiol 31:491–543

Bharti AK, Khurana JP (1997) Mutants of *Arabidopsis* as tools to understand the regulation of phenylpropanoid pathway and UV-B protection mechanisms. Photochem Photobiol 65:765–776

Biswal B, Joshi PN, Kulandaivelu G (1997) Changes in leaf protein and pigment contents and photosynthetic activities during senescence of detached maize leaves—influence of different ultraviolet radiations. Photosynthetica 34:37–44

Biswal BM, Zakaria A, Ahmad NM (2003) Topical application of honey in the management of radiation mucositis. A preliminary study. Support Care Cancer 11:242–248

Bornman JF, Vogelman TC (1991) The effect of UV-B radiation on leaf optical properties measured with fiber optics. J Exp Bot 42:547–554

Brown BA, Jenkins GI (2008) UV-B signaling pathways with different fluence-rate response profiles are distinguished in mature Arabidopsis leaf tissue by requirement for UVR8, HY5, and HYH. Plant Physiol 146(2):576–588

Caldwell MM (1981) Plant response to solar ultraviolet radiation. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology I. Encyclopedia of plant physiology. New series. Springer, Berlin, pp 169–167

Caldwell MM, Bornman JF, Ballare CL, Flint SD, Kulandaivelu G (2007) Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. Photochem Photobiol Sci 6:252–266

Chapple CC, Vogt T, Ellis BE, Sommerville CR (1992) An Arabidopsis mutant defective in the general phenylpropanoid pathway. Plant Cell 4:1413–1424

Christie JM, Arvai AS, Baxter KJ, Heilmann M, Pratt AJ, O'Hara A, Kelly SM, Hothorn M, Smith BO, Hitomi K, Jenkins GI, Getzoff ED (2012) Plant UVR8 photoreceptor senses UV-B by tryptophan-mediated disruption of cross-dimer salt bridges. Science 335:1492–1496

Dehariya P, Kataria S, Pandey GP, Guruprasad KN (2011) Assessment of impact of solar UV components on growth and antioxidant enzyme activity in cotton plant. Physiol Mol Biol Plants 17(3):223–229

Dennis C, Gitz I, Steven J, Britz JH, Sullivan JH (2013) Effect of ambient UV-B on stomatal density, conductance and isotope discrimination in four field grown Soybean [*Glycine max* (L.) Merr.] isolines. Am J Plant Sci 4:100–108

Favory JJ, Stec A, Gruber H, Rizzini L, Oravecz A, Funk M, Albert A, Cloix C, Jenkins GI, Oakeley EJ, Seidlitz HK, Nagy F, Ulm R (2009) Interaction of COP1 and UVR8 regulates UV-B-induced photomorphogenesis and stress acclimation in Arabidopsis. EMBO J 28(5):591–601

Fiscus EL, Booker FL (1995) Is increased UV-B a threat to crop photosynthesis and productivity? Photosynth Res 43:81–92

Foyer CH, Noctor G (2005) Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant Cell Environ 28:1056–1071

Foyer CH, Noctor G, Lelandais M, Lescure JC, Valadier MH, Boutin JP, Horton P (1994) Short-term effects of nitrate, nitrite and ammonium assimilation on photosynthesis, carbon partitioning and protein phosphorylation in maize. Planta 192:211–220

Frohnmeyer H, Staiger D (2003) Ultraviolet-B radiation-mediated responses in plants. Balancing damage and protection. Plant Physiol 133:1420–1428

Gerhardt KE, Lampi MA, Greenberg BM (2008) The effects of far-red light on plant growth and flavonoid accumulation in Brassica napus in the presence of ultraviolet B radiation. Photochem Photobiol 84:1445–1454

Götz M, Albert A, Stich S, Heller W, Scherb H, Krins A, Langebartels C, Seidlitz HK, Ernst D (2010) PAR modulation of the UV-dependent levels of flavonoid metabolites in *Arabidopsis thaliana* (L.) Heynh. leaf rosettes: cumulative effects after a whole vegetative growth period. Protoplasma 243:95–103

Häder DP, Kumar HD, Smith RC, Worrest RC (2003) Aquatic ecosystems: effects of solar ultraviolet radiation and interactions with other climatic change factors. Photochem Photobiol Sci 2:39–50

Han T, Sinha RP, Häder DP (2001) UV-A/blue light-induced reactivation of photosynthesis in UV-B irradiated cyanobacterium, *Anabaena* sp. J Plant Physiol 158:1403–1413

Hideg É, Strid Å (2017) The effects of UV-B on the biochemistry and metabolism of plants. In: Jordan BR (ed) UV-B radiation and plant life: molecular biology to ecology. CABI, Wallingford, pp 90–110

Hideg E, Nagy A, Oberschall A, Dudits D, Vass I (2003) Detoxification function of aldose/aldehyde reductase during drought and ultraviolet-B (280–320 nm) stresses. Plant Cell Environ 26:513–522

Hoffmann AM, Noga G, Hunsche M (2015) High blue light improves acclimation and photosynthetic recovery of pepper plants exposed to UV stress. Environ Exp Bot 109:254–263

Hollosy F (2002) Effect of ultraviolet radiation on plant cells. Micron 33:179–197

Hou X, Hou HJM (2013) Roles of manganese in photosystem II dynamics to irradiations and temperatures. Front Biol 8(3):312–322

Hung S-H, Yu C-W, Lin CH (2005) Hydrogen peroxide functions as a stress signal in plants. Bot Bull Acad Sin 46:1–10

Husain SR, Cillard J, Cillard P (1987) Hydroxyl radical scavenging activity of flavonoids. Phytochemistry 26:2489–2491

Jansen RP, Dowser C, Michaelis C, Galova M, Nasmyth K (1996) Mother cell-specific HO expression in budding yeast depends on the unconventional myosin and other cytoplasmic proteins. Cell 84:687–697

Jenkins GI (2009) Signal transduction in responses to UV-B radiation. Annu Rev Plant Biol 60:407–431

Jenkins GI (2014) The UV-B photoreceptor UVR8: from structure to physiology. Plant Cell 26:21–37

Jordan BR (1996) The effects of ultraviolet-B radiation on plants: a molecular perspective. Adv Bot Res 22:97–162

Jordan BR, James PE, Strid A, Anthony RG (1994) The effect of ultraviolet-B radiation on gene-expression and pigment composition in etiolated and green pea leaf tissue: UV-B-induced changes are gene-specific and dependent upon the developmental stage. Plant Cell Environ 17:45–54

Joshi AK, Vijay-Shanker K, Weir D (1991) The convergence of mildly context-sensitive grammatical formalisms. In: Sells P, Shieber S, Wasow T (eds) Foundational issues in natural language processing. MIT Press, Cambridge, MA

Kadur G, Swapan B, Kataria S, Sanjeev Y, Arjun T, Sanjay B, Abhinav R, Mohanty P (2007) Growth enhancement of soybean (*Glycine max*) upon exclusion of UV-B and UV-B/A components of solar radiation: characterization of photosynthetic parameters in leaves. Photosynth Res 94:299–306

Karpinski S, Escobar C, Karpinski B, Creissen G, Mullineaux P (1997) Photosynthetic electron transport regulates the expression of cytosolic ascorbate peroxidase genes in Arabidopsis during excess light stress. Plant Cell 9:627–640

Kataria S, Guruprasad KN, Ahuja S, Singh B (2013) Enhancement of growth, photosynthetic performance and yield by exclusion of ambient UV components in C3 and C4 plants. J Photochem Photobiol B 127:140–152

Kataria S, Jajoo A, Guruprasad KN (2014) Impact of increasing Ultraviolet-B (UV-B) radiation on photosynthetic processes. J Photochem Photobiol B 137:55–66

Khudyakova AY, Kreslavski VD, Shirshikova GN, Zharmukhamedov SK, Kosobryukhov AA, Allakhverdiev SI (2017) Resistance of *Arabidopsis thaliana* L. photosynthetic apparatus to UV-B is reduced by deficit of phytochromes B and A. J Photochem Photobiol B 169:41–46

Klem K, Aˇc A, Holub P, Kováˇc D, ˇSpunda V, Robson TM, Urban O (2012) Interactive effects of PAR and UV-radiation on the physiology, morphology and leaf optical properties of two barley varieties. Environ Exp Bot 75:52–64

Kobzar' EF, Kreslavski VD, Muzafarov E (1998) Photomorphogenetic responses to UV-radiation and short-time red light in lettuce seedlings. Plant Growth Regul 26:73–76

Kolli BK, Tiwari S, Mohanty P (1998) Ultraviolet-B induced damage to photosystem II in intact filaments of *Spirulina platensis*. Z Naturforsch 53:369–377

Kosobryukhov AA, Lyubimov VY, Kreslavski VD (2015) Adaptive mechanisms of photosynthetic apparatus to UV-radiation. In: Stress responses in plants. Mechanisms of toxicity and tolerance. Springer, Berlin, pp 59–78

Kreslavski VD, Ivanov AA, Kosobryukhov AA (2004) Low energy light in the 620–660 nm range reduces the UV-B-induced damage to photosystem II in spinach leaves. Biofizika (Russian) 49:767–771

Kreslavski VD, Carpentier R, Klimov VV, Murata N, Allakhverdiev SI (2007) Molecular mechanisms of stress resistance of the photosynthetic apparatus. Biochemistry 1(3):185–205

Kreslavski VD, Carpentier R, Klimov VV, Allakhverdiev SI (2009) Transduction mechanisms of photoreceptor signals in plant cells (review). J Photochem Photobiol C: Photochem Rev 10:63–80

Kreslavski VD, Khristin MS, Shabnova NI, Lyubimov VY (2012) Preillumination of excised spinach leaves with red light increases the resistance of photosynthetic apparatus to UV-radiation. Russ J Plant Physiol 59:719–737

Kreslavski VD, Shirshikova GN, Lyubimov VY, Shmarev AN, Boutanaev AM, Kosobryukhov AA, Schmitt F-J, Friedrich T, Allakhverdiev SI (2013a) Effect of preillumination with red light on photosynthetic parameters and oxidant-/antioxidant balance in *Arabidopsis thaliana* in response to UV-A. J Photochem Photobiol B 127:229–236

Kreslavski VD, Lyubimov VY, Schirshikova GN, Shmarev AN, Kosobryukhov AA, Schmitt FJ, Friedrich T, Allakhverdiev SI (2013b) Preillumination of lettuce seedlings with red light enhances the resistance of photosynthetic apparatus to UV-A. J Photochem Photobiol B 122:1–6

Kreslavski VD, Kosobryukhov AA, Shmarev AN, Aksenova NP, Konstantinova TN, Golyanovskaya SA, Romanov GA (2015) Introduction of the Arabidopsis *PHYB* gene increases resistance of photosynthetic apparatus in transgenic *Solanum tuberosum* plants to UV-B radiation. Russ J Plant Physiol 62:204–209

Kreslavski VD, Schmitt FJ, Keuer C, Friedrich T, Schirshikova GN, Zharmukhamedov SK, Kosobryukhov AA, Allakhverdiev SI (2016) Response of the photosynthetic apparatus to UV-A and red light in the phytochrome B-deficient *Arabidopsis thaliana* L. hy3 mutant. Photosynthetica 54:321–330

Kreslavski VD, Los DA, Schmitt FJ, Zharmukhamedov SK, Kuznetsov VV, Allakhverdiev SI (2018a) The impact of the phytochromes on photosynthetic processes. Biochim Biophys Acta Bioenerg 1859:400–408

Kreslavski VD, Shmarev AN, Lyubimov VY, Semenova GA, Zharmukhamedov SK, Schirshikova GN, Khudyakova AY, Allakhverdiev SI (2018b) Response of photosynthetic apparatus in *Arabidopsis thaliana* L. mutant deficient in phytochrome A and B to UV-B. Photosynthetica 56:418–426

Krins A, Langebartels C, Seidlitz HK, Ernst D (2010) PAR modulation of the UV-dependent levels of flavonoid metabolites in *Arabidopsis thaliana* (L.) Heynh. leaf rosettes: cumulative effects after a whole vegetative growth period. Protoplasma 243:95–103

Krizek DT (2004) Influence of PAR and UV-A in determining plant sensitivity and photomorphogenic responses to UV-B radiation. Photochem Photobiol 79(4):307–315

Lau OS, Deng LXW (2012) The photomorphogenic repressors COP1 and DET1: 20 years later. Trends Plant Sci 17(10):584–593

Li J, Ou-Lee TM, Raba R, Amundson RG, Last RL (1993) Arabidopsis flavonoid mutants are hypersensitive to UV-B radiation. Plant Cell 5:171–178

Lidon FC, Teixeira M, Ramalho JC (2012) Decay of the chloroplast pool of ascorbate switches on the oxidative burst in UV-B irradiated rice. J Agron Crop Sci 198:130–144

Lingakumar K, Kulandaivelu G (1993a) Regulatory role of phytochrome on ultraviolet B (280–315 nm) induced changes in growth and photosynthetic activities of *Vigna sinensis* L. Photosynthetica 29:341–351

Lingakumar K, Kulandaivelu G (1993b) Changes induced by ultraviolet-b radiation in vegetative growth, foliar characteristics and photosynthetic activities in *Vigna unguiculata*. Aust J Plant Physiol 20:299–308

Lyubimov V (2010) Stress reaction on primary carboxylases of C3 and C4 plants after short-term UV-B irradiation of whole leaves. In: XVIII congress of the federation of European societies of plant biology, Valencia, Spain, 4–9 July 2010

Mark U, Tevini M (1996) Combination effects of UV-B radiation and temperature on sunflower (*Helianthus annuus* L, cv Polstar) and maize (*Zea mays* L, cv Zenit 2000) seedlings. J Plant Physiol 148(1–2):49–56

McKenzie RL, Aucamp PJ, Bais AF, Björn LO, Ilyas M, Madronich S (2011) Ozone depletion and climate change: impacts on UV radiation. Photochem Photobiol Sci 10:182–198

Melis A, Nemson JA, Harrison MA (1992) Damage to functional components and partial degradation of PS II reaction centre protein upon chloroplast exposure to ultraviolet-B radiation. Biochim Biophys Acta Bioenerg 1109:313–320

Mishra S, Khurana JP (2017) Emerging roles and new paradigms in signaling mechanisms of plant cryptochromes. Crit Rev Plant Sci 36:89–115

Murali NS, Teramura AH (1986) Intraspecific differences in *Cucumis sativus* sensitivity to ultraviolet-B radiation. Physiol Plant 68:673–677

Nawkar GM, Maibam P, Park JH, Sahi VP, Lee SY, Kang CH (2013) UV-induced cell death in plants. Int J Mol Sci 14:1608–1628

Nedunchezhian N, Kulandaivelu G (1996) Effects of ultraviolet-B enhanced radiation and temperature on growth and photochemical activities in *Vigna unguiculata*. Biol Plant 38(2):205–214

Nishiyama Y, Allakhverdiev SI, Murata N (2011) Protein synthesis is the primary target of reactive oxygen species in the photoinhibition of photosystem II. Physiol Plant 142:35–46

Niyogi KK (1999) Photoprotection revisited: genetic and molecular approaches. Annu Rev Plant Physiol Plant Mol Biol 50:333–359

Nogues S, Allen DJ, Morison JIL, Baker NR (1998) Ultraviolet-B radiation effects on water relations, leaf development, and photosynthesis in droughted pea plants. Plant Physiol 117(1):173–181

Ohgishi M, Sajit K, Okada K, Saka T (2004) Functional analysis of each blue light receptor, cryl, cry2, photi, and phot2, by using combinatorial multiple mutants in Arabidopsis. Proc Natl Acad Sci U S A 101(8):2223–2228

Qing L, Callaghan TV, Yuanyuan Z (2004) Effects of elevated solar UV-B radiation from ozone depletion on terrestrial ecosystems. J Mt Sci 1:276–288

Rodrigues GC, Jansen MAK, Van den Noort ME, Van Rensen JJS (2006) Evidence for the semireduced primary quinone electron acceptor of photosystem II being a photosensitizer for UVB damage to the photosynthetic apparatus. Plant Sci 170:283–290

Saewan N, Jimtaisong A (2013) Protection of natural flavonoids. J Appl Pharm Sci 3(09):129–141

Schmitt F-J, Renger G, Friedrich T, Kreslavski VD, Zharmukhamedov SK, Los DA, Kuznetsov VV, Allakhverdiev SI (2014) Reactive oxygen species: re-evaluation of generation, monitoring and role in stress-signaling in phototrophic organisms. Biochim Biophys Acta Bioenerg 1837(6):835–848

Schreiner M, Mewis I, Huyskens-Keil S, Jansen MAK, Zrenner R, Win-kler JB, OBrien N, Krumbein A (2012) UV-B-induced secondary plant metabolites – potential benefits for plant and human health. Crit Rev Plant Sci 31:229–240

Schumaker MA, Bassman JH, Robberecht R, Radamaker GK (1997) Growth, leaf anatomy, and physiology of *Populus* clones in response to solar ultraviolet-B radiation. Tree Physiol 17(1):617–626

Shaish A, Avron M, Pick U, Ben-Amotz A (1993) Are active oxygen species involved in the induction of β-carotene in *Dunaliella bardawil*? Planta 190:363–368

Sharma R, Sopory SK, Guha-Mukherjee S (1976) Phytochrome regulation of peroxidase activity in maize. Plant Sci Lett 6:69–75

Sicora C, Mate Z, Vass I (2003) The interaction of visible and UV-B light during photodamage and repair of photosystem II. Photosynth Res 75:127–137

Solovchenko A, Merzlyak M (2008) Screening of visible and UV radiation as a photoprotective mechanism in plants. Russ J Plant Physiol 55(6):719–737

Solovchenko AE, Schmitz-Eiberger M (2003) Significance of skin flavonoids for UV-B-protection in apple fruits. J Exp Bot 54:1977–1984

Strid AW, Chow WS, Anderson JM (1994) UV-B damage and protection at the molecular level in plants. Photosynth Res 39:475–489

Szilárd A, Sass L, Deák Z, Vass I (2007) The sensitivity of Photosystem II to damage by UV-B radiation depends on the oxidation state of the water-splitting complex. Biochim Biophys Acta Bioenerg 1767:876–882

Takeuchi A, Yamaguchi T, Hidema J, Strid A, Kumagai T (2002) Changes in synthesis and degradation of Rubisco and LHCII with leaf age in rice (*Oryza sativa* L.) growing under supplementary UV-B radiation. Plant Cell Environ 25:695–706

Teklemariam T, Blake TJ (2004) Phenylalanine ammonia-lyase induced freezing tolerance in jack pine (*Pinus banksiana*) seedlings treated with low, ambient levels of ultraviolet-B radiation. Physiol Plant 122:244–253

Teramura AH, Sullivan JH (1994) Effects of UV-B radiation on photosynthesis and growth of terrestrial plants. Photosynth Res 39:463–473

Teramura AH, Ziska LH (1996) Ultraviolet-B radiation and photosynthesis. In: Baker NR (ed) Photosynthesis and the environment. Kluwer Academic, Dordrecht, pp 435–450

Tevini M, Braun J, Fieser G (1991) The protective function of the epidermal layer of rye seedlings against ultraviolet-B radiation. Photochem Photobiol 53:329–333

Tilbrook K, Arongaus AB, Binkert M, Heijde M, Yin R, Ulm R (2013) The UVR8 UV-B photoreceptor: perception, signaling and response. In: Arabidopsis book, p e0164. https://doi.org/10.1199/tab.0164

Tyystjarvi E (2008) Photoinhibition of photosystem II and photodamage of the oxygen evolving manganese cluster. Coord Chem Rev 252:361–376

Tyystjärvi E, Vass I (2000) Inhibition of photosynthetic electron transport by UV-A radiation targets the photosystem II complex. Photochem Photobiol 72:513–520

Urban O, Tuma I, Holub P, Marek MV (2006) Photosynthesis and growth response of *Calamagrostis arundinacea* and *C. villosa* to enhanced UV-B radiation. Photosynthetica 44:215–220

Vass I, Sass L, Spetea C, Bakou A, Ghanotakis D, Petrouleas V (1996) UV-B induced inhibition of photosystem II electron transport studied by EPR and chlorophyll fluorescence. Impairment of donor and acceptor side components. Biochemistry 35:8964–8973

Vass I, Szilard A, Sicora C (2005) Adverse effects of UV-B light on the structure and function of the photosynthetic apparatus. In: Pessarakli M (ed) Handbook of photosynthesis, 2nd edn. Marcel Dekker, New York, pp 827–843

Wade HK, Bibikova TN, Valentine WJ, Jenkins GI (2001) Interactions within a network of phytochrome, cryptochrome and UV-B phototransduction pathways regulate chalcone synthase gene expression in Arabidopsis leaf tissue. Plant J 25:675–678

White AL, Jahnke LS (2002) Contrasting effects of UV-A and UV-B on photosynthesis and photoprotection of beta-carotene in two *Dunaliella* spp. Plant Cell Physiol 43(8):877–884

Wilson MI, Greenberg BM (1993) Protection of the D1 photosystem II reaction center protein from degradation in ultraviolet radiation following adaptation of *Brassica napus* L. to growth in ultraviolet-B. Photochem Photobiol 57:556–563

Zhang WJ, Björn LO (2009) The effect of ultraviolet radiation on the accumulation of medicinal compounds in plants. Fitoterapia 80(4):207–218

Ziska LH, Teramura AH, Sullivan JH, McCoy A (1993) Influence of ultraviolet-B (UV-B) radiation on photosynthetic and growth characteristics in field-grown cassava (*Manihot esculentum* Crantz). Plant Cell Environ 16:73–79

Zsiros O, Allakhverdiev SI, Higashi S, Watanabe M, Nishiyama Y, Murata N (2006) Very strong UV-A light temporally separates the photoinhibition of photosystem II into light-induced inactivation and repair. Biochim Biophys Acta Bioenerg 1757:123–129

Chapter 19
UVB and UVB/White-Light-Induced Inhibition of Thylakoid Electron Transfer Reactions Studied by Fluorescence Induction and Fluorescence Decay: Damage to Donor and Acceptor Side Components of PSII

Roberto Barbato

Contents

Abstract Approximately 1.5% of the solar radiation reaching the Earth's surface is accounted for by wavelengths in the ultraviolet-B range (280–320 nm) and its amount is increasing as a consequence of stratospheric ozone depletion linked to human activity. This radiation is known to be harmful to all biological organisms and even a modest increase in its level may induce adverse effects on the biosphere, with plants particularly sensitive. In this study we report new data on the effect of ecologically significant level of UVB light, alone or in combination with visible light, on photosynthetic electron transfer reactions in the stress-tolerant organism *Thellungiella salsuginea*. We could confirm that UVB light harms the donor side of photosystem II, but also electron transfer beyond the acceptor side of the photosystem (i.e., cytochrome b_6/f or photosystem I) is affected. In the presence of background visible light, the effect of UVB is rather different and a main target became electron transfer between Q_A and Q_B.

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Keywords UV-B light · photosynthesis · *Thellungiella salsuginea*

19.1 Introduction

Even though light is essential for photosynthesis, when in excess, it may harm the photosynthetic apparatus itself (Li et al. 2018). Not only the amount of light, but also its quality in terms of wavelength, may have adverse effects on photosynthesis. In particular, the ultraviolet-B light component of the electromagnetic spectrum (280–315 nm) has been shown to be very dangerous to photosynthesis, as it affects a number of electron transfer steps and biochemical reactions with a very high quantum yield (Zavafer et al. 2015). These include damage to the quinone acceptors (Jansen et al. 1996), damage to the Mn cluster of the oxygen evolving complex (Barbato et al. 1995, Hakala et al. 2005), and increased degradation of reaction center D1-protein with concomitant inhibition of its synthesis (Barbato et al. 2000).

An increase in the level of ultraviolet-B light reaching the Earth's surface has been measured as a consequence of stratospheric ozone depletion (Allen et al. 1998). Since its discovery, this fact has been causing much concern as it may have strong and adverse effects on ecosystems (Caldwell et al. 2007) and have to be considered as one of main face of climate global changes. In line with this view, it seems important to understand, at any level, the effect of this light on photosynthesis. In line with this view, here we report the result from a study based on fluorescence induction and fluorescence decay after a single turnover flash, in which the effect of visible, ultraviolet-B (UVB), and a mixture of the two kinds of light (visible/UVB) is noted on the photosynthetic apparatus of *Thellungiella salsuginea*, a model organism in the field of plant environmental stress physiology. Our results indicated that the effect of ultraviolet-B light is different depending on whether visible light is present or not in the background. We found that ultraviolet-B light affects mainly the donor side of photosystem II and electron carriers beyond Q_B; however, when it was administrated together with visible light (which, per se, did not have any adverse effect), electron transfer between Q_A and Q_B was affected too.

19.2 Materials and Methods

Thellungiella salsuginea was grown as described by Goussi et al. (2018). Leaves from 4-week-old plants were used in all experiments. For irradiation, detached leaves were left to float on water and exposed to different kinds of light for either 1 or 3 h. Control leaves were kept in the dark until the end of experiments. Irradiation conditions were as follows: white light, 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and UVB light (from a Vilber-Lourmat lamp), 1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Before acquisition of fluorescence transients, plants were dark adapted for at least 30 min. Measurements were carried out as described by Pagliano et al. (2006) and analysis of chlorophyll transients performed as described by Strasser and Srivastava (1995). Statistical analysis was carried out by using the Origin software package, version 9.

19.3 Results

Irradiation of *Thellungiella salsuginea* leaves under our experimental conditions brought about a different effect depending on the particular light treatment. In terms of F_V/F_M, the intensity of visible white light used in this study did not significantly affect the maximal efficiency of PSII, whereas the presence of UVB, alone or in combination with white light, caused a marked decrease on F_V/F_M, depending on irradiation time (Table 19.1). This decrease, similar in both irradiation conditions (UVB, visible/UVB), was due to both an increase in F_0 and a decrease in F_M (Table 19.1 and Fig. 19.1a,b).

In Fig. 19.1a,b, chlorophyll transients (recorded after 30 min of dark adaptation) from leaves treated with visible, ultraviolet-B (UVB), or ultraviolet-B in combination with visible light (visible/UVB) for 1 h (1A) or 3 h (1B) are shown. The fluorescence F_t of the dark-adapted control leaves showed a typical OJIP transient (Strasser et al. 2004). As stated above, UVB treatment, alone or combined with background white light (visible/UVB), induced an increase in F_0; at the same time, a considerable decrease of F_M was observed. The effect was slightly more pronounced after 3 h of irradiation. At variance, irradiation with white light did not produce any major adverse effects.

To further investigate this point, transients shown in Fig. 19.1a,b were normalized at F_0 and F_M and then plotted as relative variable fluorescence, V_{OP} (Fig. 19.2a,b). While visible light did not affect the shape of the transients, UVB light produced a strong effect, which was different depending on the presence or absence of background white light. When administrated alone, ultraviolet-B light produced a general loss fluorescence (decrease of all phases, i.e., OJ, Ji, and IP); at variance, when visible light was present together with UVB light, a strong increase of the OJ and a

Table 19.1 Absolute (Fo, Fm, Fm, Fk, Fj) and relative (Fv/Fm, Fk/Fj) values of chlorophyll fluorescence from control and light-treated plants

	Fo	Fm	Fv	Fv/Fm	Fk	Fj	Fk/Fj
Control	678	3642	2964	0.814	1214	1848	0.657
1 h w	623	3251	2628	0.808	1205	1720	0.700
1 h u	898	2650	1752	0.661	1254	1572	0.798
1 h uw	741	2551	1810	0.710	1245	1591	0.783
3 h w	664	2930	2266	0.779	1111	1572	0.665
3 h u	923	2178	1185	0.576	1175	1385	0.848
3 h uw	884	1822	938	0.515	1161	1397	0.831

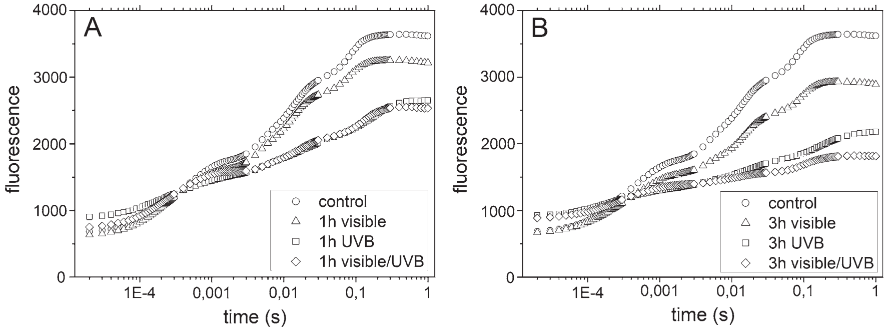

Fig. 19.1 Unnormalized chlorophyll fluorescence transients recorded from plants treated either for 1 h (**a**) or 3 h (**b**) with white light (up triangles), UVB (squares), and with W/UVB (diamonds). Transient from dark control (circles) is also reported

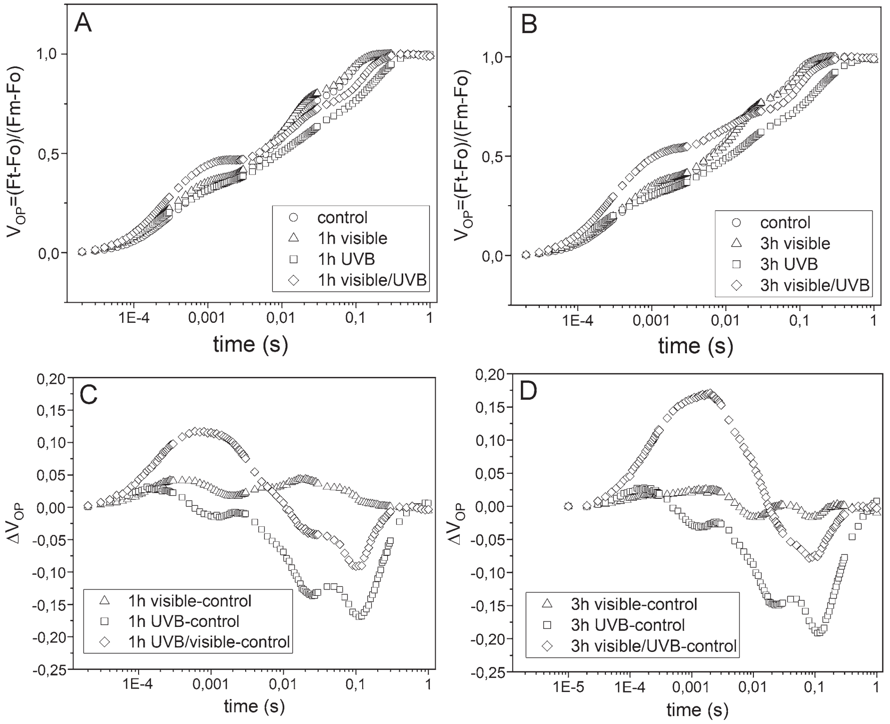

Fig. 19.2 Normalized (Fo, Fm) chlorophyll fluorescence transients (V_{OP}) from plants treated either for 1 h (**a**) or 3 h (**b**) with white light (up triangles), UVB (squares), and with W/UVB (diamonds). Transient from dark control (circles) is also reported. ΔV_{OP} was calculated as $V_{OP\ (treated)}$-$VO_{OP(control)}$; plants were treated either for 1 h (**c**) or 3 h (**d**). Triangles, white-light-treated minus dark control; squares, UVB-treated minus dark control; diamonds, white/UVB-treated minus dark control

decrease in the JI and IP phases was observed. This effect was qualitatively similar at 1 and 3 h of irradiation, but after 3 h it was more pronounced. By calculating ΔV_{OP} (Fig. 19.2c,d) it became clear that the presence of visible light (visible/UVB) brought about a strong band peaking at about 2–3 ms, whose intensity increased with irradiation time; the appearance of this band was a specific effect of irradiation with visible/UVB, as it was induced neither by UVB nor by visible light alone. In addition, irrespective of the presence of visible light, UVB light brought about the appearance of two negative bands peaking about at 20 and 100 ms, corresponding to a decrease of phases JI and IP, respectively.

To further elucidate, at least semiquantitatively, the observed differences in fluorescence kinetics, main bands occurring from O to P transients were analyzed separately. This was achieved by double normalizing curves between 0 and 300 µs (L band, between O and K steps, Fig. 19.3a,b) and between 0 and 2 ms (K band, between O and J steps, Fig. 19.4a,b). K (Fig. 19.3c,d) and L (Fig. 19.4c,d) bands were obtained, and then plotted, as the difference between treated plants with

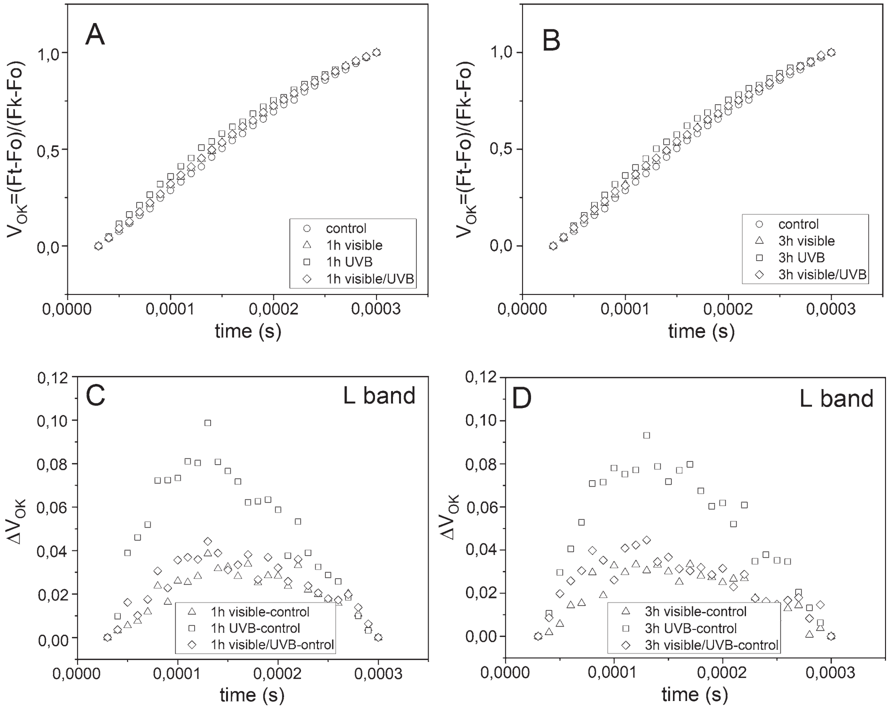

Fig. 19.3 Normalized (Fo, Fk) chlorophyll fluorescence transients (V_{OK}) from plants treated either for 1 h (**a**) or 3 h (**b**) with white light (up triangles), UVB (squares), and with W/UVB (diamonds). Transient from dark control (circles) is also reported. ΔV_{Ok} (L band) was calculated as $V_{OK\ (treated)}$-$VO_{OK\ (control)}$; plants were treated either for 1 h (**c**) or 3 h (**d**). Triangles, white-light-treated minus dark control; squares, UVB-treated minus dark control; diamonds, white/UVB-treated minus dark control

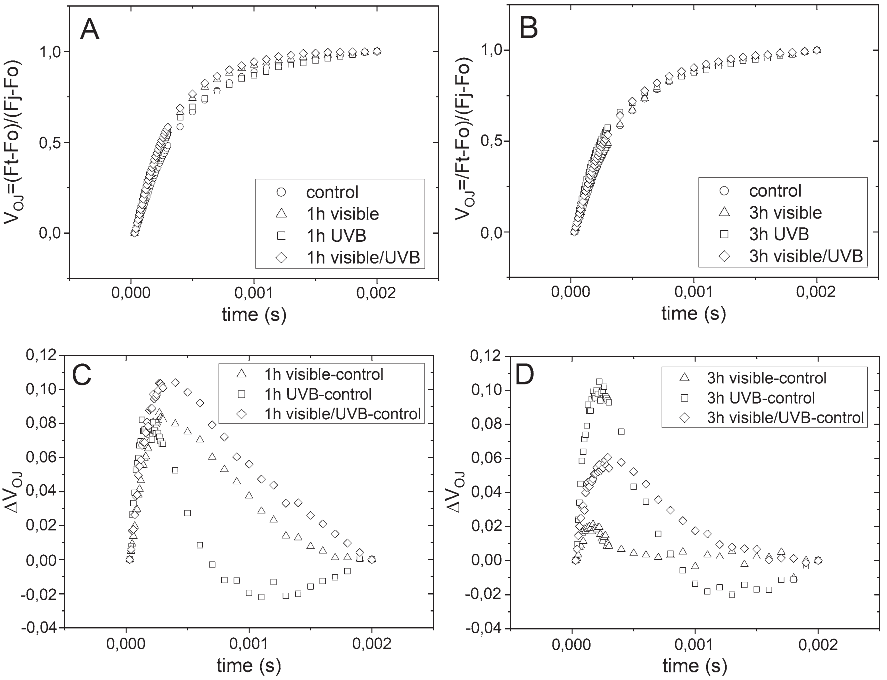

Fig. 19.4 Normalized (Fo, Fj) chlorophyll fluorescence transients (V_{Oj}) from plants treated either for 1 h (**a**) or 3 h (**b**) with white light (up triangles), UVB (squares), and with W/UVB (diamonds). Transient from dark control (circles) is also reported. ΔV_{OI} (K band) was calculated as $V_{OI\ (treated)}$-$VO_{OI\ (control)}$; plants were treated either for 1 h (**c**) or 3 h (**d**). Triangles, white-light-treated minus dark control; squares, UVB-treated minus dark control; diamonds, white/UVB-treated minus dark control

ultraviolet-B (either in the presence or absence of visible light) and dark control. After 1 h of irradiation, ΔV_{OK} revealed a positive L band, peaking between 100 and 200 µs. The maximum amplitude of the L band was after irradiation with UVB after 3 h, whereas when present together with white light, the effect of UVB was much mitigated, very similar to that observed with just white light. The kinetic difference of V_{OJ} revealed the so-called K band in treated plants, which appeared as a peak between 250 and 300 µs.

Changes in IP phase have been measured by transient normalization to the time range of 30–200 ms and expressed as $V_{IP} = (F_t - F_I) / (F_m - F_I)$ (Fig. 19.5a,b). Upon treatment with UVB light, a loss of IP phase was observed, bigger when visible light was present. Irradiation with visible light did not produce any adverse effect on this phase of the transient (Fig. 19.5a,b). Finally, fluorescence decay after a single turnover flash (in the µs range) was investigated. Visible light did not affect fluorescence decay, whereas UVB light, particularly when visible light was present in the background, produced a strong slowing down of fluorescence decay (Fig. 19.6).

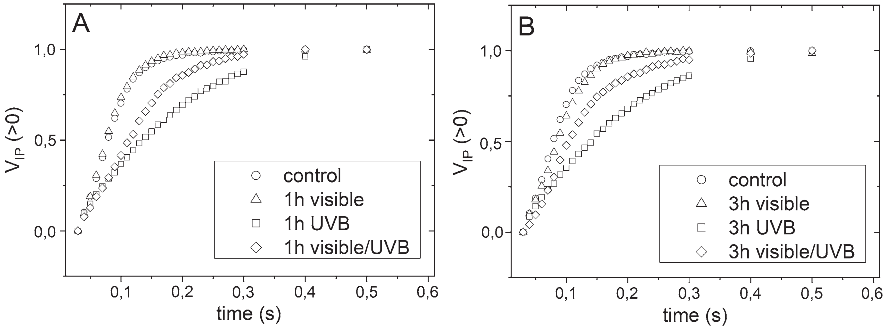

Fig. 19.5 Normalized (Fi, Fp) chlorophyll fluorescence transients (V_{IP}) from plants treated either for 1 h (**a**) or 3 h (**b**) with white light (up triangles), UVB (squares), and with W/UVB (diamonds). Transient from dark control (circles) is also reported

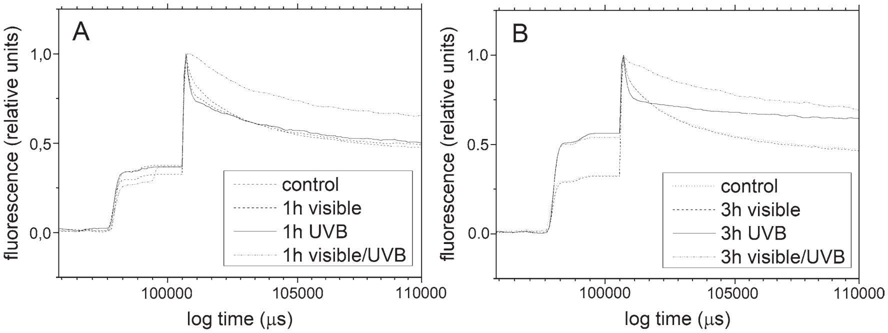

Fig. 19.6 Fluorescence decay in leaves treated for either 1 h (a) or 3 h (**b**) in plants treated with white light (dashed line), UVB light (solid line), or W/UVB light (dash dot line). Fluorescence decay from dark control is also shown (dotted line)

19.4 Discussion

The effect of UVB on photosynthetic apparatus has widely been investigated. There seems to be a number of different targets in the thylakoid membranes for this kind of radiation. Damage to the Mn cluster (Barbato et al. 1995; Hakala et al. 2005; Vass 2012; Vass et al. 1996) associated with cleavage of the D1 protein originating a 23-kDa C-terminal fragment (Barbato et al. 1995, 2000) is considered as the main target for this radiation, but additional target, such as the Q_B site (Trebst and Depka 1990; Vass et al. 1996) has been suggested. The effect of irradiation with a mixture of the two lights has been less investigated, but available data (Sicora et al. 2003) indicate that, even though administrated at the same time, the two kinds of radiations might have different and noninteracting targets. Results reported in this study suggest a slightly different view. UVB irradiation, apparently, did not affect Q_B site, as the rising in fluorescence in the 0–3 ms (OJ phase) is similar to the control. At variance, when analysis is restricted to the first 300 μs or the Fk/Fj ratio is considered (i.e., the time required for water to diffuse to the donor side of the photosystem), UVB adversely affects the chlorophyll transient, confirming the donor side of PSII as a main target for UVB light. However, when white light is superimposed to UVB, the appearance of a strong band in the first 3 ms of the transient suggests that additional targets are hit, most likely the Q_B site. Accordingly, decay of fluorescence after a single saturating flash supports this possibility. Thus, we suggest that under mixed light conditions (at least when the light intensities here reported are used), electron transfer between Q_A and Q_B may be one main target. Clearly, if sensibility to UVB light increases when white light is present, it is likely that the actual target is a reduced or semireduced form of quinones.

The effect of UVB on the second part of the chlorophyll transient (JI, IP) instead seems to be essentially independent on the presence of visible light. In fact, a decrease in both JI and IP phases is observed. These phases are thought to describe electron transfer steps beyond quinone acceptor leading to reduction of PSI acceptors. If so, we have to conclude that cytochrome b6/f and/or PSI could be specifically targeted for damage. This possibility remains to be investigated.

References

Allen DJ, Nogués S, Baker NR (1998) Ozone depletion and increased UV-B radiation: is there a real threat to photosynthesis? J Exp Bot 49:1775–1788

Barbato R, Bergo E, Slzabò I, Dalla Vecchia F, Giacometti GM (2000) Ultraviolet B exposure of whole leaves of barley affects structure and functional organization of photosystem II. J Biol Chem 275:109976–110982

Barbato R, Friso G, Frizzo A, Rigoni F, Giacometti GM (1995) Degradation of the D1 protein of Photosystem II Centre by ultraviolet-B radiation. Requires the presence of functional manganese on the donor side. Eur J Biochem 227:723–729

Caldwell MM, Bornman JF, Ballare CL, Flint DS, Kulandaivelu G (2007) Terrestrial ecosystems, increased ultraviolet radiation, and interaction with brother climate change factors. Photochem Photobiol Sci 6:252–266

Goussi R, Manaa A, Derbali W, Cantamessa S, Abdelly C, Barbato R (2018) Comparative analysis of salt stress, duration and intensity, on the chloroplast ultrastructure and. Photosynthetic apparatus in *Thellungiella salsuginea*. J Photochem Photobiol B Biol 183:275–288

Hakala M, Tuominen L, Keränen M, Tyystjärvi T, Tyystjärvi E (2005) Evidence for the role of the oxygen-evolving manganese complex in photoinhibition of photosystem II. Biochim Biophys Acta 1706:68–80

Jansen MAK, Gaba V, Greenberg BM, Mattoo AK, Edelman M (1996) Low threshold levels of ultraviolet-B in a background of photosynthetically active radiation trigger rapid degradation of the D2 protein of photosystem-II. Plant J 9:693–699

Li L, Aro E-M, Mikkar AH (2018) Mechanism of photodamage and protein turnover in photo inhibition. Trend Plant Sci 23:667–676

Pagliano C, Raviolo M, Dalla Vecchia F, Gabbrielli R, Gonnelli C, Rascio N, Barbato R, La Rocca N (2006) Evidence for PSII donor side damage and photoinhibition induced by cadmium treatment on rice (*Oryza sativa*). J Photochem Photobiol B Biol 84:70–78

Sicora C, Maté Z, Vass I (2003) The interaction of visible light during photodamage and repair of Photosystem II. Photosynth Res 75:127–137

Strasser RJ, Srivastava A (1995) Polyphasic chlorophyll *a* fluorescence transient in plants and cyanobacteria. J Photochem Photobiol B Biol 61:32–42

Strasser RJ, Tsimilli-Michael M, Srivastava A (2004) Analysis of the Chlorophyll a Fluorescence Transient. In: Papageorgiou GC, Govindjee (eds) Chlorophyll a fluorescence. Advances in photosynthesis and respiration, vol 19. Springer, Dordrecht pp 3211–362

Trebst A, Depka B (1990) Degradation of the D1-protein subunit of Photosystem II. In isolated thylakoids by UV light. Z Naturforsch 45:765–771

Vass I (2012) Molecular mechanisms of photodamage in the photosystem II complex. Biochim Biophys Acta 1817:209–217

Vass I, Sass L, Spetea C, Bakou A, Ghanotakis DF, Petrouleas V (1996) UV-B induced inhibition of Photosystem II electron transport studied by EPR and chlorophyll fluorescence. Impairment of donor and acceptor side components. Biochemistry 35:8964–89873

Zavafer A, Chow WS, Chea MH (2015) The action spectrum of photosystem II photoinactivation in visible light. J Photochem Photobiol B: Photobiol 152:247–260

Chapter 20
Climate Change and Plant Abiotic Stress: Responses, Sensing, and Signaling

Syed Damin Abbas Hamdani, Duaa Ahmad Khan, Abdul Qadir Rafiq, and Mustafeez Mujtaba Babar

Contents

Abstract Climate change is the single most prominent abiotic stress factor that yields to devastating effects on flora, fauna, and geography alike. It initiates a cascade of events, ultimately leading to the destruction of the biogeographical platform for the growth of plants throughout the globe. The adverse effects may be presented in the form of extreme fluctuation in temperature, increased concentration of salts and metals in the soil and water, elevation in carbon dioxide content, and drought and flooding among many others. Plants, being the primary natural source of sustenance, are badly affected by these conditions leading to a decrease in the overall quality and quantity of the plant yield. They have evolved themselves to naturally overcome and respond to these stress factors. This chapter provides a detailed introduction of the concept of climate change in terms of geographical and temporal

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aspects. The adverse aspects of climate change as an abiotic stress factor have been discussed thereafter. Towards the end of the chapter, various natural and artificial mitigation and interventional strategies have been reviewed.

Keywords Climate change · Abiotic stress · Plant responses · Environmental biotechnology

Abbreviations

ABA	Abscisic acid
APX	Ascorbate peroxidase
CDPKs	Calcium-dependent protein kinases
CRT	C-repeat class
DRE	Dehydration responsive element
HSPs	Heat stress proteins
LEA	Late embryogenesis abundant
MAP	Mitogen-activated protein
MAPK	Mitogen-activated protein kinase
MAPKK	Mitogen-activated protein kinase kinase
NPK1	Nicotiania protein kinase 1
OHC	Ocean heat content
P5CS	[delta] pyrroline 5 carboxylate synthetase (P5CS)
QTL	Quantitative trait locus
RNA	Ribonucleic acid
ROS	Reactive oxidative species
SA	Salicylic acid
SOD	Superoxide dismutase
SOS	Salt overly sensitive
SSS	Sea surface salinity
SST	Sea surface temperature

20.1 Introduction

Human activities have been the main cause of global warming since the mid-twentieth century. This is mainly attributable to the increase in greenhouse gas concentration. The burning of fossil fuels, including coal and oil, coupled with the massive excavation of natural resources, has led to a prodigious environmental disaster. Over the past two centuries, the average global surface temperature has increased by approximately 1 °C. Many areas have an even higher regional-scale warming with 20–40%

of the global population having experienced over 1.5 °C of warming within a year. Conversely, the rise in temperature has also resulted in intense changes to human and natural systems presented, for instance, as floods, droughts, extreme temperatures, elevated sea levels, and loss of biodiversity (Field et al. 2012). People living in the low-income and middle-income countries are mainly affected by the climate change on an everyday basis. Global warming and climate change has led to food insecurity ultimately contributing to a rise in poverty and associated population migration (Field et al. 2012). Both settled and unsettled regions, including megacities, villages, islands, mountains, and coastal regions, are equally affected by the climate change. This has led to a significant impact on the ecosystems and living species of animals and plants. An increase in the awareness of global warming and its implications on the human health and economy has led to the initiation of worldwide response at the personal and institutional level.

It is estimated that by the year 2050, the demand for agricultural products would rise by 70% (Noble and Ruaysoongnern 2010). It is, therefore, necessary to increase the crop yield in the limited arable land. However, many biotic and abiotic stress factors have led to a decrease in crop production. Among the abiotic stress factors, extremes of temperature, drought, and salinity are of prime importance. Global warming and climate change lead to further worsening of these stress factors. Estimates have shown that by the year 2050, salinity and drought would affect more than 50% of the cultivable land (Boyer 1982). Abiotic stress leads to a wide range of physiological, morphological, molecular, and biochemical changes that adversely affect the growth and yield of a plant. Salinization and drought, for instance, induce osmotic stress, which results in the loss of homeostasis and disruption of ion distribution in the cell (Serrano et al. 1999; Zhu 2001a, b). Similarly, oxidative stress may result in the denaturation of structural and functional proteins (Smirnoff 1998). These stress factors therefore initiate a series of cell signaling pathways and cellular responses that result in a further increase in the stress of the plant (Shinozaki and Yamaguchi-Shinozaki 2000; Knight and Knight 2001).

Plants have developed a number of processes to address the changes in atmospheric and climatic conditions. However, these changes can only provide limited protection to the plant. A number of biotechnological approaches are being exploited and developed to improve the response of plants to climatic stress factors. These approaches are generally based on the manipulation of genes that maintain and protect the structure and function of cellular components. The bioengineering strategies depend on the overexpression of specific genes that are responsible for maintaining signaling and regulatory pathways. These, therefore, contribute to the synthesis of structural and functional protectants, such as antioxidants, osmolytes, or other tolerance-inducing proteins. Though the current strategies have been able to address the issues of abiotic stress to a considerable degree, the genetically complex phenomena of abiotic stress tolerance and the possible unfavorable side effects make this task much difficult. The current chapter reviews the threat of climate change to the living systems and the molecular, morphological, and physiological mechanisms by which it causes adverse effects on the plants.

20.2 Climate Change Around the World

Climate change is a global phenomenon which nonselectively affects all the geographical regions of the world. The year 2017, for instance, was the warmest year since 1981 in North America (Arguez et al. 2012). Similar statistics were reported for Mexico and other South American countries as well (Sánchez-Lugo et al. 2017). There has been a marked difference in other climatic indicators as well. Annual precipitation, for instance, showed marked variation across the same geographical zones. In 2017, the precipitation across the western parts of Canada recorded below average precipitation rates, while the eastern parts had significantly higher ones. In North America, the dry and warm conditions contributed to the largest forest fires ever recorded in Canada. During 2017, the United States spent over 1 billion dollars on each of the 16 climate and weather events, which was the highest number of climatic events since 1980 (Bissolli et al. 2018).

The major part of South America experienced an upward trend in the temperature with an increase of at least 1.0 °C or higher over 30 years from 1981 to 2010. However, a gradual decrease in the temperatures have been noted in Suriname, northern Colombia, and parts of southern Brazil (Sánchez-Lugo et al. 2017). Similarly, the precipitation pattern varied across the different parts, with significantly wetter conditions observed across the coasts of Peru. Conversely, northern Brazil has been reported to be considerably drier than normal conditions (Bissolli et al. 2018).

As per the statistics of 2017, there was an average rise of 0.3–1.8 °C in most of the regions of the African continent. A few areas of Southern and Western Africa, however, noticed a drop in the temperature. With regards to the annual precipitation, Central, Western, and parts of Eastern Africa experienced annual precipitation above normal. The equatorial regions, however, reported a significantly lower rainfall (Sánchez-Lugo et al. 2017). Extreme events, including heavy downpour and flooding, have been reported in many parts of the region. In Niger, Gambia, and Nigeria, every year, heavy rainfalls during August and September have been recorded. In Morocco, however, wetter Februarys and Decembers have been reported. A rise in the number of tropical cyclone events has been observed in Zimbabwe and Mozambique. In 2017, Madagascar and Réunion Island were also affected by another cyclone originating from the southern Indian Ocean (Bissolli et al. 2018).

In Europe, 2017 was observed as the fifth warmest year with an anomaly of +1.3 °C since 1851. Over most of the parts of the continent, the rise in the temperature changes was homogeneously distributed, with local temperature anomalies varied mostly between +1 and + 2 °C (Sánchez-Lugo et al. 2017). Few regions including northeastern Germany, western Russia, and northern Poland received an above-average precipitation (base period 1981–2010) which totaled up to nearly 167% higher than the previous periods. Conversely, most of the parts of Europe had near-normal annual precipitation. Though the Iberian Peninsula and Italy received about 20–40% less precipitation than normal average, the Middle Eastern region received

40–60% less than normal precipitation (Bissolli et al. 2018). During winter 2016–2017, southern Balkan states, Turkey, and Greece recorded temperature changes of minus 2 °C, while Scandinavia faced exceptionally mild winter conditions with temperature anomalies reaching more than +4 °C.

In most of the regions of Asia, the annual mean surface temperature during 2017 remained above normal (Sánchez-Lugo et al. 2017). Precipitation pattern varied across different parts of the continent, with lower annual precipitation in central Asia and Eastern Siberia. The same trend continued in the Korean Peninsula, Northeastern China, and Mongolia. However, above higher rainfall was reported in the Indochina Peninsula, Malay Peninsula, Western China, Northeastern India, and the Maritime Continent (Bissolli et al. 2018). There was a significant season-wise variation in the climate though in most of Asia, and a positive trend has been observed. Colder and wetter springs have been reported over the past decades in Southwestern China. Similarly, an even colder winter and summer has been recorded in Siberia. Autumn was recorded to be of negative temperature anomalies from central Siberia to Japan. In Southeast Asia and western regions of Tibetan Plateau, the seasonal precipitation was recorded to be persistently above normal. However, it was below normal in the Korean Peninsula and Northeastern China from spring to autumn (Bissolli et al. 2018).

These climatic changes are not limited to the land surface only. During 2017, the climatic conditions continued to vary in the Pacific Ocean. In the western tropical Pacific, a continuous increase in ocean heat content (OHC), sea surface temperatures (SSTs), and sea level was recorded contrary to the eastern tropical Pacific. Similarly, Sea Surface Salinity (SSS) recorded a saltier trend in the east, while it became fresher in the west. The flux of carbon dioxide and chlorophyll from the atmosphere to ocean were increased in the eastern equatorial Pacific. All these climatic variations were consistent with 2016–2017 tendencies in freshwater flux and regional wind stress. In 2017, across much of the North Pacific, increase in surface temperatures ocean, heat content, and sea level was observed. Effects included destructive flooding in Hawaii. During 2017, in southeast of Greenland, OHC, SSTs, and sea level all remained below average. However, along the east coast of North America, these variables were on the higher side (Hartfield et al. 2018). In the Indian Ocean, SSTs and SSS were both below average in the east and high in different parts of the western side. Sea level rise in the north of ~10°S in the Indian Ocean and rise in the south of the latitude were recorded during 2016–2017. These climatic changes, hence, have affected the geographical properties and the botanical, zoological, and agricultural conditions of the respective regions as well as globally.

20.3 Climate Change: A Spatiotemporal Phenomenon

Climate change has been undergoing ever since the birth of the world. The gradual change in the climatic parameters have led to prominent changes in flora and fauna alike. This ecological distress has led to severe loss in the agricultural yield resulting in the disturbance of the overall food cycle. Consequently, newer strategies, including even intense agriculture efforts, have been developed to address the problems being presented, which again negatively affect the climatic conditions. However, the climate change phenomenon has become more prominent over the past couple of centuries owing to the harmful human activities. The earth's surface, for instance, has become warm by 0.7–0.9 °C per century. The rate of warming over a hundred years, however, has become nearly double since 1975 (Sánchez-Lugo et al. 2017). The average temperature of 2017 is 0.38–0.48 °C above than the 1981–2010 average. Recent data of 2017 show the average temperatures across ocean and land surface were 0.84 °C above the 1901–2000 average. By the year 2020, it is projected that the global surface temperature will be more than 0.5 °C warmer as compared to the 1986–2005 average. The planet is likely to continue to warm over this century and beyond. By 2100, average temperature could be between 1 and 5.4 °C warmer than it is today (Hartfield et al. 2018). Figure 20.1 represents the increase in temperature over the last 130 years.

Increasing carbon dioxide levels is the most important cause of the rise in global temperature (Shakun et al. 2012). Burning of fossil fuels such as coals is the leading cause of the increase in CO_2 atmospheric levels (Houghton 2008). A continuous increase in global atmospheric CO_2 levels is being observed. The global rate of atmospheric CO_2 was around 0.6 to 0.1 ppm per year in the 1960s. Over the past 10 years, however, it has been increased to 2.3 ppm per year. The global atmospheric carbon dioxide reached to a new level of 405.0 ppm in 2017. Over the past 60 years, the per annum increase in the rate of atmospheric carbon dioxide level is about 100 times more than the earlier years (Hartfield et al. 2018).

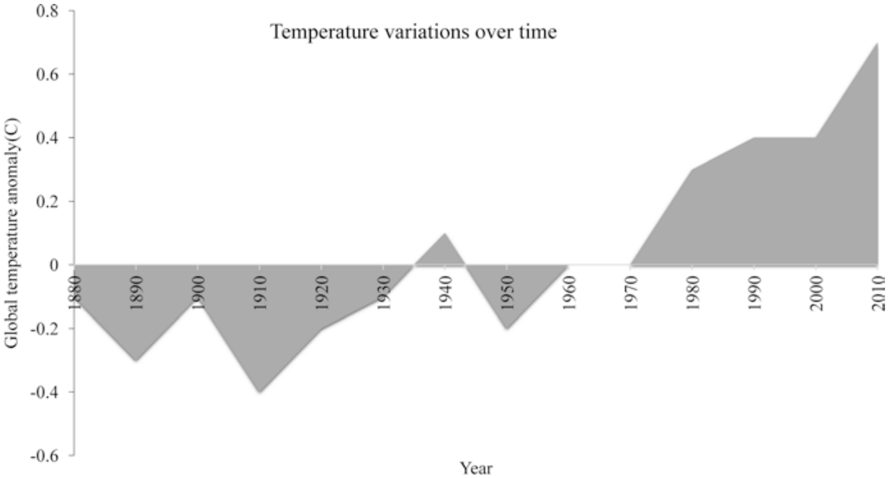

Fig. 20.1 Graph representing the global temperature anomaly with year 1901–2000 as base period (OAA National Centers for Environmental information, Climate at a Glance: Global Time Series, published February 2019, retrieved on February 21, 2019 from https://www.ncdc.noaa.gov/cag/)

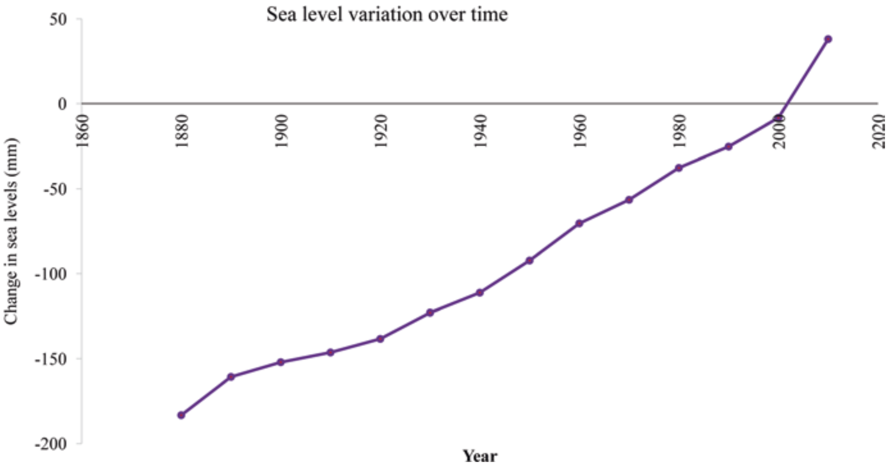

Fig. 20.2 Graph representing the average rise in global sea level from 1880 to 2010 (Church et al. 2011)

Figure 20.2 summarizes the rise in the average sea levels owing to the melting of glaciers due to ever-increasing global temperatures.

Earth's climate warming is evident from disintegration and disappearance of glaciers around the world (Thompson 2010). More than one hundred thousand glaciers are documented in the World Glacier Documentary (Haeberli et al. 2000), but only a few of these, known as reference glaciers, around 40 in number, are periodically measured over longer periods to estimate the climate-associated changes in their size or mass. It is estimated that during 1980–2016, the cumulative mass balance in these glaciers' loss has been around −19.9 m. In 2016, these reference glaciers lost the equivalent of 33 in. of water, implying the same depth of water that would be produced from the quantity of melted ice or snow (Hartfield et al. 2018). The melting of glacier mass has accelerated in the past few decades. It has increased from 226 gigatons per year to 275 gigatons per year from 1993 to 2009. The major ice loss occurred from Antarctic ice that has been accelerated from 30 gigaton per year between 1992 to 2001 to 147 gigatons per year from 2002 to 2011. Over the past century, sea level has been rising, and in recent decades, the rate has increased dramatically (Holgate and Woodworth 2004). Since 1993, the average rate of rising in sea level has been about 3.1 mm per year, 2017 was marked as the year of the highest annual average rise, and the sea level was recorded to be more than 77 m above the 1993 average. This increase in average can be the result of the warming of the global ocean and an increase in the global mean steric sea level. By 2100, it is projected that global mean sea level will rise at least 8 in. but not more than 6.6 ft (Hartfield et al. 2018). Keeping in view the above information, it is imperative that the climate change mechanism is a global phenomenon that tends to affect all the regions of the world over centuries. The effects of climate change can be altered but it cannot be halted completely. Climate change and the accompanying abiotic stress factors, hence, serve as a constant threat to the living organisms. Understanding the effects of this stress factor can, hence, aid in developing mitigation strategies to address the threat.

20.4 Climate Change as an Abiotic Stress Factor

Abiotic stress, due to changing climatic conditions, in the form of heat, cold, salinity, and drought causes changes in the biochemical, molecular, physiological, and morphological characteristics of plants, thus adversely affecting their productivity and growth. The mechanisms adopted by the plants to combat this abiotic stress has been briefly explained.

20.4.1 Sensors and Signal Transduction Pathways

Signal transduction pathways are stimulated by various stress signals. Which are perceived initially by sensors which are special molecules within the plant body. Sensors either alter the intracellular signaling by suppressing or initiating the signaling cascade or increasing the specific gene expression by activating nuclear transcription factors (Xiong et al. 2002). Various climatic stresses cause a temporary rise in intracellular Ca^{2+}, due to release from internal spaces or apoplastic space. Channels are the sensors which facilitate Ca^{2+} influx. Ligand-sensitive calcium channels are responsible for the release of Ca^{2+} from internal stores. These ligands are secondary messengers. Signaling molecules and secondary messengers such as abscisic acid produced due to early Ca^{2+}-mediated signals produce Ca^{2+} influx, which is an important characteristic of Ca^{2+} signaling (Xiong and Zhu 2001).

During environmental stress, pathways for signal transduction activate mechanisms to combat stress by repairing and protecting proteins and membranes and maintaining homeostasis. Three major types of signal transduction pathways include, firstly, the signaling due to oxidative stress by reactive oxygen species (ROS) that uses MAPK which cause osmolyte, antioxidant, and ROS-neutralizing enzyme production. Secondly, signaling can be due to Ca^{2+} that causes stress-responsive protein production by LEA genes such as DRE/CRT and, lastly, ion regulation response due to signals produced by the salt overly sensitive (SOS) pathway depending on Ca^{2+} (Xiong et al. 2002). The mechanism of initiation of stress responses has been summarized in Fig. 20.3.

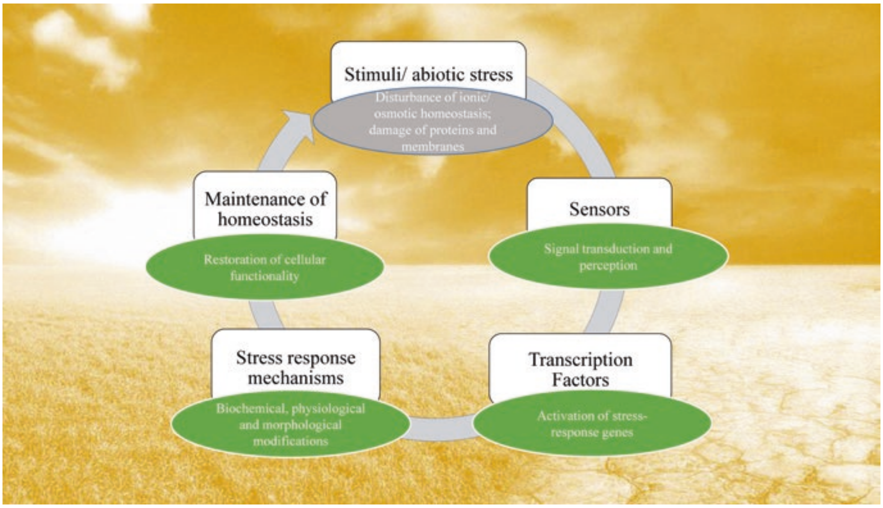

Fig. 20.3 Schematic representation of downstream processes activated in response to climate change within the plant body

20.4.1.1 Oxidative/Osmotic Stress Signaling

Oxidative stress due to climate change involves ROS production. ROS such as hydroxyl and superoxide radicals damage plants by disrupting their cellular components and functions such as photosynthesis (Sunkar et al. 2003). These ROS cause stress injury, leading to the activation of various protective mechanisms and production of ROS scavengers. In order to scavenge these toxic compounds and protect themselves from stress injury, plants have developed various antioxidation strategies. ROS scavengers are enzymatic, e.g., catalase, ascorbate peroxidase (APX), glutathione reductase, and superoxide dismutase (SOD), and nonenzymatic, e.g., anthocyanins, glutathione, carotenoids and ascorbate, and amphiphilic molecules (e.g., tocopherol), proteins, and osmolytes.

ROS signaling is mediated by MAPK pathways. In response to osmotic pressure, the receptors/sensors such as histidine kinases, transmembrane receptors, and protein tyrosine kinases activate the MAPK pathway. It results in increased osmolyte production that helps in the adjustment of osmotic pressure by regulating turgor pressure in cells hence adjusting the water gradient. MAPK upon activation either directly activates the transcription factor in nucleus or regulates the activity of cytoskeleton-associated proteins and gene expression by initiating various other signals (Xiong et al. 2002). New studies have reported that some solutes, such as proline (Pro), glycine betaine (GB), di-methylsulfoniopropionate, and mannitol, stabilize proteins and membranes directly by scavenging free radicals or by acting as chemical chaperons (Wang et al. 2003). Osmotic stress due to climatic variations leads to activation of several protein kinases along with mitogen-activated kinases. Osmotic stress also activates a number of phospholipid systems, which results in the production of various messenger molecules that work upstream of the activated protein kinases. Furthermore, it regulates the biosynthesis of abscisic acid (ABA) at various stages. The stress signaling, either ABA-independent or ABA-dependent, initially alters expressed transcription factors that leads to transcriptional activator expression which ultimately activates effector genes that play a part in stress tolerance (Zhu 2002).

20.4.1.2 Calcium-Dependent Signaling

Ca^{2+} plays an important role in various intracellular signaling processes in plants and animals. When there is no stimulus, cytoplasmic Ca^{2+} levels are low; when there is a stimulus present, Ca^{2+} enters the cell via several Ca^{2+} channels or released from intracellular stores. Rise in cytoplasmic Ca^{2+} concentration via channels is seen when there are environmental stresses. Calcium-dependent protein kinases (CDPKs) are Ca^{2+} influx sensors of significance in plants when there are stress conditions. Multigene families encode them whose expression is controlled temporally and spatially during the course of development. Moreover, external stimuli also affect the response of some CDPK genes. The CDPK pathway increases the LEA protein expression for the anti-desiccation purpose (Serrano et al. 2003). LEA-type gene activation is regulated by various pathways such as the dehydration-responsive element (DRE)/C-repeat (CRT), apart from osmolyte generation pathways. Such gene activation is part of damage repair pathways. LEA-type genes also play their role when natural desiccation occurs during maturation and development. In higher plants, under conditions of severe desiccation, high osmolality, and low temperatures, LEA proteins are found to be accumulated in higher concentrations (Xiong and Zhu 2002). These LEA proteins are involved in the preservation of protein structure and membrane integrity by binding water, sequestering ions in stressed tissues, and preventing protein denaturation. LEA proteins and chaperones also provide dehydration protection to various macromolecules such as mRNAs, enzymes, and lipids (Yamaguchi-Shinozaki 2002). Similarity in sequence of a minimum of six LEA protein families becomes the basis of their sequence identification.

20.4.1.3 Calcium-Dependent Salt Overly Sensitive (SOS) Signaling

SOS signaling depending upon calcium provides protection during salt stress from ionic perspective. Ion transporters that maintain homeostasis of ions are targeted mainly in this signaling pathway. Activation of the SOS pathway occurs in response to excess amounts of intracellular or extracellular sodium ions, which in some way triggers a cytoplasmic Ca^{2+} signal. As a result of activation, it causes changes in activity and expression of ion transporters such as sodium (Na^+), potassium (K^+), and hydrogen ions (H^+). As a whole, signal transduction during salt stress due to climatic changes involves regulation of ionic and osmotic signaling pathways and pathways leading to detoxification and control of growth. The SOS pathway controls signaling involving ions during salt stress (Zhu 2002). SOS1, SOS2, and S0S3 act via a similar pathway to improve tolerance during stress. The protein kinase complex, composed of calcium-binding subunit SOS3 and kinase subunit SOS2, in response to calcium controls the activity and expression of ion transporters like SOS1. In the model plant, Arabidopsis, the SOS3-SOS2 protein kinase complex is genetically proved to be involved in the mediation of the SOS1 gene in salt stress, thus leading to the regulation of the SOS1 transporter. The complex is also involved in direct phosphorylation and activation of the SOS1 transporter (Xiong et al. 2002; Serrano et al. 2003). Studies reporting the sequence of the SOS1 protein and showing growth comparison of plants of wild and mutant type during salt stress have suggested that Na^+/H^+ ion exchangers or antiporters are encoded by SOS1 on the cell membrane (Shi et al. 2000). A number of homologs of SOS2 and SOS3 have been identified for their roles in the activation of different pathways that transduce various other stress signals. Arabidopsis, along with SOS2 and SOS3, has been identified with 8 Ca^{2+}-binding proteins similar to SOS3 and 22 protein kinases similar to SOS2 (Guo et al. 2001). Various proteins that bind calcium sense the rise in Ca^{2+} concentration in the cytosol. During climatic stress, the SOS3 family of Ca^{2+} sensors and CDPKs is reported to play an important role in signal transduction leading to specific protein phosphorylation cascades. Hence, during salt stress, Ca^{2+} signaling is thought to have a vital role in stress tolerance (Xiong et al. 2002). Ca^{2+} level can be modulated by various second messengers, which results in the initiation of various phosphorylation pathways that activates cellular protection proteins or transcriptions factors (TF). These TFs regulate some specific stress-responsive genes. Such type of genes is involved in the regulation of synthesis of various hormones like ethylene, salicylic acid (SA), and abscisic acid (ABA). Their synthesis is increased during stress and they help in stress tolerance and signaling in plants. Stress signals, mainly salt and drought, activate genes that encode enzymes involved in ABA synthesis. It results in an increased ABA accumulation and biosynthesis, which can metabolize quickly when stress is relieved. As a feedback, expression of ABA biosynthetic gene can be stimulated by ABA itself via phosphoprotein cascade dependent on Ca^{2+} (Zhao et al. 2001). As a result of these regulatory molecules, another signaling pathway following the previously mentioned pathway can be initiated. The secondary signals and components, as well as output, can differ from primary stimuli in their specificity. Therefore, multiple signaling pathways can be activated by primary stress signals, which can differ in space, time, and outputs. These multiple pathways due to some similar components can form interlinked networks (Xiong et al. 2002; Wang et al. 2003, 2003). Probable results of pathways involved in osmotic signaling include water and osmolyte transport systems, gene expression, and activation of enzymes involved in the biosynthesis of osmolytes. Other changes are thought to be the result of detoxification signaling due to such climatic stress. In detoxification signaling, LEA-type genes, proteinases, and molecular chaperones are expressed, phospholipid hydrolysis occurs, and enzymes that take part in the removal and generation of ROS and various other proteins involved in detoxification are activated (Zhu 2002).

20.4.2 Abiotic Stress-Inducible Genes

A variety of molecular mechanisms and specific gene sets in plants take part in stress response induced by various abiotic factors. Drought stress due to climate induces a number of genes that are involved in the synthesis of metabolic proteins which protect cells from dehydration. Moreover, genes involved in signal transduction are also regulated sequentially (Xiong and Zhu 2002; Yamaguchi-Shinozaki 2002; Shinozaki et al. 2003). Three main groups of products produced as a result of gene regulation during stress can be classified as: (a) products directly providing cellular protection to plants, e.g., chaperones, LEA proteins, antifreeze proteins, heat stress proteins (HSPs), osmoprotectants, free radical scavengers, detoxification enzymes, etc.; (b) products regulating transcription and involved in signaling pathways, e.g., CDPK, phospholipases, MAPK (Frank et al. 2000; Ludwig et al. 2004), SOS kinase (Shinozaki and Yamaguchi-Shinozaki 2000; Zhu 2001a, b), and transcriptional factors (Choi et al. 2000; Shinozaki and Yamaguchi-Shinozaki 2000); and (c) products taking part in transport and uptake of water and ions such as ion transporters and aquaporins (Blumwald 2000). These genes cause an increase in the response against abiotic stress factors by mainly inducing the expression of TFs.

20.4.3 Transcription Factors

Transcription factors (TFs) are micromolecules that regulate gene expression by attaching to DNA at specific sites. Genomes of plants consist of a number of transcription factors, for instance, around 5.9% of the Arabidopsis genome encodes more than 1500 TFs (Riechmann et al. 2000). Numerous TFs are from a limited number of large multigene families. Response to several stress stimuli is often different in some specific members of a similar family, but in some members' response to various stresses might be the same as gene expression profiles overlap significantly (Bohnert et al. 2001; Seki et al. 2001; Chen et al. 2002; Fowler and Thomashow 2002). As a result, during climatic stresses, similar signaling pathways and cellular responses are often activated, such as increase in the levels of osmoprotectants, stress-responsive protein synthesis, and increased production of ROS scavengers (Knight and Knight 2001). The presence of TFs among the stress-inducible genes suggests their regulatory roles in various stress signal transduction pathways (Knight and Knight 2001; Zhu 2002). Once activated, these molecules bring about morphological, anatomical, biochemical, and physiological changes in the plant body in order to facilitate their survival in such harsh conditions. However, there is a limit to which these plant responses can contain the effects of the environmental and climatic stress factors. Appropriate intervention strategies have to be developed to address them.

20.5 Mitigation and Interventional Strategies to Address Climate Change

A variety of procedures and strategies have been developed by the concerned legislative, regulatory, and scientific bodies to decrease the effects of climate change on the living organisms and vice versa. Laws aiming at decreasing the carbon footprint have been approved and applied by a number of countries throughout the world, which have demonstrated short-term positive outcomes. Similarly, from the biotechnological perspective, an increased effort has been made to understand and employ mitigation strategies to decrease the effects of climate change on plants.

In case of exposure of the plant to environmental stress due to changing climate, a variety of genes get activated, which causes upregulation of several metabolites and proteins, which provide defense against stressful conditions. Continuous efforts for obtaining plant breeds with improved stress tolerance profiles are being made. To enhance the breeding programs, advance molecular techniques involving use and identification of molecular markers are being employed. However, unwanted features from donor parents are expressed, which is the major drawback in the introduction of genomic portions (QTLs) that improves tolerance to stresses. Hence, improvement of genetically engineered plants is required either by addition or overexpression of specific genes (Allen 1995).

Various possible targets for engineering the plants to enhance their stress tolerance profiles include genes that are part of regulatory and signaling pathways (Seki et al. 2003; Shinozaki et al. 2003), or genes that code for stress tolerance proteins (Wang et al. 2004), or enzymes that are involved in the synthesis of structural and functional metabolites (Park et al. 2004). Recent developments in plant engineering for the production of stress-tolerant plants have to led to various important attainments, yet the complexity of genetic processes involved in environmental stress tolerance makes it hard to achieve the goal. Therefore, the integration of biotechnology with classical breeding and physiology is needed (Wang et al. 2003; Flowers 2004).

20.5.1 Stress Regulatory and Signaling Pathways

Genes that control transcription and signaling cascades, such as mitogen-activated protein kinases (MAPK), salt overly sensitive (SOS) kinases, and various transcription factors, have been widely studied in plants for their possible roles in response to climatic stresses (Zhang et al. 2004). Alteration of these, as a result of genetic engineering, can result in the production of transgenic plants that are more tolerant to abiotic stress (Vinocur and Altman 2005). Recent studies have reported that nicotiana protein kinase/mitogen- activated protein kinase kinase kinase (NPK1/MAPKKK) expression in maize plant activates an oxidative signal cascade that leads to better tolerance during salinity and thermal stress in transgenic plants (Shou et al. 2004).

20.5.2 Heat-Shock Proteins and Chaperones

During climatic stresses, heat-shock proteins (HSPs), molecular chaperones, and late embryogenesis abundant (LEA) protein families are reported to be vital in producing a stress-tolerance response (Wang et al. 2003; Flowers 2004). Increase in expression of these can enhance the plant ability to tolerate abiotic stress (Sun et al. 2002). Genetically transformed rice plants, with overexpression of HSP101 gene from Arabidopsis, have shown significant progress in growth during retrieval from heat stress (Katiyar-Agarwal et al. 2003). Improved dehydration tolerance is also found in genetically engineered rice plants through the overexpression of the HVA1 isolated form *Hordeum vulgare* L plant (Babu et al. 2004).

20.5.3 Reactive Oxygen Species

In the presence of stresses, whether abiotic or biotic, reactive oxygen species (ROS) production and the associated oxidative damage to plants can be alleviated by the use of various ROS scavengers and antioxidants (Mittler 2002). In transgenic plants, overexpression of ROS scavengers and antioxidants like *Chlamydomonas* glutathione peroxidase, such as in transgenic tobacco, conferred increased oxidative stress tolerance induced by several stress signals (Yoshimura et al. 2004). Recent studies have reported the improvement in tolerance to various abiotic stresses such as heat, heavy metal salt, and hydrogen peroxide in genetically transformed plants due to overexpression of aldehyde dehydrogenase, which increases the metabolism of toxic aldehydes generated by the reaction of ROS with proteins and lipids (Sophos and Vasiliou 2003).

20.5.4 Stress-Associated Metabolites

A variety of metabolites such as amines (glycine), amino acids (Pro), and various sugars (mannitol) have been identified to help in providing tolerance against stress in plants. Increased generation of some required substances and reduction in the levels of toxic substances are two major strategies which can be employed in metabolic engineering (Capell and Christou 2004). Increased levels of Pro are also linked to better stress tolerance in plants. Transgenic tobacco plants overexpressing [delta] pyrroline 5 carboxylate synthetase (P5CS) show rise in Pro levels. However, upregulation of Pro dehydrogenase can cause a decrease in Pro levels (Konstantinova et al. 2002). In Arabidopsis, knockout of Pro dehydrogenase or transformation with its antisense results in increased levels of Pro, leading to better environmental stress tolerance (Mani et al. 2002).

Amines like GB have been recognized as osmoprotectants; the accumulation of these resulted in an increase in plant stress tolerance abilities. Transgenic plants of tobacco with betaine aldehyde decarboxylase from *Suaeda liaotungenis* were significantly resistant to salt stress. Mutant rice plants transformed with the choline dehydrogenase gene, which codes for the product that facilitates choline oxidation to GB, showed better recovery from salt stress than that in wild type (Mohanty et al. 2002). Co-targeting, the multiple steps of one pathway, was shown to be an effective approach for overexpressing GB in bacteria and plants. Certainly, the stress tolerance ability was increased in tobacco plants and *E. coli* with the aldehyde-choline dehydrogenase fusion protein. Polyamines, in plants, have also been recognized to play a vital role in stress tolerance (Nahar et al. 2016). Genetic engineering studies targeted to increase the levels of polyamines can result in the production of stress-tolerant plants as evident from proceeding examples. Overexpression of ornithine decarboxylase, *S*-adenosyl-methionine decarboxylase, and arginine decarboxylase (ADC) results in a significant increase in putrescine levels and a small increment in spermine and spermidine levels. During stress conditions of drought, higher levels of putrescine are observed in genetically modified rice plants overexpressing *Datura stramonium* ADC, which leads to increased spermine and spermidine synthesis and ultimately the protection of plant against drought conditions (Capell et al. 2004). Similarly, transgenic Arabidopsis overexpressing spermidine synthase cDNA from *Cucurbita ficifolia* have shown improved stress tolerance (Kasukabe et al. 2004). Genetic transformation of carbon metabolism and a variety of sugars, due to their possible roles in stress responses, can result in the production of more stress-tolerant plants. A nonreducing sugar – trehalose – is found in some desiccation-tolerant plants and in a number of bacteria. Increased expression of trehalose in transgenic rice plants has shown the development of high stress-tolerant abilities, implied by a reduction in photo-oxidative damage and higher rates of photosynthesis during stress conditions (Garg et al. 2002). Mannitol, an important sugar alcohol, helps alleviate salt and water stress. Expression of mannitol-1-phosphate dehydrogenase gene resulted in more stress-tolerant transgenic wheat plants as evident from an increase in number of tillers, plant height, and biomass. Employment of biotechnological tools to enhance the production of agents that can decrease the effects of climate change should, hence, be exploited to enhance the quality and quantity of the agricultural products.

20.6 Conclusion

Climate change, as discussed, is a spatiotemporally prevalent global scenario that tends to affect all the living organisms. Plants have developed various mechanisms to address the issues arising due to climate change. However, these responses are temporary and cannot prevent the plants in extremes of climatic conditions. The employment of biotechnological approaches can help in the screening, detection, dissecting, mitigating, and modifying the natural defense mechanisms to address the threats of these abiotic stress factors. Latest techniques like RNA interference technology, chromosome engineering, and targeted gene replacement in addition to the omics tools can be used to derive maximum benefits from the minimum resources in a safe and effective manner. Globally harmonized legislative and scientific efforts are needed to exploit the possibilities of newer interventional strategies.

References

Allen RD (1995) Dissection of oxidative stress tolerance using transgenic plants. Plant Physiol 107(4):1049

Arguez A, Durre I, Applequist S, Vose RS, Squires MF, Yin X, Heim RR Jr, Owen TW (2012) NOAA's 1981–2010 US climate normals: an overview. Bull Amer Meteor Soc 93(11):1687–1697

Babu RC, Zhang J, Blum A, Ho T-HD, Wu R, Nguyen H (2004) HVA1, a LEA gene from barley confers dehydration tolerance in transgenic rice (*Oryza sativa* L.) via cell membrane protection. Plant Sci 166(4):855–862

Bissolli P, Ganter C, Li T, Mekonnen A, Sanchez-Lugo A (2018) 7. Regional climates. Bull Amer Meteor Soc 99(8):S193–S193

Blumwald E (2000) Sodium transport and salt tolerance in plants. Curr Opin Cell Biol 12(4):431–434

Bohnert HJ, Ayoubi P, Borchert C, Bressan RA, Burnap RL, Cushman JC, Cushman MA, Deyholos M, Fischer R, Galbraith DW (2001) A genomics approach towards salt stress tolerance. Plant Physiol Biochem 39(3–4):295–311

Boyer JS (1982) Plant productivity and environment. Science 218(4571):443–448

Capell T, Bassie L, Christou P (2004) Modulation of the polyamine biosynthetic pathway in transgenic rice confers tolerance to drought stress. Proc Natl Acad Sci 101(26):9909–9914

Capell T, Christou P (2004) Progress in plant metabolic engineering. Curr Opin Biotechnol 15(2):148–154

Chen W, Provart NJ, Glazebrook J, Katagiri F, Chang HS, Eulgem T, Mauch F, Luan S, Zou G, Whitham SA (2002) Expression profile matrix of Arabidopsis transcription factor genes suggests their putative functions in response to environmental stresses. Plant Cell 14(3):559–574

Choi H-I, Hong J-H, Ha J-O, Kang J-Y, Kim SY (2000) ABFs, a family of ABA-responsive element binding factors. J Biol Chem 275(3):1723–1730

Church JA, White NJ, Konikow LF, Domingues CM, Cogley JG, Rignot E, Gregory JM, van den Broeke MR, Monaghan AJ, Velicogna I (2011) Revisiting the Earth's sea-level and energy budgets from 1961 to 2008. Geophys Res Lett 38(18):L18601 (1–8)

Field C, Barros V, Stocker T, Qin D, Dokken D, Ebi K, Mastrandrea M, Mach K, Plattner G-K, Allen S (2012) IPCC, 2012: Managing the risks of extreme events and disasters to advance climate change adaptation A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change CUP. 30(11):7575–7613

Flowers T (2004) Improving crop salt tolerance. J Exp Bot 55(396):307–319

Fowler S, Thomashow MF (2002) Arabidopsis transcriptome profiling indicates that multiple regulatory pathways are activated during cold acclimation in addition to the CBF cold response pathway. Plant Cell 14(8):1675–1690

Frank W, Munnik T, Kerkmann K, Salamini F, Bartels D (2000) Water deficit triggers phospholipase D activity in the resurrection plant *Craterostigma plantagineum*. Plant Cell 12(1):111–123

Garg AK, Kim J-K, Owens TG, Ranwala AP, Choi YD, Kochian LV, Wu RJ (2002) Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses. Proc Natl Acad Sci U S A 99(25):15898–15903

Guo Y, Halfter U, Ishitani M, Zhu J-K (2001) Molecular characterization of functional domains in the protein kinase SOS2 that is required for plant salt tolerance. Plant Cell 13(6):1383–1400

Haeberli W, Cihlar J, Barry RG (2000) Glacier monitoring within the global climate observing system. Ann Glaciol 31:241–246

Hartfield G, Blunden J, Arndt DS (2018) State of the climate in 2017. Bull. Amer. Meteor. Soc 99(8):Si–S310

Holgate S, Woodworth P (2004) Evidence for enhanced coastal sea level rise during the 1990s. Geophys Res Lett 31(7)

Kasukabe Y, He L, Nada K, Misawa S, Ihara I, Tachibana S (2004) Overexpression of spermidine synthase enhances tolerance to multiple environmental stresses and up-regulates the expression of various stress-regulated genes in transgenic *Arabidopsis thaliana*. Plant Cell Physiol 45(6):712–722

Katiyar-Agarwal S, Agarwal M, Grover A (2003) Heat-tolerant basmati rice engineered by overexpression of hsp101. Plant Mol Biol 51(5):677–686

Knight H, Knight MR (2001) Abiotic stress signalling pathways: specificity and cross-talk. Trends Plant Sci 6(6):262–267

Konstantinova T, Parvanova D, Atanassov DD (2002) Freezing tolerant tobacco, transformed to accumulate osmoprotectants. Plant Sci 163(1):157–164

Ludwig AA, Romeis T, Jones JD (2004) CDPK-mediated signalling pathways: specificity and cross-talk. J Exp Bot 55(395):181–188

Mani S, Van de Cotte B, Van Montagu M, Verbruggen N (2002) Altered levels of proline dehydrogenase cause hypersensitivity to proline and its analogs in Arabidopsis. Plant Physiol 128(1):73–83

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7(9):405–410

Mohanty A, Kathuria H, Ferjani A, Sakamoto A, Mohanty P, Murata N, Tyagi A (2002) Transgenics of an elite indica rice variety Pusa basmati 1 harbouring the codA gene are highly tolerant to salt stress. Theor Appl Genet 106(1):51–57

Nahar K, Hasanuzzaman M, Rahman A, Alam M, Mahmud J-A, Suzuki T, Fujita M (2016) Polyamines confer salt tolerance in mung bean (*Vigna radiata* L.) by reducing sodium uptake, improving nutrient homeostasis, antioxidant defense, and methylglyoxal detoxification systems. Front Plant Sci 7:1104

Noble AD, Ruaysoongnern S (2010) The nature of sustainable agriculture. In: Dixon GR, Tilston EL (eds) Soil microbiology and sustainable crop production. Springer, Netherlands, pp 1–25

Park EJ, Jeknić Z, Sakamoto A, DeNoma J, Yuwansiri R, Murata N, Chen TH (2004) Genetic engineering of glycinebetaine synthesis in tomato protects seeds, plants, and flowers from chilling damage. Plant J 40(4):474–487

Riechmann JL, Heard J, Martin G, Reuber L, Jiang C-Z, Keddie J, Adam L, Pineda O, Ratcliffe O, Samaha R (2000) Arabidopsis transcription factors: genome-wide comparative analysis among eukaryotes. Science 290(5499):2105–2110

Sánchez-Lugo A, Morice C, Berrisford P, Argüez A (2017) Global surface temperatures [in "state of the climate in 2016"]. Bull. Amer. Meteor. Soc 98(8):S11–S13

Seki M, Kamei A, Yamaguchi-Shinozaki K, Shinozaki K (2003) Molecular responses to drought, salinity and frost: common and different paths for plant protection. Curr Opin Biotechnol 14(2):194–199

Seki M, Narusaka M, Abe H, Kasuga M, Yamaguchi-Shinozaki K, Carninci P, Hayashizaki Y, Shinozaki K (2001) Monitoring the expression pattern of 1300 Arabidopsis genes under drought and cold stresses by using a full-length cDNA microarray. Plant Cell 13(1):61–72

Serrano R, Gaxiola R, Ríos G, Forment J, Vicente O, Ros R (2003) Salt stress proteins identified by a functional approach in yeast. Monatsh Chem 134(11):1445–1464

Serrano R, Mulet JM, Rios G, Marquez JA, De Larrinoa IF, Leube MP, Mendizabal I, Pascual-Ahuir A, Proft M, Ros R (1999) A glimpse of the mechanisms of ion homeostasis during salt stress. J Exp Bot 50:1023–1036

Shakun JD, Clark PU, He F, Marcott SA, Mix AC, Liu Z, Otto-Bliesner B, Schmittner A, Bard E (2012) Global warming preceded by increasing carbon dioxide concentrations during the last deglaciation. Nature 484(7392):49

Shi H, Ishitani M, Kim C, Zhu J-K (2000) The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na+/H+ antiporter. Proc Natl Acad Sci 97(12):6896–6901

Shinozaki K, Yamaguchi-Shinozaki K (2000) Molecular responses to dehydration and low temperature: differences and cross-talk between two stress signaling pathways. Curr Opin Plant Biol 3(3):217–223

Shinozaki K, Yamaguchi-Shinozaki K, Seki M (2003) Regulatory network of gene expression in the drought and cold stress responses. Curr Opin Plant Biol 6(5):410–417

Shou H, Bordallo P, Fan J-B, Yeakley JM, Bibikova M, Sheen J, Wang K (2004) Expression of an active tobacco mitogen-activated protein kinase kinase kinase enhances freezing tolerance in transgenic maize Proc Natl Acad Sci 101(9):3298–3303

Smirnoff N (1998) Plant resistance to environmental stress. Curr Opin Biotechnol 9(2):214–219

Sophos NA, Vasiliou V (2003) Aldehyde dehydrogenase gene superfamily: the 2002 update. Chem Biol Interact 143:5–22

Sun W, Van Montagu M, Verbruggen N (2002) Small heat shock proteins and stress tolerance in plants. Biochim Biophys Acta -Gene Structure and Expression 1577(1):1–9

Sunkar R, Bartels D, Kirch HH (2003) Overexpression of a stress-inducible aldehyde dehydrogenase gene from Arabidopsis thaliana in transgenic plants improves stress tolerance. Plant J 35(4):452–464

Thompson LG (2010) Climate change: the evidence and our options. The Behav Anal 33(2):153–170

Vinocur B, Altman A (2005) Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. Curr Opin Biotechnol 16(2):123–132

Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218(1):1–14

Wang W, Vinocur B, Shoseyov O, Altman A (2004) Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. Trends Plant Sci 9(5):244–252

Xiong L, Schumaker KS, Zhu J-K (2002) Cell signaling during cold, drought, and salt stress. Plant Cell 14(suppl 1):S165–S183

Xiong L, Zhu JK (2001) Abiotic stress signal transduction in plants: molecular and genetic perspectives. Physiol Plant 112(2):152–166

Xiong L, Zhu JK (2002) Molecular and genetic aspects of plant responses to osmotic stress. Plant Cell Environ 25(2):131–139

Yamaguchi-Shinozaki K (2002) Biological mechanisms of drought stress response. JIRCAS Work Rep 23:1–8

Yoshimura K, Miyao K, Gaber A, Takeda T, Kanaboshi H, Miyasaka H, Shigeoka S (2004) Enhancement of stress tolerance in transgenic tobacco plants overexpressing Chlamydomonas glutathione peroxidase in chloroplasts or cytosol. Plant J 37(1):21–33

Zhang JZ, Creelman RA, Zhu JK (2004) From laboratory to field. Using information from Arabidopsis to engineer salt, cold, and drought tolerance in crops. Plant Physiol 135(2):615–621

Zhao Z, Chen G, Zhang C (2001) Interaction between reactive oxygen species and nitric oxide in drought-induced abscisic acid synthesis in root tips of wheat seedlings. Funct Plant Biol 28(10):1055–1061

Zhu J-K (2001a) Cell signaling under salt, water and cold stresses. Curr Opin Plant Biol 4(5):401–406

Zhu J-K (2001b) Plant salt tolerance. Trends Plant Sci 6(2):66–71

Zhu J-K (2002) Salt and drought stress signal transduction in plants. Annu Rev Plant Biol 53(1):247–273

Chapter 21
Plant Signaling Under Adverse Environment

Qurat ul ain Sani, Wajahat Maqsood, Faiza Munir, Adil Hussain, and Rabia Amir

Contents

Abstract Plants are the primary producers for all different types of ecosystems on earth. They use abiotic sources of energy such as light and inorganic chemical compounds to build organic molecules which are used as carbon and energy source by all other organisms. Evolutionary biologists have long considered plant domestication by humans as a coevolutionary process between plants and human beings in which both the partners have changed over time. However, there are other important

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factors that seem to have been ignored while discussing the "*plant-hominin coevolutionary continuum*." These are the different environmental conditions including various biotic and abiotic factors that have changed so much over time. These changes range from fast, short-term, or acute to slow, gradual, long-term, or chronic changes. Plants that adapted to these changing environmental conditions were favored by humans for domestication and hence they exist today, whereas those that could not cope with environmental changes went extinct. The genetic record of such adaptations is carried by today's plant genomes. These adaptations are the genetic legacy of hundreds of millions of years of natural selection shaped by the changing environment. Though plants affect the environment, they are shaped by the environment. Humans have recently woken up to their self-made problems of overpopulation, urbanization, pollution, indiscriminate use of fossil fuels, rising temperatures, melting glaciers, and others. All these ultimately translate into climate change. Though climate change events have been recorded throughout the history of the planet earth, every time *life* found a way to survive. But this time the situation is much worse as climate is changing at a much faster and severe rate and scientists predict that it may be impossible for the earth, humans, plants, and others to survive. In this scenario being the only primary producers, plants are as equally an important stakeholder as humans. If planet earth is to support the predicted nine billion human population by 2050, crop plants will need to tolerate and adapt to climate change at a rate and way that they have never done before. How plants sense different stresses and adapt to adverse environmental conditions are fundamental questions that need to be answered. In this chapter, we gather the important scientific studies that try to answer these questions through research, experimentation, and evidence at molecular level. We have discussed plant adaptation to adverse environment via strategies like calcium signaling, MAP kinase signaling, stress-sensing and other signaling molecules, antioxidant defense, phytohormone biosynthesis and signaling, transcriptional regulation of response cascades under stress, and the cross talk between different stress responses.

Keywords Abiotic stress signaling · Plant defense response · Transcriptional regulation

Abbreviations

ABA	Abscisic acid
ABRE	ABA-responsive element
ADC	*Arginine decarboxylase*
APX	Ascorbate peroxidase
AsA-GSH cycle	Ascorbate-glutathione cycle
BR	Brassinosteroids
bZIP	Basic leucine zipper
Ca^{2+}	Calcium ions

CaM	Calmodulin
CBK	CaM-binding protein kinase
CcaMKs	Calmodulin-dependent protein kinases
CDPKs	Ca^{2+}-dependent protein kinases
CK	Cytokinins
CNGCs	Cyclic nucleotide-gated channels
DHAR	Dehydroascorbate reductase
DRE	Dehydration-responsive element
DRE/CRT	Dehydration-responsive element/C-repeat
ET	Ethylene
GLR	Glutamate-like receptor
GPCRs	G protein-coupled receptors
GR	Glutathione reductase
GST6	Glutathione s-transferase6
GSTs	Glutathione *S*-transferases
H_2O_2	Hydrogen peroxide
JA	Jasmonic acid
LRR-RLKs	Leucine-rich repeat RLKs
MAPKs	Mitogen-activated protein kinases
NIG	NaCl-induced gene
Ocs	Octopine synthase
PA	Polyamines
PLD	Phospholipase D
RLKs	Receptor-like kinase
ROS	Reactive oxygen species
SA	salicylic acid
SAA	Systemic Acquired Acclimation
Spd	Triamine spermidine
SPDS	*Spd synthase*
Spm	Tetramine spermine
SPMS	*Spm synthase*
TFs	Transcription factors
UV	Ultraviolet

21.1 Introduction: Abiotic Stress Signaling in Plants

Plants being sessile organisms are often exposed to a plethora of abiotic stresses (Bohnert and Sheveleva 1998; Smirnoff 1998). Abiotic stresses are harmful effects caused by nonliving environmental elements that include drought, extreme cold or heat, critical pressure, intense light, salinity, change in pH, mineral deficiencies, redox reactions, acidic or alkaline soils, radiations, mechanical stresses, and extreme wind (Neha et al. 2008). Environmental adversities like water shortage have disastrous effects in plants all around the world (Garg et al. 2008).

Abiotic stresses have a profound impact on the cellular environment of plants in terms of the different types and quantity of macro- and micromolecules produced either as a stress by-product or as a cellular response mechanism. These molecules include compounds such as amino acids, proteins, nucleic acids, and carbohydrates. Response to abiotic stresses is characterized by a rapid to long-term and local to global change in the transcriptome. Several genes are induced by environmental adversities, for example, RD29A, that have been identified in many species of plants such as Arabidopsis. The overexpression of the aforementioned gene plays a role in effective response and tolerance against stress factors in planta (Hirayama and Shinozaki 2010a). Several forms of induction stages occur because of varying dependency on de novo production of signaling molecules or proteins, including abscisic acid (ABA) (Hamm 1998; Hirayama and Shinozaki 2010b; Yamaguchi-Shinozaki and Shinozaki 2006) and other phytohormones.

Gene expression profiling under abiotic stresses has become possible after successful whole genome sequencing (Kilian et al. 2007). By means of microarray experiments, many products of stress-inducible genes have been identified which can be categorized in two classes (Shinozaki et al. 2003): one consisting of those proteins which are specifically involved in abiotic stress tolerance directly such as late embryogenesis abundant (LEA) proteins and second comprising factors that regulate expression of stress-inducible genes and intracellular signaling molecules such as phosphatases, protein kinases (MAPK), several transcription factor proteins, and phospholipid metabolic enzymes. It has been presumed that the plants possess an effective cellular response system against abiotic stress factors after the successful identification of stress-inducible genes in certain signal transduction pathways (Hirayama and Shinozaki 2010a). Plant responds to stress adversities via integration of several mechanisms as shown in Fig. 21.1.

21.2 Plant Strategies to Acclimate Under Adverse Environmental Conditions

A plant is affected by stress as soon as abrupt changes occur in the environment. Unlikely, certain plant species that are highly stress tolerant respond in a different manner that is acclimating to that specific stress over time. Therefore, acclimation and stress are eventually associated with each other in plants. Stress-induced homeostasis is considered as a signal for plants to begin processes necessary for modulation of new homeostasis linked to acclimation. Plants elicit resistance or tolerance response depending on the genetic capability of that plant to maintain homeostasis in a time-dependent manner. The adjustment of homeostasis linked to a new acclimated state is not merely the result of a single physiological mechanism but rather many of them are integrated over the period of plant acclimation. Upon stress, the short-term physiological processes begin in a few seconds or minutes though they are transitory

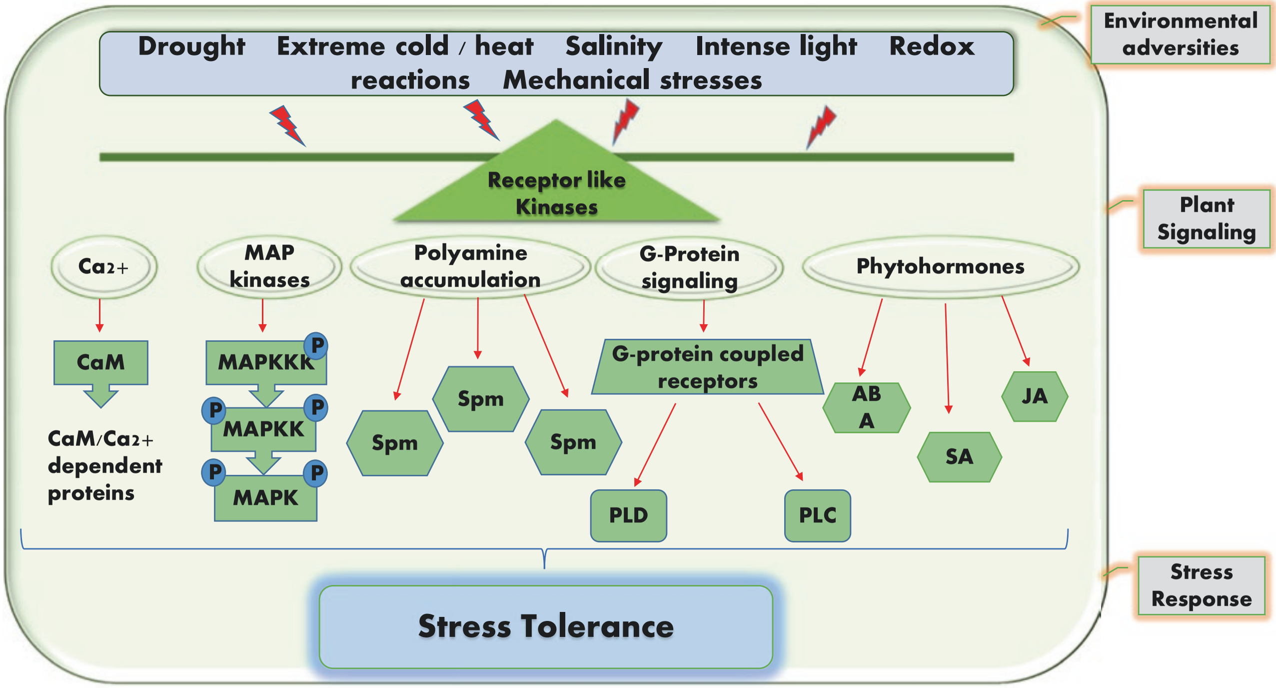

Fig. 21.1 Schematic representation of the plant response continuum under environmental stress. Plant defense response employs integration of several mechanisms in order to survive under environmental adversities. The plant cell perceives stress signals on receptor-like kinases found in the cell membrane and then transduce them down through signaling pathways including MAP kinase signaling, calcium ion signaling, G protein signaling, phytohormone signaling, and ROS signaling and through the accumulation of polyamines which turn on transcriptional factors for regulation of gene expression thus increasing the plant potential to tolerate stress. Information retrieved from (Hirayama and Shinozaki 2010a, b)

in nature. It means such processes are not only rapidly detected in stressful conditions but also vanish very soon. However, long-term physiological processes are comparably more stable, as they last longer. But in the period of plant acclimation, lifetimes of short-term and long-term processes intersect in time in such a way that the former initiate responses just after the onset of stress in contrast to long-term processes that are still detectable after some time. Thus, the pyramid of short-term and long-term processes shows that the execution of an acclimated state is a complicated process that requires time.

It is crucial to comprehend the interaction of stress-induced signaling pathways and the points of their cross talk which switch from one signaling pathway to the other. Calcium sensors are assumed as the initial response of a plant to external stimuli which generates downstream signaling. Many phytohormones also regulate stress responses, out of which abscisic acid (ABA) is the major hormone and has the ability to interact with salicylic acid (SA) and jasmonic acid (JA) signal transduction pathways. G proteins are also known to play a key role in regulating transduction pathways (Ku et al. 2018). The abovementioned components that play a key role in plant stress tolerance are described in Table 21.1.

Table 21.1 Components that play a key role in plant defense response under stress conditions

Components involved in plant signaling	Role in abiotic stress	References
Calcium ions	Act as messenger	Reddy et al. (2011);
	Regulate gene expression	Poovaiah et al. (1987)
Receptor-like kinases	Sense and perceive extracellular ligands	Osakabe et al. (2013)
	Activate the downstream signaling pathway	
Mitogen-activated protein kinases	Involved in cell division and differentiation	Tuteja and Singh (2012)
	Involved in stress responses	
	Regulate antioxidant defense system	
Polyamines	Stabilize the cell components	Todorova et al. (2015)
	Protect the macromolecules from the free radicals	Fariduddin et al. (2013)
	Component of adaptive mechanisms	
	Activate antioxidant defense system	
G proteins	Involved in transduction of extracellular signals into intracellular environment	Apone et al. (2003)
	Regulate several enzymes	Chakraborty et al. (2015)
	Regulate the expression of LEA and LEA-like genes	
Phytohormones	Mediate defense response in plants	Nakashima and Yamaguchi-Shinozaki (2013)
Transcription factors	Regulate responsive genes	Singh et al. (2002)
	Increase stress tolerance potential	

21.2.1 The Role of Calcium in Abiotic Stress Signaling

Stress causes signal-specific alterations in cellular calcium levels, which plays a role in the regulation of various physiological processes that are critical for adaptation of plants to stress. Many calcium and calmodulin (CaM)-binding transcription factors have been isolated and characterized in plants. The identified transcription factors function in signaling pathways, determined by means of functional analyses (Reddy et al. 2011). Calcium ions are not only a major nutrient but also a key ion for maintenance of cell wall rigidity, structure, and function (Hepler 2005). Plants use calcium as a messenger more than other messenger molecules of plants and animals. Through the use of a variety of technologies which can monitor free calcium in the cytosol and other cellular compartments, it has been indicated that every other signal including developmental, hormonal, or stress swiftly elevates calcium ions, mainly in the cytosol and sometimes in other cellular compartments (Reddy et al. 2011). In addition to that, alterations in the level of calcium depend on a given stress with respect to the place in the cell where change occurs, for example, in the nucleus, cytosol, other organelles, or any other place within the cell. Besides that, the duration and magnitude of elevation also depend on that particular stress (McAinsh et al. 1996). Besides growth and development, environmental responses are also highly associated with the timely expression of particular genes in related cells at the right time. Meanwhile, Ca^{2+} was found not only to serve as messengers but also as regulators of gene expression in plants (Poovaiah et al. 1987).

The level of Ca^{2+} in cells regulates gene expression by means of Ca2+ sensors (Reddy et al. 2011). Following their activation, Ca^{2+} sensors finally bind with Cz elements present in the promoter region of particular genes resulting in repression or induction of gene expression. Moreover, these sensors may also control DNA-binding proteins and finally activate or repress gene expression. Eventually, higher levels of cellular Ca^{2+} trigger associated phosphatases or protein kinases (CaM-binding protein kinase [CBK], CDPK, and CCaMK) that phosphorylates/dephosphorylates particular DNA-binding proteins to mediate gene expression. Some of the Ca^{2+} sensors are present in a nucleus, while others are transported to the nucleus as a defense response against stress. For example, At-CDPK2 and Mc-CDPK1 are triggered against osmotic and salt stress, respectively, thus suggesting significance of these proteins in the proper functioning of the nucleus. It is presumed that signal induction regulates gene expression by means of one or a combination of all of these signaling pathways (Hepler 2005; Raichaudhuri et al. 2006; Reddy et al. 2011).

It has been reported that two transcription factors (TFs), i.e., *Arabidopsis* NaCl-induced gene (NIG) and At-CaM7, directly bind with Ca^{2+}. *Arabidopsis* NaCl-induced gene (NIG) shows response against salt stress and encodes the first identified plant TF that participates in direct Ca^{2+} binding (Kim and Kim 2006). NIG1 is comprised of the N-terminal and C-terminal which contain the EF hand like the Ca^{2+}-binding motif and helix-loop-helix DNA-binding domain. This TF binds to another motif CANNTG, which is also called E-box. DNA-binding domains are also found in some additional EF hand proteins (Day et al. 2002), but their functions are not known (Reddy et al. 2011).

At-CaM7 participates actively in transcriptional regulation. It has been reported that Ca^{2+}/CaMs perform functions indirectly by triggering protein functions through their activation or deactivation. Conversely, CaM7 has been found rare as it directly coordinates with promoter regions of those genes that work in the development of a seedling (Kushwaha et al. 2008). In plants, there are light modulating genes with a promoter region that contains the Z-/G-box (ATACGTGT/CACGTG) to which CaM7 binds, thus regulating gene expression and photomorphogenesis. Nevertheless, the influence of Ca^{2+} binding on CaM7 DNA-binding activity is still under study. However, there is a chance of additional unrevealed Ca^{2+} sensors that also interact with other particular DNA sequences. Future examinations including biochemical investigations and EF hand proteins will help us in further exploration of other Ca^{2+}-binding transcriptional factors (Reddy et al. 2011).

21.2.2 MAP Kinase Signaling and Abiotic Stress Responses

These enzymes are involved in reverse phosphorylation for the transmission of signals. The MAPKKKs (MAPK kinase kinase) work by the signaling cascade in which the downstream kinase gets phosphorylated by the upstream kinases in a particular order (Xiong and Ishitani 2006). MAPK kinase kinase (MAPKKK), a MAPK kinase (MAPKK), and a MAPK are the three important components of this aforementioned cascade and interact with each other through phosphorylation. Moreover, such kinases perform both intra- and extracellular signaling in plants by shifting the information from sensors towards specific cellular responses such as cell differentiation, cell division, and stress response. MAPK signaling has also been associated with hormonal responses. In plants, MAP kinases are represented by multigene families and are involved in efficient transmission of specific stimuli and also involved in the regulation of the antioxidant defense system in response to stress signaling. These MAPK signaling pathways are triggered by different abiotic stresses (Tuteja and Singh 2012) as a representative of specificity in the system. MAPK actively participates in cell signaling cascades which are triggered by various abiotic factors including salt, heat, cold, wounding, UV, touch, heavy metals, and osmotic stress (Tuteja and Singh 2012). Additionally, CTR1, ANP1–3, and AtMEKK are three MAPKKKs found in *Arabidopsis thaliana.* Three *AtMEKK* genes are expressed under stress conditions such as cold (Knight and Knight 2001). Activation of the plasma membrane triggers MAP3Ks or MAP4Ks in response to stress (Dan et al. 2001). MAP4Ks play a vital role as mediators that interlink upstream signaling components to the central MAPK cascade. Two amino acids present in S/T-X3–5-S/T MAP3K motif are phosphorylated by serine/threonine MAP3Ks in the activation loop of MAP2Ks. MAP2Ks in turn phosphorylate the MAPKs at the tyrosine and threonine residues located in a highly conserved T-X-Y motif (Chang and Karin 2001). These kinases are capable of phosphorylating an array of substrates which also involve other types of kinases and transcriptional factors. The synthesis and stability of the MAPK cascade can also be modulated by adaptor or anchoring proteins, shared docking domains, and scaffold proteins (Takekawa et al. 2005).

Members of the MAPK signaling pathway can be triggered by various stress factors such as MPKs, for example, the *A. thaliana* AtMPK6 which is involved in H_2O_2, O_3, ABA, JA, and ethylene signal transduction pathways, and also play a role in significant developmental processes including anther and embryo development and epidermal patterning (Teige et al. 2004).

21.2.3 Role of Receptor-Like Kinases in Plant Defense

Receptor-like kinases are the type of proteins which sense environmental stimuli and relay down to inter- and intracellular networks. They belong to a large family of genes in plants and contain a cytosolic domain named as Ser/Thr kinase. These receptor proteins function in sensing and perceiving extracellular ligands and activate the downstream signaling pathway by phosphorylating the intracellular threonine/serine kinase domains (Osakabe et al. 2013). Plants also require energy for reprogramming signaling pathways so that they can employ adaptive responses under stresses (Thao and Tran 2012). Phytohormones act as endogenous signals. They coordinate and mediate biochemical as well as molecular mechanisms that enable plants to tolerate environmental stresses and manage overall development (Choudhary et al. 2012). RLKs have been shown to integrate phytohormone signaling under environmental stress conditions (Shiu 2001). During this period of growth and development in plants, the external stimuli activate a harmonized intercellular signaling for a coordinated defense response against the stress. Such an intercellular communication determines the fate of the cells and development of plant organs (Van Norman et al. 2011). Physical stimuli, ions, small organic molecules, and peptides are involved in cell-cell coordination.

Receptor-like kinases can convey the perceived signals by catalytic activity of protein kinases towards the specified proteins inside the cytoplasm of cells. The RLK family in Arabidopsis is comprised of more than 600 members, with leucine-rich repeat RLKs (LRR-RLKs) forming the largest collection (Gish and Clark 2011). These proteins are also capable of maintaining homeostasis under stress (Smith et al. 2011).

21.2.4 Abiotic Stress Sensing and Putative Sensors in Plants

Plant cells are capable of sensing numerous environmental stress stimuli by altering physiology, metabolism, and gene expression. Despite a lot of efforts, only a small number of putative sensors have been described. In part, it may be due to the fact that plant genomes consist of a large number of gene families. Each family consists of multiple genes with almost the same function resulting in high redundancy, and a loss or dysfunction of such genes does not produce significant effects. Hence, a direct conclusive evidence for the presence of stress sensors is hard to obtain and would be challenging to demonstrate a protein or macromolecule directly involved in sensing physical, chemical, and/or stress stimuli (Zhu 2016).

Stress factors such as high or low temperatures, osmotic stress agents, heavy metal or oxidative stress, and abscisic acid are known to cause elevation in concentrations of free cytosolic calcium that can be observed by scientists by means of other calcium reporters or genetically encoded aequorin (Zhu 2016). Plants possess a diverse family of channels such as cyclic nucleotide-gated channels (CNGCs) and another family of glutamate receptor-like (GLR) channels which generate Ca^{2+} signals upon stress (Swarbreck et al. 2013). COLD1 is a transmembrane protein and a putative sensor; recently, it has been reported that this sensor regulates cold stress sensing in rice crop (Ma et al. 2015). The authors suspect that COLD1 itself is a cold stress-sensing calcium channel or may be involved in the regulation of the calcium channel (Ma et al. 2015). But it is vague how this sensor plays a role in calcium sensing and results in cold tolerance. The fluidity of phospholipid membranes in the cell are altered by both high and low temperatures (Sangwan et al. 2002). High temperature may be detected by molecular chaperons that then bind to the misfolded proteins formed by heat denaturation (Sangwan et al. 2002). This binding would help in the release of transcription factors associated with heat stress from the chaperons thus allowing the transcription factors to trigger the heat stress-responsive genes. In plants, recently reported H2A-Z comprising nucleosomes are also proposed as thermosensory apparatus (Kumar and Wigge 2010).

Stress sensing is assumed as ligand perception; therefore, it is believed as a process occurring on the cell membrane or at the cell surface, which then relays down to other subcellular organelles like the nucleus. More effective chemical genetic approaches and cutting-edge gene editing technologies may overcome the challenge of gene redundancy. The growing interest towards the significance of several cell organelles involved in the process of stress sensing and responsiveness along with a discrete stress-sensing model may also aid in the understanding of stress resistance and stress-sensing process. However, the combination of signals from various organelles is still not clear (Zhu 2016).

21.2.5 Polyamines as Potent Modulators Against Abiotic Stresses

Polyamines (PA) are a group of compounds that exist naturally in plants and possess an aliphatic nitrogen structure. Besides having roles in various physiological processes, they also respond against several environmental adversities (Gill and Tuteja 2010). Polyamines include spermine (Spm, a tetramine), spermidine (Spd, a tetramine), and an obligate precursor called putrescine (Put, a diamine) that play a critical role in the modulation of plant physiological processes such as development

(Kusano et al. 2007). PA are also involved in the plant response system against a number of unfavorable environmental factors. Besides, polyamines stabilize the cell components and protect the macromolecules from the free radicals that are generated under adverse environmental conditions. The endogenous PA in plants also contribute in stress tolerance as a component of an adaptive mechanism in order to confer the negative effects of stress (Todorova et al. 2015). These endogenous PA have the ability to scavenge free radicals and activate an antioxidant defense system to cope with environmental adversities such as deficiency of mineral nutrients, salinity, osmotic stress and drought, high- and low-temperature stress, metal toxicity, UV irradiance, ozone stress, and herbicides (Cuevas et al. 2004; Fariduddin et al. 2013; Iriti and Faoro 2009; Katerova and Todorova 2011; Kocsy 2011; Kuthanová et al. 2004; Wimalasekera et al. 2011).

Several evidences propose that the PA function in defense against abiotic stress. Cellular polyamine level varies under stress conditions. Years ago, it was reported that PA accumulate when potassium is deficient (Richards and Coleman 1952). However, it is now known that that PA levels change in plant species in response to a broad range of stress factors such as dehydration, salinity, heat and cold stress, nutrient deficiencies, and others (Liu et al. 2007). Accumulated evidence describes that most abundant PA under abiotic stress are spermine (Spm), spermidine (Spd), and putrescine (Put) (Yang et al. 2007).

Elevated concentration of PA is observed due to de novo synthesis of the free PA against abiotic stress factors. To understand the regulation of the PA level, it is necessary to develop knowledge about biosynthetic gene expression because synthesis of PA is primarily controlled at the level of transcription. Data suggests that despite of the difference between timing and level of induction, SPDS, ADC, and SPMS are those PA biosynthetic genes that are upregulated during stress (Liu et al. 2014). Out of these biosynthetic genes, ADC is an important stress-responsive gene, identified in a wide range of plants (Wang et al. 2011). Therefore, ADC genes are considered as promising candidates to identify possible transcription mediators such as protein kinases or transcription factors. Before screening cDNA libraries via yeast one-hybrid, the first step in characterization of possible PA biosynthetic gene regulating transcription factors is the identification and in silico analysis of potential promoters. This identification usually employs characterization of putative cis-acting sequences present in the promoter. Bioinformatic analysis of the promoter from SamDC gene in rice revealed the existence of a number of putative cis-acting elements like W-box, LTRE, ABRE, and MYBR that are closely linked to several environmental factors. The evidences propose that a common group of TFs or a single TF may control PA biosynthetic gene or different genes that are involved in PA biosynthesis, respectively (Wang and Liu 2015).

Accumulated free PA coincide with the high level of PA transcripts as stated in some studies, but this statement is incongruent with other studies (Wang and Liu 2015). Due to catabolism of PA, there is inconsistency in the gene expression profile and accumulated PA. The PA biosynthetic genes also correlate with the stress tolerance in expression patterns (Pillai and Akiyama 2004).

21.2.6 G Protein Signaling Components in Abiotic Stress Responses

The G protein complex is comprised of G-alpha, G-beta, and G-gamma and this protein complex along with GPCR has been found linked with various signal transduction pathways in plants (Hamm 1998; Pandey et al. 2015). G protein-coupled receptors (GPCRs) are basically a large protein family that plays a role in the transduction of extracellular signals into intracellular environment (Kroeze et al. 2003). G proteins employ downstream effectors such as phospholipases, ion channels, phosphatases/kinases, and GTPases in order to transduce signals (Xu et al. 2015). G proteins are involved in the regulation of several enzymes including phospholipase D (PLD) and phosphatidylinositol-phospholipase C (PLC) (Apone et al. 2003), ultimately regulating the expression of LEA and LEA-like genes against various environmental stress factors, as studied in *Arabidopsis*, presenting the vital role of G proteins in signaling pathways (Chakraborty et al. 2015).

The G protein signaling core in plants is much simpler in contrast to animals (Urano and Jones 2014). This protein signaling core functions in many biological mechanisms such as ozone resistance, sugar stress resistance, phytohormone signaling, and seedling responses to light and germination (Chen 2008). Cell to cell communication links the plant internal environment with the external through a cascade of events regulated by various signaling molecules, and one of the most important is GPCR proteins. External stimuli received at the membrane alters the conformation of intracellular GPCR domain and triggers the linked G protein as well as downstream signaling. Activated G protein in turn acts on downstream elements, ultimately generating a cascade that leads towards altered gene expression which enables plants to confer to environmental stresses (Misra et al. 2007).

21.3 Antioxidant Defense System in Plants Exposed to Adverse Environment

Cellular metabolism in plants produces reactive oxygen species (ROS). Environmental adversities result in the production of higher concentrations of these ROS leading to oxidative damage and hence cell death. In spite of their role in destruction process, ROS are presumed to be the second messengers of various cellular mechanisms that also involve defense against several stress factors. Numerous enzymatic as well as nonenzymatic antioxidants are localized in the tissues that affect scavenging of the reactive oxygen species (Sharma et al. 2016). These ROS production and scavenging systems are present in many organelles such as peroxisomes, mitochondria, and chloroplasts, and these systems work in harmony with each other (Pang and Wang 2008). The equilibrium between formation and quenching of ROS may be affected by various environmental adversities that elevate intracellular ROS (Sharma et al. 2016). In order to avoid the oxidative damage, higher plants raise the level of endogenous antioxidant defense. In plants, it has been expected that oxidative damage is the minimum effect produced by every environmental stress apparently (Smirnoff 1995).

A significant amount of attention has been diverted towards the identification and characterization of transgenic plants and mutants that have altered antioxidant expression level. This potential approach helps in the development of understanding about its role in stress-defense response and antioxidant system itself (Sharma et al. 2016). Antioxidants work in coordination and recruit a cascade of redox reactions. For example, the harmonization between ascorbic acid and phenolic compounds and ascorbic acid and glutathione is well known. But the results contradict with the status of antioxidants in oxidative stress (Gout et al. 2001).

It has been reported that the experiments conducted on overexpression of antioxidants do not necessarily increase an antioxidative defense. Therefore, antioxidative potential does not always synchronize positively in a plant defense response (Gout et al. 2001). Competence of an antioxidant system can be indicated by the compartmentalization of ROS production and antioxidant localization, ability to induce antioxidant defense, and the formation and translocation of these antioxidants (Blokhina et al. 2003). The antioxidant defense system of plants helps in the protection of cellular organelles, nucleic acids, unsaturated membrane lipids, and other enzymes from the detrimental effect of free radicals (Larson 1988).

Among the plant species, the ascorbate-glutathione cycle is a major ROS scavenging pathway that resides in many cellular organelles including the cytosol, chloroplasts, mitochondria, peroxisomes, and apoplast. This cycle regulates the concentration of ROS in these organelles (Mittler 2002). The AsA-GSH cycle actively participates in the successive reduction and oxidation of glutathione, ascorbate, and NADPH that is catalyzed by glutathione reductase (GR), monodehydroascorbate reductase (MDAR), ascorbate peroxidase (APX), and dehydroascorbate reductase (DHAR) (Gratão et al. 2005). In this way, the AsA-GSH cycle functions in combating the oxidative stress. Many elements of the antioxidant defense system of plants have been characterized into model plants successfully. Moreover, alterations or distortions in this system are a better way to understand the various ROS comprised of signaling pathways (Caverzan et al. 2016).

21.4 Phytohormones at the Crossroad of Abiotic Stress Responses

Phytohormones are a group of small molecules derived from important metabolic pathways and serve as essential regulators for plant growth and survival. In the past decade, research has advanced to a new level which includes discovery of those regions where hormones are synthesized in plants. Moreover, the concepts of plant hormone biology, identification of receptors of these hormones, perceiving stress signals, transport of phytohormones, and their signaling have been made clear, thus offering new opportunities for carrying research on chemical specificity of phytohormone signaling in plants (Santner et al. 2009).

Plants produce various hormones, and the major ones include cytokinins (CK), auxins, abscisic acid (ABA), gibberellins (GA), jasmonates (JA), strigolactones, ethylene (ET), brassinosteroids (BR), and salicylic acid (SA). Out of these, ET, SA, ABA, and JA function in mediating defense response in plants under abiotic and biotic stresses. Basically, ABA is known to function in defense response under abiotic stresses because such stresses elevate ABA, whereas SA, ET, and JA function in maintaining defense against pathogens. But the process of defense response against any stress is not merely limited to these hormones. Cross talk of SA, ABA, ET, and JA with that of GAs, CKs, and auxins in mediating defense response has been reported recently (Nakashima and Yamaguchi-Shinozaki 2013; Nishiyama et al. 2013).

Signal transduction pathways of ET, JA, ABA, and SA cross talk at various levels, for example, hormone-responsive transcription factors (TFs), to mediate defense response in plants. Although it is remarkable that complete plant acclimation and continued growth are main features of a precise response against stress, defense response generated by plants against any stress is also dependent on the type of positive or negative cross talk in hormone signaling pathways instead of depending only on the contribution of each hormone (Verma et al. 2016). The synchronization of phytohormone metabolism, their transport, and the mediation of central signaling factor expression is critical in order to maintain the concentration of hormones in cells and tissues. Additionally, hormone metabolism is crucial for effective signaling that can provide sustained growth and development response (Waadt et al. 2015).

21.5 Transcriptional Regulation of Stress Responses

Development of stress-tolerant crop plants requires a vibrant understanding about the interactions between transcription factors, genes, and their pathway to adapt to adverse environmental conditions. Although characterization of transcription factors and their targets takes time and labor, the experimental methods used in the identification of roles of such transcription factors in stress response give reliable results. Additionally, mathematical models along with integration of computational approaches and high-throughput omics data provide a platform for new understandings (Tchagang et al. 2013). In plants, regulation of stress-responsive genes by transcription factors is the most critical means of responding to a broad range of stress factors (Singh et al. 2002b). The plant genome contributes a major volume to transcription. In a model plant such as Arabidopsis, 1500 transcription factors are encoded by its genome (Riechmann et al. 2000). These transcription factors of ten belong to large gene families, which in some cases are unique to plants (Singh et al. 2002a).

For example, ERF proteins which are a subfamily of the ethylene-responsive element-binding protein (EREBP)/APETALA2 (AP2) family of transcription factors belong only to plants (Riechmann et al. 2000). These proteins are composed of a well-conserved domain of 58–59 amino acids, known as ERF domain. It has been reported that the ERF domain binds to two analogous cis-elements: one is the GCC box found in promoters of pathogenesis-related genes involved in ethylene responsiveness and the other is dehydration-responsive element (DRE)/C-repeat motif, which confers resistance to drought and cold stress. ERF family members are linked to a wide variety of stress factors that is why they belong to a large-size family. The members of this family in one plant species are able to perform their role in other plants as well, thus increasing their stress tolerance potential (Singh et al. 2002a).

Another family of transcription factors in plants is the bZIP. This family is comprised of one class of proteins which contain octopine synthase (ocs)-element-binding factor (OBF)/TGA and are associated to stress response. They bind to the ocs element and control the gene expression of PR-1 and glutathione s-transferase6 (GST6) (Lebel et al. 1998). Other classes of the bZIP family are linked to signaling transduction against stresses such as dehydration/salinity or UV light. ABA-responsive element-binding (AREB)/ABRE-binding factors, which belong to this class of proteins, have shown responses at the level of transcription and translation, in dehydration or salinity stress (Jakoby et al. 2002).

In the past decade, a lot of effort has been put on the characterization of these factors in plants, which play a role in gene expression as a result of abiotic stresses. Sometimes, closely related transcription factors have the capability to trigger or repress the genes by means of cis-acting elements which respond against specific stress conditions (Singh et al. 2002b). High-throughput molecular technologies should keep on providing effective transcription factor candidates or their combinations that have the potential to boost up the expression of stress-responsive genes in a highly controlled and planned way, thus enhancing genetic engineering of crops which possess potent stress response abilities (Nal et al. 2001).

21.6 Cross Talk between Different Abiotic Stress Signaling Pathways

Being sessile organisms, plants continuously adapt to the changing climate at cellular, molecular, and physical level. The foremost step in such an adaptation is turning on of the molecular response by perceiving the stress signal through receptors and relaying down the information to a specific signaling pathway. The signal transduction pathways result either in physiological alterations which include closure of stomata or the expression of stress-responsive genes leading to modulation of cellular as well as molecular mechanisms and processes. In the recent era, our understanding and knowledge about signal transduction pathways starting from stimulus until final response has been advanced. These pathways are part of a complicated signaling network actually and they are triggered in response to more than one stimulus because of overlap between their branches (Knight and Knight 2001).

The perception of stress signal during environmental adversities and triggering the signaling cascade to turn on the process of adaptation are crucial steps which determine the growth and development of plants. In the past years, research has been carried out to identify all components of such transduction pathways to confer resistance against a wide range of stresses (Chinnusamy et al. 2004). It is believed that plants possess a number of signaling pathways that cross talk with each other at several levels because of the presence of specific and general stress tolerance and resistance mechanisms (Huang et al. 2012).

21.7 Conclusion and Future Prospects

Plants are exposed to numerous environmental adversities that effect their survival. Plants which are unable to survive under adverse environment consume more resources in contrast to the ones which adjust in such environment. But how the plants evolve such mechanisms that help them to acclimatize such changes is a basic query. Therefore, in order to improve agricultural production in a frequently changing environment, more resistant crop plants are required.

In plant biology, the study on plant's response to stresses is an emerging field of research, because of its dynamic consequences in the agriculture sector. Environmental adversities are the leading cause of decreased crop yield all over the world. The studies carried on model plants like Arabidopsis have provided fundamental information on molecular mechanisms behind stress responses. Moreover, important crops and wild plants including Arabidopsis are sensitive to environmental stresses, whereas some specialized crop plants such as halophytes or xerophytes are rather resistant to severe stressful conditions. Thus, there must be clear differences between tolerant and intolerant plant species in terms of efficient response mechanisms. In addition to that, the putative molecular mechanisms, expression of genes, and their roles should be discovered.

Revealing the integrated response by different signal transduction pathways would assist breeders in enhancing the production of tolerant food crops. Based on several studies, it has been presumed that the reprogramming of transcriptome is a vital aspect of adaptation and stress signaling in plants. As these stress responses are synchronized with survival and reproduction, understanding of the cross talk between signaling pathways linked with plants growth and development is important. Similarly, efforts should be made to understand the cross talk between abiotic and biotic stress signaling pathways.

References

Apone F, Alyeshmerni N, Wiens K, Chalmers D, Chrispeels MJ, Colucci G (2003) The G-protein-coupled receptor GCR1 regulates DNA synthesis through activation of phosphatidylinositol-specific phospholipase C. Plant Physiol 133(2):571–579

Blokhina O, Virolainen E, Fagerstedt KV (2003) Antioxidants, oxidative damage and oxygen deprivation stress: a review. Ann Bot 91(2):179–194

Bohnert HJ, Sheveleva E (1998) Plant stress adaptations—making metabolism move. Curr Opin Plant Biol 1(3):267–274

Caverzan A, Casassola A, Brammer SP (2016) Reactive oxygen species and antioxidant enzymes involved in plant tolerance to stress. In: Abiotic and biotic stress in plants-recent advances and future perspectives. InTech

Chakraborty N, Singh N, Kaur K, Raghuram N (2015) G-protein signaling components GCR1 and GPA1 mediate responses to multiple abiotic stresses in *Arabidopsis*. Front Plant Sci 6:1000

Chang L, Karin M (2001) Mammalian *MAP kinase* signalling cascades. Nature 410(6824):37

Chen J-G (2008) Heterotrimeric G-proteins in plant development. Front Biosci Volume(13):3321–3333

Chinnusamy V, Schumaker K, Zhu JK (2004) Molecular genetic perspectives on cross-talk and specificity in abiotic stress signalling in plants. J Exp Bot 55(395):225–236

Choudhary SP, Oral HV, Bhardwaj R, Yu J-Q, Tran L-SP (2012) Interaction of brassinosteroids and polyamines enhances copper stress tolerance in Raphanus sativus. J Exp Bot 63(15):5659–5675

Cuevas JC, Sánchez DH, Marina M, Ruiz OA (2004) Do polyamines modulate the Lotus glaber NADPH oxidation activity induced by the herbicide methyl viologen? Funct Plant Biol 31(9):921–928

Dan I, Watanabe NM, Kusumi A (2001) The Ste20 group kinases as regulators of MAP kinase cascades. Trends Cell Biol 11(5):220–230

Day IS, Reddy VS, Ali GS, Reddy A (2002) Analysis of EF-hand-containing proteins in Arabidopsis. Genome Biol 3(10):1

Fariduddin Q, Varshney P, Yusuf M, Ahmad A (2013) Polyamines: potent modulators of plant responses to stress. J Plant Interact 8(1):1–16

Garg N, Pundhir S, Prakash A, Kumar A (2008) PCR primer design: *DREB* genes. J Comput Sci Syst Biol 1:021–040

Gill SS, Tuteja N (2010) Polyamines and abiotic stress tolerance in plants. Plant Signal Behav 5(1):26–33

Gish LA, Clark SE (2011) The RLK/Pelle family of kinases. Plant J 66(1):117–127

Gout E, Boisson A-M, Aubert S, Douce R, Bligny R (2001) Origin of the cytoplasmic pH changes during anaerobic stress in higher plant cells. Carbon-13 and phosphorous-31 nuclear magnetic resonance studies. Plant Physiol 125(2):912–925

Gratão PL, Polle A, Lea PJ, Azevedo RA (2005) Making the life of heavy metal-stressed plants a little easier. Functional plant biology Funct Plant Biol 6:481–494

Hamm HE (1998) The many faces of G protein signaling. J Biol Chem 273(2):669–672

Hepler PK (2005) Calcium: a central regulator of plant growth and development. Plant Cell 17(8):2142–2155

Hirayama T, Shinozaki K (2010a) Research on plant abiotic stress responses in the post-genome era: past, present and future. Plant J 61(6):1041–1052

Hirayama T, Shinozaki K (2010b) Research on plant abiotic stress responses in the post-genome era: past, present and future. Plant J 61(6):1041–1052

Huang G-T, Ma S-L, Bai L-P, Zhang L, Ma H, Jia P, Liu J, Zhong M, Guo Z-F (2012) Signal transduction during cold, salt, and drought stresses in plants. Mol Biol Rep 39(2):969–987

Iriti M, Faoro F (2009) Chemical diversity and defence metabolism: how plants cope with pathogens and ozone pollution. Int J Mol Sci 10(8):3371–3399

Jakoby M, Weisshaar B, Dröge-Laser W, Vicente-Carbajosa J, Tiedemann J, Kroj T, Parcy F (2002) bZIP transcription factors in Arabidopsis. Trends Plant Sci 7(3):106–111

Katerova Z, Todorova D (2011) Effect of enhanced UV-C irradiation on the growth, malondialdehyde, hydrogen peroxide, free proline, polyamines, IAA and IAA-oxidase activity in pea plants (*Pisum sativum* L.). C R Acad Bulg Sci 64 (11)

Kilian J, Whitehead D, Horak J, Wanke D, Weinl S, Batistic O, D’angelo C, Bornberg-Bauer E, Kudla J, Harter K (2007) The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. Plant J 50(2):347–363

Knight H, Knight MR (2001) Abiotic stress signalling pathways: specificity and cross-talk. Trends Plant Sci 6(6):262–267

Kocsy G (2011) Regulation of free amino acid and polyamine levels during cold acclimation in wheat. Acta Biol Szeged 55(1):91–93

Kroeze WK, Sheffler DJ, Roth BL (2003) G-protein-coupled receptors at a glance. J Cell Sci 116(24):4867–4869

Ku Y-S, Sintaha M, Cheung M-Y, Lam H-M (2018) Plant hormone signaling Crosstalks between biotic and abiotic stress responses. Int J Mol Sci 19(10):3206

Kumar SV, Wigge PA (2010) H2A. Z-containing nucleosomes mediate the thermosensory response in Arabidopsis. Cell 140(1):136–147

Kusano T, Yamaguchi K, Berberich T, Takahashi Y (2007) Advances in polyamine research in 2007. J Plant Res 120(3):345–350

Kushwaha R, Singh A, Chattopadhyay S (2008) Calmodulin7 plays an important role as transcriptional regulator in Arabidopsis seedling development. Plant Cell 20(7):1747–1759

Kuthanová A, Gemperlová L, Zelenková S, Eder J, Macháčková I, Opatrný Z, Cvikrová M (2004) Cytological changes and alterations in polyamine contents induced by cadmium in tobacco BY-2 cells. Plant Physiol Biochem 42(2):149–156

Larson RA (1988) The antioxidants of higher plants. Phytochemistry 27(4):969–978

Lebel E, Heifetz P, Thorne L, Uknes S, Ryals J, Ward E (1998) Functional analysis of regulatory sequences controlling *PR-1* gene expression in Arabidopsis. Plant J 16(2):223–233

Liu J-H, Kitashiba H, Wang J, Ban Y, Moriguchi T (2007) Polyamines and their ability to provide environmental stress tolerance to plants. Plant Biotechnol 24(1):117–126

Liu J-H, Peng T, Dai W (2014) Critical cis-acting elements and interacting transcription factors: key players associated with abiotic stress responses in plants. Plant Mol Biol Report 32(2):303–317

Ma Y, Dai X, Xu Y, Luo W, Zheng X, Zeng D, Pan Y, Lin X, Liu H, Zhang D (2015) *COLD1* confers chilling tolerance in rice. Cell 160(6):1209–1221

McAinsh MR, Clayton H, Mansfield TA, Hetherington AM (1996) Changes in stomatal behavior and guard cell cytosolic free calcium in response to oxidative stress. Plant Physiol 111(4):1031–1042

Misra S, Wu Y, Venkataraman G, Sopory SK, Tuteja N (2007) Heterotrimeric G-protein complex and G-protein-coupled receptor from a legume (*Pisum sativum*): role in salinity and heat stress and cross-talk with phospholipase C. Plant J 51(4):656–669

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7(9):405–410

Nakashima K, Yamaguchi-Shinozaki K (2013) ABA signaling in stress-response and seed development. Plant Cell Rep 32(7):959–970

Nal B, Mohr E, Ferrier P (2001) Location analysis of DNA-bound proteins at the whole-genome level: untangling transcriptional regulatory networks. BioEssays 23(6):473–476

Neha G, Sachin P, Anil P, Anil K (2008) Primer designing for *DREB1A*, a cold induced gene. J Proteomics Bioinform 1:028–035

Nishiyama R, Watanabe Y, Leyva-Gonzalez MA, Van Ha C, Fujita Y, Tanaka M, Seki M, Yamaguchi-Shinozaki K, Shinozaki K, Herrera-Estrella L (2013) Arabidopsis AHP2, AHP3, and AHP5 histidine phosphotransfer proteins function as redundant negative regulators of drought stress response. Proc Natl Acad Sci 110(12):4840–4845

Osakabe Y, Yamaguchi-Shinozaki K, Shinozaki K, Tran L-SP (2013) Sensing the environment: key roles of membrane-localized kinases in plant perception and response to abiotic stress. J Exp Bot 64(2):445–458

Pandey A, Sharma M, Pandey GK (2015) Small and large g proteins in biotic and abiotic stress responses in plants. In: Elucidation of abiotic stress signaling in plants. Springer, pp 231–270

Pang C-H, Wang B-S (2008) Oxidative stress and salt tolerance in plants. In: Progress in botany. Springer, pp 231–245

Pillai M, Akiyama T (2004) Differential expression of an *S-adenosyl-L-methionine decarboxylase* gene involved in polyamine biosynthesis under low temperature stress in japonica and indica rice genotypes. Mol Gen Genomics 271(2):141–149

Poovaiah B, Reddy A, Leopold AC (1987) Calcium messenger system in plants. Crit Rev Plant Sci 6(1):47–103

Raichaudhuri A, Bhattacharyya R, Chaudhuri S, Chakrabarti P, DasGupta M (2006) Domain analysis of a groundnut calcium-dependent protein kinase nuclear localization sequence in the junction domain is coupled with nonconsensus calcium binding domains. J Biol Chem 281(15):10399–10409

Reddy AS, Ali GS, Celesnik H, Day IS (2011) Coping with stresses: roles of calcium-and calcium/calmodulin-regulated gene expression. Plant Cell 23(6):2010–2032

Richards F, Coleman R (1952) Occurrence of putrescine in potassium-deficient barley. Nature 170(4324):460

Riechmann JL, Heard J, Martin G, Reuber L, Jiang C-Z, Keddie J, Adam L, Pineda O, Ratcliffe O, Samaha R (2000) Arabidopsis transcription factors: genome-wide comparative analysis among eukaryotes. Science 290(5499):2105–2110

Sangwan V, Örvar BL, Beyerly J, Hirt H, Dhindsa RS (2002) Opposite changes in membrane fluidity mimic cold and heat stress activation of distinct plant MAP kinase pathways. Plant J 31(5):629–638

Santner A, Calderon-Villalobos LIA, Estelle M (2009) Plant hormones are versatile chemical regulators of plant growth. Nat Chem Biol 5(5):301

Sharma P, Jha AB, Dubey RS (2016) Oxidative stress and antioxidative defense systems in plants growing under abiotic stresses. In: Handbook of plant and crop stress. CRC Press, pp 109–158

Shinozaki K, Yamaguchi-Shinozaki K, Seki M (2003) Regulatory network of gene expression in the drought and cold stress responses. Curr Opin Plant Biol 6(5):410–417

Shiu S-H (2001) Plant receptor-like kinase gene family: diversity, functions. and signaling Sci STKE 18:113–122

Singh KB, Foley RC, Oñate-Sánchez L (2002a) Transcription factors in plant defense and stress responses. Curr Opin Plant Biol 5(5):430–436

Singh KB, Foley RC, Oñate-Sánchez L (2002b) Transcription factors in plant defense and stress responses. Curr Opin Plant Biol 5(5):430–436

Smirnoff H (1995) Antioxidant systems and plant response to the environment. Environment and plant metabolism

Smirnoff N (1998) Plant resistance to environmental stress. Curr Opin Plant Biol 9(2):214–219

Smith LM, Bomblies K, Weigel D (2011) Complex evolutionary events at a tandem cluster of *Arabidopsis thaliana* genes resulting in a single-locus genetic incompatibility. PLoS Genet 7(7):e1002164

Swarbreck SM, Colaço R, Davies JM (2013) Plant calcium-permeable channels. Plant Physiol 163(2):514–522

Takekawa M, Tatebayashi K, Saito H (2005) Conserved docking site is essential for activation of mammalian MAP kinase kinases by specific MAP kinase kinase kinases. Mol Cell 18(3):295–306

Tchagang AB, Phan S, Famili F, Pan Y, Cutler AJ, Zou J (2013) A generic model of transcriptional regulatory networks: Application to plants under abiotic stress. In: 2013 IEEE International Workshop on Genomic Signal Processing and Statistics, 2013. IEEE, pp 28–31

Teige M, Scheikl E, Eulgem T, Dóczi R, Ichimura K, Shinozaki K, Dangl JL, Hirt H (2004) The MKK2 pathway mediates cold and salt stress signaling in Arabidopsis. Mol Cell 15(1):141–152

Thao NP, Tran L-SP (2012) Potentials toward genetic engineering of drought-tolerant soybean. Crit Rev Biotechnol 32(4):349–362

Todorova D, Katerova Z, Alexieva V, Sergiev I (2015) Polyamines–possibilities for application to increase plant tolerance and adaptation capacity to stress. Genet Plant Physiol 5(2):123–144

Tuteja N, Singh GS (2012) Plant acclimation to environmental stress. Springer Science & Business Media

Urano D, Jones AM (2014) Heterotrimeric G protein–coupled signaling in plants. Annu Rev Plant Biol 65:365–384

Van Norman JM, Breakfield NW, Benfey PN (2011) Intercellular communication during plant development. Plant Cell 23(3):855–864

Verma V, Ravindran P, Kumar PP (2016) Plant hormone-mediated regulation of stress responses. BMC Plant Biol 16(1):86

Waadt R, Hsu PK, Schroeder JI (2015) Abscisic acid and other plant hormones: methods to visualize distribution and signaling. BioEssays 37(12):1338–1349

Wang J, Sun P-P, Chen C-L, Wang Y, Fu X-Z, Liu J-H (2011) An arginine decarboxylase gene *PtADC* from *Poncirus trifoliata* confers abiotic stress tolerance and promotes primary root growth in *Arabidopsis*. J Exp Bot 62(8):2899–2914

Wang W, Liu J-H (2015) Genome-wide identification and expression analysis of the polyamine oxidase gene family in sweet orange (*Citrus sinensis*). Gene 555(2):421–429

Wimalasekera R, Tebartz F, Scherer GF (2011) Polyamines, polyamine oxidases and nitric oxide in development, abiotic and biotic stresses. Plant Sci 181(5):593–603

Xiong L, Ishitani M (2006) Stress signal transduction: components, pathways and network integration. In: Abiotic stress tolerance in plants. Springer, pp 3–29

Xu DB, Chen M, Ma YN, Xu ZS, Li LC, Chen YF, Ma YZ (2015) A G-protein β subunit, AGB1, negatively regulates the ABA response and drought tolerance by down-regulating AtMPK6-related pathway in Arabidopsis. PLoS One 10(1):e0116385

Yamaguchi-Shinozaki K, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. Annu Rev Plant Biol 57:781–803

Yang J, Zhang J, Liu K, Wang Z, Liu L (2007) Involvement of polyamines in the drought resistance of rice. J Exp Bot 58(6):1545–1555

Zhu J-K (2016) Abiotic stress signaling and responses in plants. Cell 167(2):313–324

Chapter 22
Plant-Based Biostimulants and Plant Stress Responses

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Contents

Abstract Plants face a variety of biotic and abiotic stresses throughout their life cycle that adversely affect their growth and production. These stresses decrease the annual crop yield up to 70% globally and had created a problem of food shortage as well as the malnutrition for ever-increasing world population. Different strategies are being practiced to overcome these problems and found successful up to some extent. Exogenous use of plant growth promoters through different modes is one such among them that found helpful to improve the plant growth and production under stressful conditions and is being employed at commercial level to obtain better production. However, most of them are the inorganic chemicals and are found toxic for organism and are not environmental friendly. Trend is increasing toward

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the use of organic and environmental-friendly biostimulants with the ability to improve production and stress tolerance induction. Studies have revealed that exogenous use of these biochemicals through different modes (seed soaking, foliar spray, or as soil application) is found helpful in improving the plant growth and production under stressful conditions. These biostimulants include the chelation of macro- or micro-nutrients with different organic compounds, plant growth regulators of microbial origin, and plant-based biostimulants that are found helpful in improving the plant growth and production under stressful conditions. These include humic acids (humic and fulvic acid), chitosan, phosphites, bio-char, and plant-based extracts, including algal extracts and of different plant parts. These biostimulants along with the improvement of plant growth and production also found helpful to improve the yield and yield nutritional quality when applied exogenously through different modes. Improvements in the attribute due to the exogenous use of biostimulants under stressful condition are associated with their role in different physio-biochemical attributes, including plant antioxidative defense mechanism, plant photosynthetic efficiency, and plant water relation through the accumulation of different osmotica (osmolytes and osmoprotectants) that help to maintain cellular osmotic potential and better nutrient uptake and mobility. Plant-based biostimulants improve the plant growth due to the presence of different phytohormones and other secondary metabolites, vitamins, antioxidants, and the inorganic nutrients in the extract that directly affect the plant growth and production through improving the plant tolerance against abiotic stresses. Exogenous use of biostimulants through different modes also improves the plant growth, yield as well as the yield nutritional quality under stressful conditions. However, studies revealed that the effective dose for the induction of stress tolerance of these biostimulants is plant species, growth stage, and stress type specific. Moreover, the use of biostimulants for the effective improvement is also dependent on the mode of application. Although large work has been done to study the role of biostimulants in improving plant growth and production, still more is required for final recommendations. More attention is required in this regard and in future due to their non-toxic and environmental-friendly nature.

Keywords Biostimulant · Exogenous application · Extracts · Abiotic stresses

22.1 Introduction

During their life cycle plants face a variety of different biotic and abiotic stresses that adversely affect the plant growth and final yield. Among different abiotic stresses, drought, salinity, heavy metal, high and low temperatures are the major ones that plants face during their life cycle (Ali and Ashraf 2011; Jamil et al. 2015; Ali et al. 2018; Noman et al. 2018a). It is estimated that collectively these stresses decreased the plant yield up to 70% that has created the problem of food security for the increasing world population (Erni 2015). The first and the foremost effect of different abiotic stresses (drought, salinity, heat, and cold stress) is the change in plant water relations that affects the cellular turgor pressure (Lata et al. 2018). Changes in plant water relations directly affect the photosynthetic rate, processes of assimilation, and other metabolic activities that ultimately decrease the plant growth (Akram et al. 2018; Haworth et al. 2018). This also affects the efficiency of PSII subunits that leads to lipid peroxidation of cellular membrane due to over production of reactive oxygen species (ROS) under stressful conditions (Ebele and Emodi 2016; He et al. 2018).

However, plants have developed certain mechanisms to counteract the adverse effects of different abiotic stresses (Kamanga and Mndala 2019). These include the maintenance of leaf water content through the production/accumulation of different osmolytes and osmoprotectants, hormonal regulation of different metabolic activities as well as the development of well-defined antioxidative defense mechanism for the scavenging of over-produced ROS. These include the over-production of different enzymatic and non-enzymatic antioxidants that helps in scavenging of ROS (Kumar and Trivedi 2018).

During the last few decades a tremendous change in plant nutrient management has been developed by different techniques for the induction of stress tolerance for better crop production. Exogenous use of biostimulants through different modes is one of these that are being used for the improvement in plant growth and production under varying environmental conditions. In available literature the word biostimulants was firstly used by Kauffman et al. (2007). He defined biostimulants as "the materials other than the fertilizers that improve the plant growth when is applied in low quantities." There are many different available forms of biostimulants but they are divided into three major categories. These include humic substances (HS), hormone-containing products (HCP) along with the secondary metabolites and amino acid containing products (AACP). Biostimulants are beneficial for plant growth without being the nutrients, pesticides, or soil improvers (Calvo et al. 2014; Du Jardin 2015; Halpern et al. 2015). Biostimulants may be of synthetic or of natural origin including the microorganisms such as plant growth-promoting rhizobacteria (PGRs) (Zhang et al. 2003) and include the beneficial fungi (Halpern et al. 2015). The major plant biostimulants are humic and fulvic acids, protein hydrolysates, seaweed extracts, chitosan, inorganic compounds, beneficial fungi (i.e., arbuscular mycorrhizal fungi; AMF and *Trichoderma* spp.) and plant growth-promoting bacteria (Habib et al. 2013; Noman et al. 2018a; Canellas et al. 2015; Rouphael et al. 2015; Ruzzi and Aroca 2015).

22.2 Role of Different Plant-Based Biostimulants in Stress Tolerance

22.2.1 Humic Acid

Humic substances are formed by the chemical and biological decomposition of animal and plant matter by the microbial activity (Tilman et al. 2011). Humic acid plays a key role in ecological and environmental processes. It regulates both the soil carbon and nitrogen cycle and affects the growth of plants and microorganisms (Nigania et al. 2017). Humic acid is a humus compound that is easily soluble in an alkaline solution but becomes precipitated in acidic (pH 1–2) solution (Hayes 2006).

Increase in plant growth with the exogenous application of humic acid is cited in available literature by many researchers (Nardi et al. 2002, 2009; Chen et al. 2004; Canellas and Olivares 2014; Meganid et al. 2015; Matuszak-Slamani et al. 2017). In an experiment by Rose et al. (2014), it was found that exogenous application of humic acid increased the root and shoot weight of different plant species up to 22%. It was also found that the effect of exogenous application of humus is plant species specific (Trevisan et al. 2010; Haghighi et al. 2012; El-Bassiouny et al. 2014). For example, the effect of humus extracted by the brown coal is less effective than the humus isolated from the peat (Canellas and Olivares 2014).

Plants face an evolutionary pressure to increase the surface area under stress for the absorption of water and nutrients in order to match the enhanced photosynthetic activity (Canellas and Olivares 2014). It is hypnotized that the positive effect of humic substances on plant growth is directly linked with the change in root architecture. Fine roots directly release the H^+ ions in soil through H^+-ATPase and organic acids in rhizosphere that change the soil pH in rhizosphere and increase the nutrient uptake by the roots through active or passive transport (Morsomme and Boutry 2000). The H^+-ATPase causes the hydrolysis of cytoplasmic ATP that results in the release of H^+ ions in the apoplast that lead to the loosening of cell membrane. This is the basis of acid growth hypothesis that is induced by the auxins involvement (Nardi et al. 2000). Since cell growth is linked with the extracellular acidification, the activation of H^+-ATPase is directly or indirectly linked with root hair proliferation (Canellas et al. 2008). This mechanism is especially observed in maize that in the presence of humic acid the maize seedlings changed their organic acid exudations (Ohno et al. 2004; Canellas et al. 2008; Puglisi et al. 2009).

Humic acids have been found effective in improving the growth by endogenous increased biosynthesis or through exogenous use through different modes and nutrition of different crop plants. It is also helpful in improving the antioxidative defense mechanism of different crop plants that found effective in improving the plant growth under different environmental stresses (Table 22.1). However, this improvement in plant growth is species specific and also depends upon the applied concentration of humic acid. In maize it was studied that the exogenous use of humic acid improved the fresh and dry biomasses that was found associated with the improved leaf chlorophyll content and increased proline accumulation under drought and salt

Table 22.1 Roles of humic acids in plant stress tolerance

Type of stress	Plant species	Type of biostimulants used	Concentration used	Mode of application	Growth medium	Improvements	References
Salt stress	Maize	Humic acid	100 mM	Foliar application and pre-sowing seed treatment	In sand culture (pot experiment)	Increased biomass, F_v/F_m, chlorophyll pigments and proline accumulation, increased activity of SOD, POD, CAT, MDA and H_2O_2 content	Kaya et al. (2018)
Drought stress	Lima bean	Humic acid	0, 1, 3 and 6 L ha^{-1}	Foliar application	Field experiment	Increased photosynthetic activity, carotenoids, membrane stability, LRWC, proline, and soluble sugars content	Beheshti and Tadayyon (2017)
Heat stress	Tomato	Humic acid	4.8, 9.6 and 14.4 kg ha^{-1}	Mixed in soil	Soil	Increased plant height, biomass, number of flower cluster, and total number of flowers	Abdellatif et al. (2017)
Drought stress	Marjoram	Humic acid	0, 1% humic acid	Foliar application	Pots filled with soil	Improved plant height, leaves dry weight and essential oil percentage	El-Khateeb et al. (2017)
Drought stress	Fennel	Humic acid	0, 1, 2 and 3 kg ha^{-1}	Mixed with soil	Field experiment	Increased seed yield, essential oil percentage, *p*-cymene, Gama terpinene, and thymoquinone	Ariafar and Forouzandeh (2017)
Drought and salt stress	Peanut	Humic acid, salicylic acid	0–1.5 mM	Foliar application	Field experiment	Increased the Na^+/K^+ ratio	Nigania et al. (2017)
Drought stress	Sunflower	Humic acid and zinc	0, 4 L h^{-1}	Mixed with water	Field experiment	Increased grain yield, grain weight, and number of seeds per head	Hatami (2017)
Drought stress	Black cumin	Humic acid	0, 1, 2, 3 kg ha^{-1}	Soil application	Field experiment	Increased seed yield, essential oil percentage, *p*-cymene, γ-terpinene, and thymoquinone	Ariafar and Forouzandeh (2017)

(continued)

Table 22.1 (continued)

Type of stress	Plant species	Type of biostimulants used	Concentration used	Mode of application	Growth medium	Improvements	References
Salt stress	Soya bean	Humic acid	<30 or > 30 kDa	Mixed in Hogland's nutrient solution	Hydroponic solution	Improved total leaf area, plant height, fresh and dry masses, and chlorophyll content	Matuszak-Slamani et al. (2017)
Drought stress	Okra	Putrescine and humic acid	0, 0.5, 1 and 1.5 mM	Foliar application	Field experiment	Increased fruit yield, LRWC, vitamin C and proline contents, CAT and POD activities and WUE	Barzegar et al. (2016)
Natural conditions	Dill	Humic acid and indole acetic acid	0 and 400 ppm	Foliar application	Field experiment	Improved survival %, plant height, number of branches, number of umbels, and seed oil yield	Said-Al Ahl et al. (2016)
Drought stress	Wheat	Humic acid	220 ml HF plus 10 L of water for 1 ton seeds	Pre-sowing seed treatment and foliar	Field experiment	Increased seed yield	Shahryari (2017)
Natural conditions	Lettuce	Humic acid	0, 70, 500, 4000, 6000, 14,000, and 42,000 mg L^{-1}	Mixed with Hogland's nutrient solution	Plant growing media	Increased plant height, root length, and biomass production	Verdi et al. (2015)
Salt stress	Common bean	Humic acid	3 g L^{-1}	Mixed in soil	Soil	Plant height, number of leaves, root length, fresh and dry biomass, and photosynthetic pigments	Meganid et al. (2015)
Drought stress	Rapeseed	Humic acid	0, 3, 6 mg L^{-1}	Mixed with irrigation water	Field experiment	Improved photosynthetic pigments, PSII efficiency, and antioxidant activity	Lotfi et al. (2015)

Drought stress	Wheat	Humic acid	13 mg L^{-1}	Foliar and seed priming	Sandy soil	Increased plant height, number of leaves, fresh and dry biomass, photosynthetic pigment, total soluble sugar, carbohydrates, free amino acids, proline, and nutrient uptake	El-Bassiouny et al. (2014)
Nitrogen stress	Maize	Humic acid	0, 100, 200 mg ha^{-1}	Hoagland solution	Petri plates	Improved fresh and dry mass and antioxidant activity (SOD, POD, CAT, and APx)	Zhang et al. (2013)
Drought stress	Maize	Humic acid	0, 150, 300, 450 ppm	Foliar application	Field experiment	Positively affected the plant height, yield components, seed yield, biological yield, and harvest index	Moghadam et al. (2014)
Salt stress	Cotton	Putrescine and humic acid	0, 1, 2%	Foliar application	Pot experiment in soil	Increase in plant height, number of leaves, leaf area, fruiting branches per plant, biomass, as well as number of bolls, seed and fiber yield/plant, lint percentage, and seed index	Ahmed et al. (2013)
Drought stress	Pistachio	Humic acid	0, 500, 1000, 1500 ppm	Foliar application	Field experiment	Increased leaf photosynthetic pigments, LRWC, proline accumulation, abscisic acid (ABA) in fresh leaf, and root dry weight	Kasmani et al. (2013)
Drought and salt	Cumin and basil	Humic acid	0, 1000, 2000 mg L^{-1}	Mixed with Hogland's nutrient solution	Petri-plates	Improved seed germination and root and shoot length	Haghighi et al. (2012)
Drought stress	Wheat	Humic acid and fluvic acid	33.23 g L^{-1} of humic acid and 9.02 g L^{-1} of fulvic acid	Mixed with irrigation water	Field experiment	Increased seed yield	Ranjbar et al. (2012)

(continued)

Table 22.1 (continued)

Type of stress	Plant species	Type of biostimulants used	Concentration used	Mode of application	Growth medium	Improvements	References
Salt stress	Maize	Humic acid	Soil application as 0, 2 and 4 g kg^{-1} and foliar spray as 0, 0.1 and 0.2%	Soil and foliar	Soil	Increased the uptake of P, K, Mg, Na, Cu, and Zn	Khaled and Fawy (2011)
Salt stress	Pepper seedlings (cv. Demre)	Humic acid and phosphorous	0, 750, 1500 mg/kg	Mixed in peat	Peat	Increased uptake of N, P, K^+, Ca^{2+}, Mg^{2+}, S, Mn^{2+}, and Cu^{2+} contents in of root and shoot	Çimrin et al. (2010)

stress. It also found associated with improved the activities of antioxidant enzymes, including SOD, POD, CAT, and APX. Exogenous use of humic acid as foliar spray also improved the nutrient uptake in maize under salt and drought stress (Khaled and Fawy 2011; Zhang et al. 2013; Moghadam et al. 2014; Kaya et al. 2018). In wheat exogenous application of humic acid as foliar spray also improved the growth and seed yield in wheat (Ranjbar et al. 2012; El-Bassiouny et al. 2014). Improved photosynthetic activity, carotenoid contents, and membrane stability were found in lima bean by the exogenous application of humic acids (Beheshti and Tadayyon 2017). It also improved the number of flowers and flower cluster in tomato (Abdellatif et al. 2017). In relation to these, exogenous use of humic acid was also found helpful in improving the plant growth in marjoram (El-Khateeb et al. 2017), fennel (Ariafar and Forouzandeh 2017), peanut (Nigania et al. 2017), Sunflower (Hatami 2017), black cumin (Ariafar and Forouzandeh 2017) as well as improved the growth and yield in soya bean, okra, dill, rape seed, and cotton plants (Matuszak-Slamani et al. 2017; Barzegar et al. 2016; Said-Al Ahl et al. 2016; Lotfi et al. 2015; Ahmed et al. 2013). Exogenous use of humic acid also improved the growth as well as nutrient uptake in pepper seedlings under natural environmental conditions (Çimrin et al. 2010). In pistachio, exogenous application of humic acid increased the proline and ABA accumulation in leaves that resulted in its improved stress tolerance (Kasmani et al. 2013).

22.2.2 *Fulvic Acid*

Fulvic acid is mainly produced by the biodegradation of lignin-containing organic compounds (Malan et al. 2015). It helps in improving the cation exchange capacity of agriculture land (Malan et al. 2015). Due to its high solubility in water it can be easily leached down. It is present in very low concentration (0.2–1% w/v) in the soil (Malan et al. 2015) but has large impact on the soil fertility and plant growth. It is a non-toxic organic fertilizer that acts as mineral ion chelating agent and increases the water holding capacity of soil that ultimately increases the nutrient uptake by the roots and as a result enhanced plant productivity (Malan et al. 2015: Lotfi et al. 2015). Fulvic acid has high attraction toward the water molecules that keep the soil moist and as a result increases the water availability for absorption to roots (Khang 2011). Fulvic acid easily binds or chelates the mineral elements like Ca^{2+}, Cu^{2+}, Zn^{2+}, Mn^{2+}, K^{+}, and Mg^{2+} and facilitates their translocation to the plants (Shahid et al. 2012).

Fulvic acid protects the plant against stress by increasing the soil efficiency by imparting its role in changing the soil pH and nutrient profile (Goatley and Schmidt 1990). Presence of fulvic compounds in soil chelates the mineral ions present in rhizosphere and improves their translocation in plants through roots that ultimately improve the plant growth, yield, and yield nutritional quality (Stevenson 1994). It has been also found that the fulvic acid can also function as a phytohormone that helps in regulating many physiological and biochemical processes taking place in cell (Akıncı and Öngel 2011). Fulvic acid helps to cope with salt stress by increasing the buffering properties of plants against available soil salts as well as the soil acidity (Gezgin and Sanal 2012). It has been found that the exogenous application of fulvic acid as a biostimulant increased the drought stress tolerance in wheat (Yu-ling and LiJian-hua 1999). It was also found that the fulvic acid protects plant against oxidative damages by increasing the plant antioxidative capacity (Anjum et al. 2011a, b).

It has also been found that the exogenous application of fulvic acid has also been found effective in alleviating the abiotic stress tolerance in many crop plants as has been depicted from a lot of available literature. For example, exogenous application of fulvic acid is found effective in increasing the plant growth of crop plants grown under various different abiotic stresses (Shahid et al. 2012: Lotfi et al. 2015: Husein et al. 2015: Dinler et al. 2016: Moradi et al. 2017).

For crops fulvic acids act as chelators. They bound with minerals to make them into organic compounds that can be absorbed and translocated by plants more easily. They also enable the soil to hold more water, that is, they improve the soil field capacity and increase the water infiltration of the soil. Additionally, humic and fulvic acids reduce the toxicity of toxins present in the soil by reducing the amount of these harmful substances that reach the crop's roots. Exogenous application of fulvic acid as foliar spray increases the plant oxygen uptake capacity that is directly linked with the increased chlorophyll content and the membrane stability under abiotic stress conditions as well as increases the nutrient uptake by the roots. Exogenous application of fulvic acid also found helpful in regulating the stomatal opening and closing with improved transpiration and respiration rate of the plants under stressful environments (Table 22.2).

Exogenous application of fulvic as foliar spray and seed priming was found helpful in improving seed germination rate, development of root and shoot, improved resistance against fungal attack, improved cell division, respiration rate as well as improved crop growth and final yield. Under natural environmental conditions, exogenous application of fulvic acid as foliar spray was found helpful in improving plant yield attributes such as the number of seeds, seed weight, harvest index, and seed oil percentage (Moradi et al. 2017). It was found that the under salt stress, foliar application of fulvic acid was found helpful in improving the plant growth, contents of chlorophyll, protein, proline accumulation, as well as improved nutrient uptake by the roots in citrus and grapevines (Mahmoudi and Aryee 2015; El-Kenawy 2017), respectively. Under heat stress, foliar application of fulvic acid was also found helpful in enhancing the seed germination rate as well as antioxidant activity of soya bean seedlings (Dinler et al. 2016). Exogenous use of fulvic acid as foliar spray was also found helpful in enhancing the plant growth through improving the PSII efficiency by decreasing the lipid peroxidation of cellular membrane with an increase in the antioxidative defence mechanism under drought stress in rapeseed (Lotfi et al. 2015). Exogenous use of fulvic acid was also found helpful in reducing the adverse effects of toxic heavy metals by decreasing their uptake by the roots in broad bean plants (Violante et al. 2010; Shahid et al. 2012; Tang et al. 2014).

Table 22.2 Roles of fulvic acids in plant stress tolerance

Type of stress	Plant species	Type of biostimulant	Concentration used	Mode of application	Growth medium	Improvements	References
Natural conditions	Safflower	Fluvic acid	0, 0.5 and 1 kg ha^{-1}	Foliar application	Field experiment	Improved number of seeds in head, 1000 seed weight, seed yield, harvest index, and oil percent	Moradi et al. (2017)
Salt stress	Thompson seedless grapevines	Chitosan, salicylic acid, and fulvic acid	0, 500 ppm	Foliar application	Field experiment	Improved shoot length, leaf surface area, leaf chlorophyll content and total soluble protein, percentages of N, P, and K^+ in leaves as well as enhanced yield per vine, cluster weight, berry weight, soluble solids content and total phenols while reduced total acidity, cluster weight loss %, berry shatter % and berry decay% and total % loss in cluster weight	El-Kenawy (2017)
Heat and salt stress	Soya bean	Fulvic acid	0, 2.0 mg L^{-1}	Pre-sowing seed treatment	Petri dishes	Increased LRWC, antioxidant enzyme activities (SOD, APX, GST), decreased levels of H_2O_2 and MDA	Dinler et al. (2016)
Salt stress	Citrus	Fulvic acid		Soil application	Pot experiment	Improved the proline accumulation and chlorophyll content	Mahmoudi and Aryee (2015)
	Unshu						
Natural conditions	Tomato	Fulvic acid, humic, and calcium	0, 4%	Foliar application	Field experiment	Improved vegetative growth, yield, and fruit quality	Husein et al. (2015)
Drought	Rapeseed	Fluvic acid	0, 300, and 600 mg L^{-1}	Foliar application	Field experiment	Improved the maximum quantum efficiency of PSII (*Fv/Fm*) and performance index (PI) and significantly decreased the lipid peroxidation of the membrane	Lotfi et al. (2015)
Heavy metal stress	Broad bean	Fulvic acid	0, and 25 mg L^{-1}	Mixed with Hogland's solution	Hydroponic solution	Fulvic acid reduced Pb toxicity by reducing its uptake	Shahid et al. (2012)

22.2.3 Chitosan

Chitosan is derivative of chitin, a compound present in cell wall of fungi and also the major component of the insect's exoskeleton and crustacean's shells. Chitosan has a wide use in agriculture and medicine industry. In many crops including the ornamentals and cereals, exogenous application of chitosan has been studied but depending upon the type of the chitosan molecule, its concentration, type of plant species, and the plant developmental stage (Limpanavech et al. 2008; Kananont et al. 2010; Pornpienpakdee et al. 2010). The major role of chitosan in plant is studied as its activity to inhibit the microbial growth and decreased microbial membrane integrity that protects the plants from many diseases (Bautista-Baños et al. 2003; Prapagdee et al. 2007; Ali et al. 2015; Li et al. 2009; Maqbool et al. 2010). However, its activity as biostimulant has also been reported.

Chitosan is also regarded as a major component of the plant defense repose against wounds during healing and the pathogenic attack in pea and tomato (Bautista-Baños et al. 2003; Ferrari et al. 2013). It was found that upon wounding the chitosan triggers the accumulation of ROS (reactive oxygen species) and PRPs (pathogenesis related proteins) that protect the plants against the pathogenic attack (Mejía-Teniente et al. 2013; Pastor et al. 2013; Malerba and Cerana 2015). It was also studied that the exogenous application of chitosan caused an increase in production of hydrogen peroxide (H_2O_2) that found effective to protect the plant cells from the oxidative damage caused by the over-production of ROS (Zhao et al. 2007). This increased concentration of H_2O_2 leads to increased production of plant defensive enzymes that enhances the biosynthesis of phenolic compounds. This mechanism has been studied in many different crops, including papaya (Ali et al. 2012), sweet basil (Kim et al. 2005), grapes (Meng and Tian 2009), and tomato (Liu et al. 2007; Badawy and Rabea 2009).

The other mechanisms to induce the stress responses in plants are by the nitric oxide (NO) pathway (Raho et al. 2011; Zhang et al. 2013; Zhao et al. 2007). For example, in tobacco, chitosan reduces the accumulation of TMV (tobacco mosaic virus) and induces the TMV resistance (Zhao et al. 2007) by the production of NO. In this case, NO is first produced in the chloroplast, then to the nucleus and later spread in the whole cell (Zhang et al. 2017). Furthermore, exogenous application of chitosan is found effective in increasing the plant growth and stress tolerance in many crops, including wheat (Zeng and Luo 2012), maize (Rahman Al-Tawaha et al. 2018), mung bean (Ray et al. 2015), rice (Agrawal et al. 2002; Pongprayoon et al. 2013), and many others (Karimi et al. 2013; Sharifa and Abu-Muriefah 2013; Malekpoor et al. 2016; Bistgani et al. 2017).

Chitosan is commercially developed from chitin. Antibacterial and antifungal properties of chitosan have been studied extensively as a natural antimicrobial agent as used in various pharmaceuticals, cosmetic, and agriculture. In addition, it has been found that the exogenous use of chitosan through different modes induces positively many physiological and biochemical changes in plants by altering different metabolic processes. However, the effect was specific to plant growth stage, plant species, and the used concentration of chitosan (Tables 22.3 and 22.4). Exogenous application of chitosan improves the plant antioxidative defense responses in different crops by enhancing the H_2O_2 accumulation as signaling molecule. This increased concentration of H_2O_2 leads to the synthesis of different secondary metabolites such as polyphenolics, lignin, flavonoids, and phytoalexins in many crops, including tomato (El-Tantawy 2009), wheat (Zeng and Luo 2012), and rice (Pongprayoon et al. 2013).

It has been found that under natural environmental conditions, exogenous use of chitosan through different modes improved the plant growth in tomato by increasing the biosynthesis of photosynthetic pigment and efficiency of PSII (El-Tantawy 2009). It has been found that exogenous use of chitosan also reduced the plant transpiration rate that resulted in improved grain yield under natural environmental conditions in pepper plant (Bittelli et al. 2001) and wheat (Abdel-Aziz et al. 2018).

Exogenous use of different concentrations of chitosan through different modes improved the plant growth and antioxidative defense mechanism under salt stress in different crops (Guan et al. 2009). Chitosan applied exogenously improved the plant growth by enhancing the photosynthetic activity, proline accumulation, improvement in antioxidative defense mechanism as well as improved nutrient uptake under salt stress in mung bean (Ray et al. 2015), rosemary (Helaly et al. 2018), and maize (Rahman Al-Tawaha et al. 2018). However, under drought stress, exogenous use of chitosan through different modes improved plant growth and yield quality by changing antioxidative defense mechanism as well as nutrient uptake in different crops, including common bean (Sharifa and Abu-Muriefah 2013), rice (Pongprayoon et al. 2013), ricinus (Karimi et al. 2013) wheat (Zeng and Luo 2012), basil (Malekpoor et al. 2016), and thyme (Bistgani et al. 2017).

22.2.4 Phosphite

Among others, phosphites are also essential for all the living organisms on earth, including higher and lower plants due to their major proportion in DNA, RNA, ATP, and cell membranes. Phosphite groups play a key role in genetic hereditary, membrane structure, signal transduction pathway, and cellular metabolism. Phosphate is the sole phosphorous containing group that is essential for plant optimal plant growth and development (López-Arredondo et al. 2014). Phosphite (Phi $H_2PO_3^-$) or its conjugate phosphorous acid (H_3PO_3) is being used as insecticide, supplemental fertilizer, and biostimulant from past three decades (Hanrahan et al. 2005). Phi as biostimulant enhances the plant stress tolerance, nutrient assimilation, and yield quality under abiotic stress. Phi is also being used for the control of pathogens in many countries (McDonald et al. 2015; Thao and Yamakawa 2009).

It has been clear from many studies that the foliar application of Phi improved the plant growth, yield, and yield nutritional quality of many crops, including onion (Gómez-Merino and Trejo-Téllez 2015), potato (Lovatt and Mikkelsen 2006), and pepper (Varadarajan et al. 2002). It has been found that the foliar application of Phi

Table 22.3 Roles of chitosan in plant stress tolerance

Type of stress	Plant species	Type of biostimulants used	Concentration used	Mode of application	Growth medium	Improvements	References
Natural conditions	Wheat	Nano chitosan	400, 500, and 600 ppm	Foliar application	Soil experiment	Improved grain quality	Abdel-Aziz et al. (2018)
Salt stress	Rosemary	Chitosan or zeolite application		Soil and foliar application	Pot experiment	Shoot and root length, branches number, biomass production, photosynthetic pigments, minerals, and essential oil yield	Helaly et al. (2018)
Salt stress	Maize	Chitosan	10 mg L^{-1}	Mixed with Hogland's solution	Hydroponic	Improved fresh and dry biomass, plant height, and leaf areas	Rahman Al-Tawaha et al. (2018)
Drought stress	Thyme	Chitosan	0, 200, and 400 µg L^{-1}	Foliar application dissolved in acetic acid	Pot experiment under green house	Increased the essential oil concentration in seed	Bistgani et al. (2017)
Drought stress	Basil	Chitosan	0, 0.2 and 0.4 g L^{-1}	Foliar application	Pot experiment	Improved growth and photosynthetic pigments	Malekpoor et al. (2016)
Salt stress	Mung bean	Chitosan	25 ppm/pot	Mixed with soil	Pot experiment	Improved protein and antioxidant activity	Ray et al. (2015)
Drought stress	Common bean	Chitosan	0, 100, 200, 400 mg L^{-1}	Foliar application	Pot sand culture	Increased growth, yield and its quality	Sharifa and Abu-Muriefah (2013)
Drought stress	Rice	Chitosan	40 mg L^{-1}	Pre-sowing seed treatment	Sand	Enhanced plant growth and better maintenance of the photosynthetic pigments	Pongprayoon et al. (2013)
Drought stress	Wheat	Chitosan	0, 0.2, 0.4, 0.6, 0.8, and 1%	Seed coating	Field experiment	Antioxidative defense mechanism and chlorophyll content	Zeng and Luo (2012)

Drought	Ricinus.	Chitosan	0, 5 g L^{-1}	Foliar application	Field experiment	Improved antioxidant activities (SOD, POD and CAT), also improved the proline accumulation	Karimi et al. (2013)
Natural conditions	Tomato	Chitosan	25 m^3/fed	Foliar application	Field conditions	Plant height, number of branches and leaves/plant, biomass production, photosynthetic pigments, yield/plant, and marketable yield	El-Tantawy (2009)
Natural conditions	Pepper plant	Chitosan	1 g L^{-1}	Foliar application	Field conditions	Reduced transpiration rate	Bittelli et al. (2001)

Table 22.4 Roles of phosphite in plant stress tolerance

Type of stress	Plant species	Type of biostimulants used	Concentration used	Mode of application	Growth medium	Improvements	References
Drought stress	*Eucalyptus*	Phosphite	0, 5 L ha^{-1}	Foliar spray	Pot experiment in soil	Improved ETR and the transpiration rate and leaf lipoperoxide content	Gonçalves et al. (2014)
Fungal infection	European ash	Phosphite	20–25 cm^3 of inoculum per 1000 cm^3 of the soil mixture	Peat and perlite	Pot experiment	Enhanced the production of triterpenes (ursolic and oleanolic acid), and decreased production of phenols (tyrosol) and sterols (−sitosterol) in seedlings infected with *H. fraxineus*. Treatment with Actifos caused seedlings to enhance their response to pathogen(s) attack and increase their survival probability	Keča et al. (2018)
Growth room conditions	Potato	Phosphite		Foliar application	Pot experiment	Phosphite-triggered response to confer long-lasting resistance against *P. infestans*	Burra et al. (2014)
Growth room conditions	Maize	Phosphite	52 μm, 644 μm	Mixed with Hogland's solution	Hydroponic	Increased seedlings phosphorous concentration	Ávila et al. (2011)
Growth room conditions	Strawberry	Phosphite	1.02 g phosphorous/ rhizobox	Mixed with peat	Pot experiment	Improved root and shoot length and increased phosphorous content	Glinicki et al. (2010)
Heavy metal	Ascomycete fungus	Rock phosphate	1–6 g L^{-1}	Petri-plates	Growth medium	Growth, amino acids and protein content was increased	Hasan (2007)
Natural and growth room conditions	Maize	Phosphite	0 and 45 kg ha^{-1}	Soil and foliar application	Pot and field experiment	An inhibited growth of the maize plants was observed, after potassium phosphite was applied as the sole P source. The negative effects ranged from a stunted growth of the plants to the complete die off	Schroetter et al. (2006)

may induce the sugar metabolism that disturbs the internal metabolic activity and induce the shikimic pathway that results in increased floral intensity and improved yield and yield quality (Lovatt and Mikkelsen 2006).

Under stressful condition, exogenous use of phosphite is found helpful in alleviating the plant stress tolerance. Exogenous use of phosphite is found effective against pathogenic bacteria, oomycetes, and many pathogenic fungi that significantly affect the crop growth and production. As a biostimulant exogenous use of phosphite was found helpful in improving the crop yield and yield nutritional quality in different crop species, including potato (Burra et al. 2014), maize (Ávila et al. 2011), and strawberry (Glinicki et al. 2010). However, the improvement in growth is dependent upon crop species as well as applied concentration of phosphite. Exogenous use of phosphite induces abiotic stress tolerance in plants by improving the plant photosynthetic rate and antioxidant activity (Gonçalves et al. 2014).

Under different abiotic and biotic stresses, exogenous use of phosphite improved plant growth and production. Under drought stress, foliar application of phosphite improved the plant growth by improving the transpiration rate, PSII efficiency, and antioxidant activity in *Eucalyptus* (Gonçalves et al. 2014). Exogenous application of phosphite under room growth condition with different concentration increased the growth rate, phosphorous concentration, and also improved the root and shoot length of the strawberry (Glinicki et al. 2010) and while also increasing phosphorous concentration and enhancing the seedling in hydroponic condition in maize (Ávila et al. 2011). Under natural and room condition soil and foliar application of phosphite inhibited growth of the maize (Schroetter et al. 2006). Exogenous application of phosphite also improved the plant tolerance against fungal infection by increasing the production of phenols and sterols in European ash plant (Keča et al. 2018). Under heavy metal stress, exogenous application of phosphite also improved the plant growth by improving the protein (Hasan 2007).

22.2.5 Algal Extracts

About 10,000 species of macro-algae (seaweeds) have been found that cover almost 10% of marine productivity. However, a small portion of seaweeds has a significant role as a food for humans and animals and also has a potential role in agriculture as organic fertilizers (Craigie 2011a, b; Khan et al. 2012; Rönnbäck et al. 2007). Studies have revealed that seaweeds are being used by the humans for many other purposes, including medicines, cosmetics, and coloring dyes in textile industry as well along with the food and agriculture industry (Coulter and Turner 2013). Ancient romans were familiar with the fertilizing nature of seaweeds as columella (the most noted writer in the roman history) depicted that the plant roots were wrapped by the seaweeds to retain the greenness of the seedlings (Battacharyya et al. 2015). Recently, the trend is moving toward the use of seaweeds as organic manure in many countries for reclamation of soil with better production as alternate source of nutrients for soil in place of chemical fertilizers (Wells et al. 2007). Seaweeds are now designated as plant biostimulants due to rich source of many important secondary metabolites (Craigie 2011a, b). It has been found that exogenous use of seaweed alters the many metabolic processes even in very low concentration that improved the plant growth, flowering and final yield and yield nutritional quality (Khan et al. 2012). Furthermore, the large number of available literature depicted that the exogenous use of seaweeds extracts through different modes also helpful in improving the plant tolerance against many abiotic stresses, including drought, salinity, heat and cold, as well as heavy metal stress (Kim et al. 2015; Khairy and El-Shafay 2013).

Commercially available seaweed extracts have a diverse range of organic and inorganic components, including nitrogen, phosphorous, potassium, calcium, iron, magnesium, zinc, sodium, and sulfur, while organic components include the different osmolytes, betaines, amino acids, antioxidants and proteins, as well as the phytohormone in some cases (MacKinnon et al. 2010). For example, brown algae extract also contains a proportion of amino acids and proteins. Dry weight of brown algae contains about 10–47% proteins (Nagahama et al. 2009). In addition, brown algae also contain significant amount of secondary metabolites and vitamin precursors that have potential to enhance the plant growth and production when applied exogenously (Craigie 2011a, b).

Brown algae extract also contain a large amount of phenolic compounds, which protect the cell and cellular components from the adverse effects of stresses (Wang et al., 2009). Phenolic compounds also play significant role in scavenging the reactive oxygen species produced under stressful conditions (Belattmania et al. 2016). Seaweed extract is available in different forms, including liquid and or as soluble powder form that can be applied as foliar and pre-sowing seed treatment. It can also be mixed with irrigation water and/or can also be applied by drip irrigation to the crops. It has been found that the foliar application of seaweed extract has improved the growth of many crops, including potato, tomato, plum, cherry, almonds, mango, etc. (Haider et al. 2012) but the effect was the treatment and growth level specific. Furthermore, the mode of application for improvement in crop growth is growth stage specific at which the extract was applied. Exogenous use of seaweed extract can also improve the yield nutritional quality and shelf life of fruit by improving the flavonoids accumulation (Fan et al. 2011). For example, exogenous application of seaweed extract as foliar application just before the 7–14 days of the harvesting improved the flavonoid concentration in spinach (Fan et al. 2011; Ferrari et al. 2013). It also improved the productivity, quality, and nutrient status of olives (Chouliaras et al. 2009). The foliar application of seaweed extract also improved the olive oil quality by improving the linoleic and oleic acid content with a decrease in oil palmitoleic acid. Exogenous application of seaweed extract enhanced the shelf life of avocado and pears (Kamel 2014).

There are many compounds present in algal biomass that act as active compounds at different stages of plant growth. These can be used as plant biostimulants through different modes but depend upon the plant species and the stage of plant growth (Table 22.5). The mechanism behind for the improvement in plant growth through exogenous use of seaweed extract was the high proportion of phytohormones (cytokinins, auxins and auxin-like compounds, indole acetic acid, abscisic

Table 22.5 Roles of algal extracts in plant stress tolerance

Type of stress	Plant species	Type of extract	Concentration used	Mode of application	Growth medium	Improvements	References
Natural condition	Arabidopsis	Green seaweed extract	0–1%	Foliar application	Lab experiment	Inhibited root growth due to inhibition of lateral root development	Ghaderiardakani et al. (2019)
Drought stress	Arabidopsis	Seaweed extract	3 g/L	Hydroponics system	Polystyrene trays	Plants able to maintain a strong stomatal control and relatively higher values of both water use efficiency (WUE) and mesophyll conductance	Santaniello et al. (2017)
Drought stress	Soya bean	Seaweed extract	κ$^-$, λ-, and ι$^-$OCs	Foliar application	Seed trays	Improved LRWC and higher stomatal conductance, improved antioxidant activity	Shukla et al. (2016)
Salt stress	Pepper	*Padina pavonica* and *Jania rubens* extracts	0, 3, 12 g/L	Pre-sowing seed treatment	Petri-plate experiment	Improved seed germination	Rinez et al. (2018)
Salt stress	Wheat		0, 1, 5, 10%	Pre-sowing seed treatment	Lab experiment in petri-plates	Improved activity of (SOD, CAT), while decreased activity of APX and GR	Ibrahim et al. (2014)
Salt stress	*Sargassum dentifolium*	Seaweed extract	1%	Pre-sowing seed treatment	Petri plates experiment in growth room	Increased fresh, dry biomass, and photosynthetic pigments contents (Chl. *a*, Chl. *b* and car.), activity of SOD, CAT, POD, and APx	Shaddad et al. (2014)
Drought stress	Tomato	Micro-algae extract	–	Soil application	Pot experiment in soil	Better development of root length, increased number of leaves number, and leaves area	Oancea et al. (2013)

(continued)

Table 22.5 (continued)

Type of stress	Plant species	Type of extract	Concentration used	Mode of application	Growth medium	Improvements	References
Natural condition	Sunflower	Seaweeds extract	0, 0.4, 0.6%	Foliar application	Field experiment	Increased both root and shoot fresh and dry biomass, plant height, head diameter, seed index (1000 seed weight), seed yield, highest growth improvement was recorded in plants treated by 0.6% extract	Osman and Salem (2011)
Pathogenic attack	Potato and tobacco	Chilean marine macro-algae extracts	0.1–10 mM	Exogenous application	In vitro	Improved anti-fungal and anti-microbial activity	Jiménez et al. (2011)

acid) in the extract (Khan et al. 2009; Gorka et al. 2013; Wieczorek et al. 2013; Michalak and Chojnacka 2015). It has been found that exogenous use of algal extracts increases the plant growth, fresh and dry biomass, biosynthesis of photosynthetic pigments, and carotenoid content as well as improves the root development (Michalak and Chojnacka 2016; Khan et al. 2009). Exogenous use of algal extracts as foliar spray, seed priming, or soil application is also found helpful in plants to increase their resistance against different abiotic stresses (Khan et al. 2009). Huge literature has been cited that depicts the role of algal extract as biostimulant to improve the plant growth and yield under abiotic stress conditions (Santaniello et al. 2017; Shukla et al. 2016; Rinez et al. 2018; Ibrahim et al. 2014). Furthermore under natural environmental conditions, exogenous use of green algal extract in *Arabidopsis* inhibited the root growth and lateral root development (Ghaderiardakani et al. 2019), while in sunflower exogenous use of algal extracts as foliar spray improved the plant growth and final yield (Osman and Salem 2011). Under drought stress, the use of seaweed extract as foliar spray was found helpful to improve the plant growth by improving the leaf relative water content, stomatal conductance, and water use efficiency in Arabidopsis (Shukla et al. 2016) and soya bean (Santaniello et al. 2017). In tomato exogenous application of seaweed extract as soil application improved the root development and number of leaves in plants (Oancea et al. 2013). Under salt stress, exogenous use of seaweed extract as foliar spray was found helpful for improving the plant growth, antioxidant activity, seed yield, yield nutritional quality, and the nutrient uptake in pepper (Rinez et al. 2018), wheat (Ibrahim et al. 2014; El-Baky 2009), and *Sargassum dentifolium* (Shaddad et al. 2014). Exogenous use of algal extract was also found helpful in improving the plant resistance against pathogenic attack in potato and tobacco (Jiménez et al. 2011).

22.2.6 Plant-Based Extracts

The world fertilizing trend is moving toward the use of eco-friendly fertilizers for the crop plants. Exogenous use of the plant extracts as biostimulants is one of them (Pourhadi et al. 2018). There are two major classes of plant-based biostimulants, seaweed extracts, and extracts of different plant parts that are being used for the better crop production through different modes. Extracts of different plant parts (roots, shoots, seeds) show a differential response depending upon the mode of application and concentration used as well as the type of plant species (Chojnacka et al. 2015). Different plant parts contain different chemical compositions that alter the plant growth when applied exogenously (Rouphael et al. 2018). They may contain phytohormones, nutrients as well as the antifungal and anti-microbial agents that protect the plant against the biotic and abiotic stress. Plants are source of different bioactive compounds and secondary metabolites, including nitriles, flavonoids, alkaloids, and antioxidant agents (Ahmed et al. 2016). For example, sugar beet roots contain a large amount of sucrose as well as GB and fleuric acid that improves the crop growth. GB is naturally occurring amino acid that is involved in osmoregulation under abiotic stress and enhances the activity of PSII (Malekzadeh 2015). Under abiotic stress like drought and salinity, plants accumulate GB in contents in their chloroplast resulting in improvement of stress tolerance (Raza et al. 2012). Fleuric acid in sugar beet also has antioxidant activity that improves plant growth when applied exogenously (Abbas et al. 2010).

Phyto-extracts of various plants contain organic and inorganic compounds, including mineral elements like potassium, calcium, sulfur, magnesium, phosphorus, vitamins, and amino acids. Therefore, phyto-extracts give more satisfying results as compared to synthetically manufactured chemicals. Similarly, plant-based extract contains a variety of phytohormones, including zeatin, a purine adenine derivative of plant hormone group cytokinin (Makkar et al. 2007). Zeatin improves the antioxidant properties of many enzymes and protects the cell from oxidative damage under stressful condition (Schäfer et al. 2015). Similarly, improvement in plant growth is also improves by the exogenous use of plant-based extract due to the presence of cytokinin (Wahid 2007).

Numerous plant species have been reported that improve the plant growth by their exogenous use as foliar spray. Rady and Mohamed (2015) studied that the exogenous use of moringa seed extract as foliar spray improved the seed germination and antioxidant properties of *Capsicum annuum* L. under heavy metal stress. They reported that this improvement may be due to the accumulation of phytohormones, proline, sugars, ascorbic acid, glutathione, vitamins, and mineral nutrient as well. Similarly, exogenous use of moringa leaf extract improved the plant growth and fiber quality in cotton (Arif et al. 2019). Huge amount of available literature has depicted the role of plant-based extracts from different plant species to improve the crop growth, that is, wheat (Farooq et al. 2017), fenugreek (Latef et al. 2017), sorghum (Ahmad et al. 2016a, 2016b), and common bean (Latif and Mohamed 2016).

Environmental constraints are the major factors that limit the plant growth. Different abiotic and biotic stresses limit the plant growth and production (Liu et al. 2010; Abdel Latef and Miransari 2014; Ahmad et al. 2016a, b). To counteract the adverse effects of these biotic and abiotic stresses, plants have developed certain mechanisms that maintain the proper plant growth under such stressful conditions. Accumulation of certain osmolytes and osmoprotectants including proline, GB, total free amino acids, soluble protein, and soluble sugar is one of them (Abdel and Trasn 2016; Ahmad et al. 2016a, b; Liu et al. 2010). In relation to these, uptake of certain inorganic ions K^+, Cl^-, Na^+ is also helpful in osmoregulation during stressful condition to maintain a proper plant growth and production (Table 22.6).

Exogenous application of different plant extracts through different modes has been found helpful to reinforce the proper plant growth under abiotic stress. However, the effect is concentration and the plant species specific (Tomar and Agarwal 2013). Different compounds extracted from the plants showed a variety of compounds depending upon the plant part used for the extraction (Yasmeen et al. 2013; Rady and Mohamed 2015). These extracts showed a great potential as antioxidant activity as well as osmoprotectants and osmoregulators (Noman et al. 2018a). These compounds in extracts collectively improve the plant antioxidative properties as well as plant growth. For example, foliar application of plant extracts

Table 22.6 Roles of plant-based extracts in plant stress tolerance

Type of stress	Plant species	Type of biostimulant used	Concentration used	Mode of application	Growth medium	Improvements	References
Heavy metal + salt stress	Pepper plant	Moringa leaf extract	5 times diluted	Soil application and foliar application	Field experiment	Improved growth, leaf photosynthetic pigments, proline accumulation, total soluble sugar, and nutrient uptake	Rady and Mohamed (2015)
Drought	Wheat	Sugar beet extract	0, 10, 20, 30, 40, and 50%	Pre-sowing seed treatment	Lab experiment and field experiment	Improved plant growth, biomass production, content of photosynthetic pigment, antioxidant activity, and nutrient uptake	Noman et al. (2018a)
Heat and drought stress	Wheat	Sunflower, sorghum and brassica	3%	Foliar application	Pot experiment in soil medium	Improvement in grain yield, water-use efficiency, and transpiration efficiency as well as antioxidant activity	Farooq et al. (2017)
Salt stress	Fenugreek	Moringa leaf extract	25%	Foliar application	Pot experiment in soil medium	Improved fresh and dry biomass, antioxidants activity (POD, CAT, APx) while SOD remained unchanged	Latef et al. (2017)

(continued)

Table 22.6 (continued)

Type of stress	Plant species	Type of biostimulant used	Concentration used	Mode of application	Growth medium	Improvements	References
Chilling stress	Maize	Salicylic acid, sorghum water extract, and moringa leaf extract	10 times diluted	Foliar application	Field experiment	Improved crop growth, leaf index, leaf area, and final yield	Waqas et al. (2017)
Natural environmental conditions	Sorghum	Moringa leaf extract and sorghum extract	3%	Foliar application and seed priming	Field experiment	Improved growth and yield	Ahmad et al. (2016a, b)
Salt stress, heat stress	Common bean	Moringa leaf extract	30 times diluted	Foliar application	Pot experiment in soil medium	Improved growth, photosynthetic pigments, fresh and dry biomass, and the antioxidant activity	Latif and Mohamed (2016)
Growth room conditions	Plumed cockscomb	*Senna alata* L. leaf extract	5, 10, 12, 25, 30, 40, 50, 75%	Pre-sowing seed treatment	Pot experiment in soil medium	Improved plant growth, seedling height, fresh and dry biomass, and induced early flowering	Agbagwa (2014)
Drought stress	Moringa and alfalfa	Algal extract	0.5%	Foliar application	Field experiment	Foliar application of extract 300 g fed^{-1} achieved the highest values of fresh and dry weight (g plant^{-1}) and a remarkable increase of biomass production	El Sayed et al. (2014)

Salt stress	Wheat	Moringa leaf extract	30 times diluted	Foliar application	Field experiment	Improved growth, biomass production, decreased Na^+ and Cl^-, improved K^+ uptake	Yasmeen et al. (2013)
Allelopathic stress	Wheat and corn	Walnut leaf extract	1.5, 3, and 6%	Pre-sowing seed pretreatment	Lab experiment	Improved seed germination rate, root and shoot length	Khoshvaghti and Lotfi (2013)
Growth room conditions	Range grasses	Moringa leaf extract	10, 20, 30, and 40 times diluted	Pre-sowing seed treatment	Lab experiment in petri-plates	Improved seed germination, root and shoot length, number of leaves, and seedling vigor	Noman et al. (2018b)
Drought and salt stress	Okra	Moringa leaf extract	2.5, 5 and 10%	Pre-sowing seed treatment	Petri-plate experiment	Reduced the growth of seed-born fungus	Nwangburuka et al. (2012)
Salt stress	Okra	Sugar beet extract and GB	50 mM	Foliar application	Pot experiment	Improved plant growth, photosynthetic rate, antioxidant activity, nutrient uptake, and final yield	Habib et al. (2013)
Growth room conditions	Mung bean	Moringa leaf, bark, root, fruit, and seed extracts	2.5,5,7.5, 10, 12.5, and 15%	Pre-sowing seed treatment	Lab experiment in petri-plates	Inhibited the seed germination rate	Husein et al. (2015)
Growth room conditions	Maize	Moringa leaf extract	30 and 40 times diluted	Pre-sowing seed treatment	Lab experiment in petri-plates	Improved seed germination, % emergence, root and shoot length, and root and shoot fresh and dry biomass	Basra et al. (2011)

(continued)

Table 22.6 (continued)

Type of stress	Plant species	Type of biostimulant used	Concentration used	Mode of application	Growth medium	Improvements	References
Growth room conditions	Tomato	Extracts of *Convolulus arvensis* L., *Euphorbia helioscopia* L., *Vicia sativa*, and *Anagallis arvensis* L.	10, 20, 30, 40, and 50%	Pre-sowing seed treatment	Lab experiment in petri-plates	Improved germination percent, root and shoot length and seedling vigor	Mukhtar and Bajwa (2011)
Growth room conditions	Brinjal	Aqueous leaf extracts of *Azadirachta indica, Calotropis procera, Clerodendron* spp., *Croton Spasriflorus,* leaf and seed of *Lantana camara*, leaf of *Luffa cylindrica*, *Moringa oleifera*, leaf and seed of *Putranjiva roxburghii*, leaves of *Salvadora persica, Senna alata*, *Trema orientales*, and *Trichosanthes dioica*	100% solution	Pre-sowing seed treatment	Lab experiment in petri plates	Inhibited the growth of seed born fungi, improved seed germination	Kurri et al. (2011)
Growth room conditions bean	Beans, groundnut, and common	Moringa leaf extract	100%	Pre-sowing seed treatment	Lab experiment in petri-plates	Improved seed germination decreased the length of hypocotyl	Phiri and Mbewe (2010)
Salt stress	Eggplant	GB and sugar beet extract	100%	Foliar application	Pot experiment in sand culture	Improved plant growth, root and shoot fresh and dry biomass, and nutrient uptake	Abbas et al. (2010)
Growth room conditions	Wheat	*Prosopis Juliflora* leaf extract	5 and 10%	Pre-sowing seed treatment	Lab experiment in petri-plates	Inhibited seed germination and decreased rood length	Siddiqui et al. (2009)

Growth room conditions	Gram, mustard and wheat	Moringa leaf extract	20%	Pre-sowing seed treatment	Lab experiment in petri-plates	Improved germination rate, decreased root, and shoot length	Awasthi et al. (2008)
Growth room conditions	Bitter gourd	Moringa leaf extract	2%	Pre-sowing seed treatment	Lab experiment in petri-plates	Improved seed germination	Thirusenduraselvi and Jerlin (2007)

improved the plant growth, contents of photosynthetic pigments, proline accumulation as well as the nutrient uptake under drought and salt stress, respectively, in wheat (Farooq et al. 2017). Foliar application of algal extracts remarkably improved the crop growth and biomass production under drought stress in moringa and alfalfa (El Sayed et al. 2014). Similarly, exogenous application of different plant-based extracts also improved the plant growth and production as well as final yield and yield quality under salt stress by improving the antioxidant activity, accumulation of different osmolytes and osmoprotectants, and nutrient uptake in fenugreek (Farooq et al. 2017) and common bean (Latif and Mohamed 2016). While under natural environmental conditions, exogenous use of plant extracts improved the plant growth and yield in pepper plant (Rady and Mohamed 2015). It was also studied that the exogenous use of sugar beet extract as foliar spray or pre-sowing seed treatment was found significantly helpful in improving the plant growth, photosynthetic pigment, antioxidant activity, and nutrient uptake in different crops, including wheat (Noman et al. 2018a), okra (Habib et al. 2013) and eggplant (Abbas et al. 2010). Pre-sowing seed treatment of brinjal seed with aqueous extracts of different weed inhibited the seed born pathogenic fungi and improved the seed germination rate and seedling vigor (Kuri et al. 2011). Many different studies have revealed that the exogenous use of moringa leaf extract inhibited the seed germination and root growth in many crops, including mung bean (Husein et al. 2015) and wheat (Siddiqui et al. 2009).

References

Abbas W, Ashraf M, Akram NA (2010) Alleviation of salt-induced adverse effects in eggplant (*Solanum melongena* L.) by glycinebetaine and sugarbeet extracts. Sci Hortic 125(3):188–195

Abdel LAA, Trasn LSP (2016) Impacts of priming with silicon on the growth and tolerance of maize plants to alkaline stress. Front Plant Sci 7:243

Abdel-Aziz H, Hasaneen MN, Omar A (2018) Effect of foliar application of nano chitosan NPK fertilizer on the chemical composition of wheat grains. Egypt J Bot 58(1):87–95

Abdellatif IMY, Abdel-Ati YY, Abdel-Mageed YT, Hassan MAMM (2017) Effect of humic acid on growth and productivity of tomato plants under heat stress. J Hort Res 25(2):59–66

Abu-Muriefah SS (2013) Effect of chitosan on common bean (*Phaseolus vulgaris* L.) plants grown under water stress conditions. Int R J Agri Sci Soil Sci 3(6):192–199

Agbagwa IO (2014) Crude extracts of *Senna alata* (L.) Roxb. Mimics plant growth hormones in promotion of vegetative and reproductive growth in *Celosia argentea* L. Am J Plant Sci 5(13):1918

Agrawal GK, Rakwal R, Tamogami S, Yonekura M, Kubo A, Saji H (2002) Chitosan activates defense/stress response(s) in the leaves of Oryza sativa seedlings. Plant Physiol Biochem 40(12):1061–1069

Ahmad P, Latef AAA, Hashem A, Abd_Allah EF, Gucel S, Tran LSP (2016a) Nitric oxide mitigates salt stress by regulating levels of osmolytes and antioxidant enzymes in chickpea. Front Plant Sci 7:347

Ahmad W, Noor M, Afzal I, Bakhtavar M, Nawaz M, Sun X, Zhao M (2016b) Improvement of sorghum crop through exogenous application of natural growth-promoting substances under a changing climate. Sustainability 8(12):1330

Ahmed AH, Darwish E, Hamoda SAF, Alobaidy MG (2013) Effect of putrescine and humic acid on growth, yield and chemical composition of cotton plants grown under saline soil conditions. Am Eurasian J Agric Environ Sci 13(4):479–497

Ahmed MB, Zhou JL, Ngo HH, Guo W, Chen M (2016) Progress in the preparation and application of modified biochar for improved contaminant removal from water and wastewater. Bioresour Technol 214:836–851

Akıncı İE, Öngel O (2011) Amelioration of nickel toxicity by humic acid on bean (*Phaseolus vulgaris* L.) seedling growth. Ekoloji 20(79):29–37

Akram NA, Shafiq F, Ashraf M (2018) Peanut (*Arachis hypogaea* L.): a prospective legume crop to offer multiple health benefits under changing climate. Compr Rev Food Sci Food Saf 17(5):1325–1338

Ali Q, Ashraf M (2011) Induction of drought tolerance in maize (*Zea mays* L.) due to exogenous application of trehalose: growth, photosynthesis, water relations and oxidative defence mechanism. J Agron Crop Sci 197(4):258–271

Ali A, Mohamed MTM, Siddiqui Y (2012) Control of anthracnose by chitosan through stimulation of defence-related enzymes in Eksotika II papaya (*Carica papaya* L.) fruit. J Biol Life Sci 3:114–126

Ali A, Noh NM, Mustafa MA (2015) Antimicrobial activity of chitosan enriched with lemongrass oil against anthracnose of bell pepper. Food Packag Shelf Life 3:56–61

Ali Q, Javed MT, Noman A, Haider MZ, Waseem M, Iqbal N, Perveen R (2018) Assessment of drought tolerance in mung bean cultivars/lines as depicted by the activities of germination enzymes, seedling's antioxidative potential and nutrient acquisition. Arch Agron Soil Sci 64(1):84–102

Al-Tawaha AR, Turk MA, Al-Tawaha ARM, Alu'datt MH, Wedyan M, Al-Ramamneh EADM, Hoang AT (2018) Using chitosan to improve growth of maize cultivars under salinity conditions. Bulg J Agri Sci 24(3):437–442

Anjum SA, Wang L, Farooq M, Xue L, Ali S (2011a) Fulvic acid application improves the maize performance under well-watered and drought conditions. J Agron Crop Sci 197(6):409–417

Anjum SA, Xie XY, Wang LC, Saleem MF, Man C, Lei W (2011b) Morphological, physiological and biochemical responses of plants to drought stress. Afr J Agric Res 6(9):2026–2032

Ariafar S, Forouzandeh M (2017) Evaluation of humic acid application on biochemical composition and yield of black cumin under limited irrigation condition. Bulletin de la Société Royale des Sciences de Liège 86:13–24

Arif M, Kareem SHS, Ahmad NS, Hussain N, Yasmeen A, Anwar A, Ansar M (2019) Exogenously applied bio-stimulant and synthetic fertilizers to improve the growth, yield and fiber quality of cotton. Sustainability 11(7):2171

Ávila, F. W., Faquin, V., Araújo, J. L., Marques, D. J., Júnior, P. M. R., da Silva Lobato, A. K., & Baliza, D. P. (2011). Phosphite supply affects phosphorus nutrition and biochemical responses in maize plants. Aust J Crop Sci, 5(6), 646

Awasthi OP, Singh IS, Meena SR (2008) Allelopathic influence of aqueous leaf extract of drumstick (Moringa Oleifera) on germination and seedling growth of ground storey crops. Veg Sci 35(1):100–102

Badawy ME, Rabea EI (2009) Potential of the biopolymer chitosan with different molecular weights to control postharvest gray mold of tomato fruit. Postharvest Biol Technol 51(1):110–117

Barzegar T, Moradi P, Nikbakht J, Ghahremani Z (2016) Physiological response of okra cv. Kano to foliar application of putrescine and humic acid under water deficit stress. Int J Hort Sci Technol 3(2):187–197

Basra SMA, Iftikhar MN, Afzal I (2011) Potential of moringa (Moringa oleifera) leaf extract as priming agent for hybrid maize seeds. Int J Agric Biol 13:1006–1010

Battacharyya D, Babgohari MZ, Rathor P, Prithiviraj B (2015) Seaweed extracts as biostimulants in horticulture. Sci Hortic 196:39–48

Bautista-Baños S, Hernández-López M, Bosquez-Molina E, Wilson CL (2003) Effects of chitosan and plant extracts on growth of Colletotrichum gloeosporioides, anthracnose levels and quality of papaya fruit. Crop Prot 22(9):1087–1092

Beheshti S, Tadayyon A (2017) Effects of drought stress and humic acid on some physiological parameters of lima bean (*Phaseolus lunatus* L.). J Plant Process Funct Iranian Soc Plant Physiol 6(19):1–14

Belattmania Z, Engelen AH, Pereira H, Serrão EA, Barakate M, Elatouani S, Sabour B (2016) Potential uses of the brown seaweed *Cystoseira humilis* biomass: 2-fatty acid composition, antioxidant and antibacterial activities. J Mater Environ Sci 7(6):2074–2081

Bistgani ZE, Siadat SA, Bakhshandeh A, Pirbalouti AG, Hashemi M (2017) Morpho-physiological and phytochemical traits of (*Thymus daenensis* Celak.) in response to deficit irrigation and chitosan application. Acta Physiol Plant 39(10):231

Bittelli M, Flury M, Campbell GS, Nichols EJ (2001) Reduction of transpiration through foliar application of chitosan. Agric For Meteorol 107(3):167–175

Burra DD, Berkowitz O, Hedley PE, Morris J, Resjö S, Levander F, Alexandersson E (2014) Phosphite-induced changes of the transcriptome and secretome in *Solanum tuberosum* leading to resistance against *Phytophthora infestans*. BMC Plant Biol 14(1):254

Calvo P, Nelson L, Kloepper JW (2014) Agricultural uses of plant biostimulants. Plant Soil 383(1–2):3–41

Canellas LP, Olivares FL (2014) Physiological responses to humic substances as plant growth promoter. Chem Biol Technol Agric 1(1):3

Canellas LP, Teixeira Junior LRL, Dobbss LB, Silva CA, Medici LO, Zandonadi DB, Façanha AR (2008) Humic acids crossinteractions with root and organic acids. Ann Appl Biol 153(2):157–166

Canellas LP, Olivares FL, Aguiar NO, Jones DL, Nebbioso A, Mazzei P, Piccolo A (2015) Humic and fulvic acids as biostimulants in horticulture. Sci Hortic 196:15–27

Chen Y, Clapp CE, Magen H (2004) Mechanisms of plant growth stimulation by humic substances: the role of organo-iron complexes. Soil Sci Plant Nutr 50(7):1089–1095

Chojnacka, K., Michalak, I., Dmytryk, A., Wilk, R., & Górecki, H. (2015). Innovative natural plant growth biostimulants. In Shishir S, Pant KK (eds) Advances in fertilizer technology. 452–489

Chouliaras V, Tasioula M, Chatzissavvidis C, Therios I, Tsabolatidou E (2009) The effects of a seaweed extract in addition to nitrogen and boron fertilization on productivity, fruit maturation, leaf nutritional status and oil quality of the olive (*Olea europaea* L.) cultivar Koroneiki. J Sci Food Agric 89(6):984–988

Çimrin KM, Türkmen Ö, Turan M, Tuncer B (2010) Phosphorus and humic acid application alleviate salinity stress of pepper seedling. Afr J Biotechnol 9(36)

Coulter CR, Turner P (2013) Encyclopedia of ancient deities. Routledge

Craigie JS (2011a) Seaweed extract stimuli in plant science and agriculture. J Appl Phycol 23(3):371–393

Craigie JS (2011b) Seaweed extract stimuli in plant science and agriculture. J Appl Phycol 23(3):371–393

Dinler BS, Gunduzer E, Tekinay T (2016) Pre-treatment of fulvic acid plays a stimulant role in protection of soybean (*Glycine Max* L.) leaves against heat and salt stress. Acta Biologica Cracoviensia s Botanica 58(1):29–41

Du Jardin P (2015) Plant biostimulants: definition, concept, main categories and regulation. Sci Hortic 196:3–14

Ebele NE, Emodi NV (2016) Climate change and its impact in Nigerian economy. J Sci Res Rep 10:1–13

El Sayed AI, Rafudeen MS, Golldack D (2014) Physiological aspects of raffinose family oligosaccharides in plants: protection against abiotic stress. Plant Biol 16(1):1–8

El-Baky HHA (2009) Enhancing antioxidant availability in grains of wheat plants grown under seawater-stress in response to microalgae extracts treatments. Afr J Biochem Res 3(4):077–083

El-Bassiouny HSM, Bakry BA, Attia AAEM, Allah MMA (2014) Physiological role of humic acid and nicotinamide on improving plant growth, yield, and mineral nutrient of wheat (*Triticum durum*) grown under newly reclaimed sandy soil. Agric Sci 5(08):687

El-Kenawy MA (2017) Effect of chitosan, salicylic acid and fulvic acid on vegetative growth, yield and fruit quality of Thompson seedless grapevines. Egypt J Hort 44(1):45–59

El-Khateeb MA, El-Attar AB, Nour RM (2017) Application of plant biostimulants to improve the biological responses and essential oil production of marjoram (*Majorana hortensis*, Moench) plants. Middle East J Agri Res 6(4):928–941

El-Tantawy EM (2009) Behavior of tomato plants as affected by spraying with chitosan and aminofort as natural stimulator substances under application of soil organic amendments. Pak J Biol Sci 12(17):1164

Erni C (2015) Shifting cultivation, livelihood and food security: new and old challenges for indigenous peoples in Asia. Shifting Cultivation, Livelihood and Food Security 3

Fan D, Hodges DM, Zhang J, Kirby CW, Ji X, Locke SJ, Prithiviraj B (2011) Commercial extract of the brown seaweed *Ascophyllum nodosum* enhances phenolic antioxidant content of spinach (*Spinacia oleracea* L.) which protects *Caenorhabditis elegans* against oxidative and thermal stress. Food Chem 124(1):195–202

Farooq M, Rizwan M, Nawaz A, Rehman A, Ahmad R (2017) Application of natural plant extracts improves the tolerance against combined terminal heat and drought stresses in bread wheat. J Agron Crop Sci 203(6):528–538

Ferrari PC, Souza FM, Giorgetti L, Oliveira GF, Ferraz HG, Chaud MV, Evangelista RC (2013) Development and in vitro evaluation of coated pellets containing chitosan to potential colonic drug delivery. Carbohydr Polym 91(1):244–252

Gezgin S, Sanal HT (2012) “Water-lily sign” as a rare finding of spinal hydatidosis. Spine J 12(6):e5

Ghaderiardakani F, Collas E, Damiano DK, Tagg K, Graham NS, Coates JC (2019, 1983) Effects of green seaweed extract on Arabidopsis early development suggest roles for hormone signalling in plant responses to algal fertilisers. Sci Rep 9(1)

Glinicki R, Sas-Paszt L, Jadczuk-Tobjasz E (2010) The effect of plant stimulant/fertilizer “RESISTIM” on growth and development of strawberry plants. J Fruit Ornam Plant Res 18(1):111–124

Goatley JM, Schmidt RE (1990) Seedling Kentucky bluegrass growth responses to chelated iron and biostimulator materials. Agron J 82(5):901–905

Gómez-Merino FC, Trejo-Téllez LI (2015) Biostimulant activity of phosphite in horticulture. Sci Hortic 196:82–90

Gonçalves, K. S., Sousa, A. D. P., Velini, E. D., Trindade, M. L. B., & Paz, V. D. S. (2014). Application of potassium phosphite to eucalyptus submitted to water stress. In Inovagri International Meeting

Gorka B, Lipok J, Wieczorek PP (2013) Separation and identification of biologically active compounds from algae and their use in nutrition of plants. Przemysl Chemiczny 92(6):1061–1066

Guan YJ, Hu J, Wang XJ, Shao CX (2009) Seed priming with chitosan improves maize germination and seedling growth in relation to physiological changes under low temperature stress. J Zhejiang Univ Sci B 10(6):427–433

Habib N, Ashraf M, Shahbaz M (2013) Effect of exogenously applied nitric oxide on some key physiological attributes of rice (*Oryza sativa* L.) plants under salt stress. Pak J Bot 45(5):1563–1569

Haghighi M, Kafi M, Fang P (2012) Photosynthetic activity and N metabolism of lettuce as affected by humic acid. Int J Veg Sci 18(2):182–189

Haider MW, Ayyub CM, Pervez MA, Asad HU, Manan A, Raza SA, Ashraf I (2012) Impact of foliar application of seaweed extract on growth, yield and quality of potato (*Solanum tuberosum* L.). *Soil*. Environment 31(2)

Halpern M, Bar-Tal A, Ofek M, Minz D, Muller T, Yermiyahu U (2015) The use of biostimulants for enhancing nutrient uptake. Adv Agron 130:141–174. Academic Press

Hanrahan G, Salmassi TM, Khachikian CS, Foster KL (2005) Reduced inorganic phosphorus in the natural environment: significance, speciation and determination. Talanta 66(2):435–444

Hasan HAH (2007) Role of rock phosphate in alleviation of heavy metals stress on *Fusarium oxysporum*. Plant Soil Environ 53(1):1

Hatami H (2017) The effect of zinc and humic acid applications on yield and yield components of sunflower in drought stress. J Adv Agri Technol 4(1):36

Haworth M, Marino G, Cosentino SL, Brunetti C, De Carlo A, Avola G, Centritto M (2018) Increased free abscisic acid during drought enhances stomatal sensitivity and modifies stomatal behaviour in fast growing giant reed (*Arundo donax* L.). Environ Exp Bot 147:116–124

Hayes MH (2006) Solvent systems for the isolation of organic components from soils. Soil Sci Soc Am J 70(3):986–994

He M, He CQ, Ding NZ (2018) Abiotic stresses: general defenses of land plants and chances for engineering multistress tolerance. Front Plant Sci 9

Helaly MN, Farouk S, Arafa SA, Amhimmid NB (2018) Inducing salinity tolerance of rosemary (*Rosmarinus officinalis* L.) plants by chitosan or zeolite application. Asian J Adv Agri Res 5:1–20

Husein ME, El-Hassan SA, Shahein MM (2015) Effect of humic, fulvic acid and calcium foliar application on growth and yield of tomato plants. Int J Biosci 7(1):132–140

Ibrahim WM, Ali RM, Hemida KA, Sayed MA (2014) Role of Ulva lactuca extract in alleviation of salinity stress on wheat seedlings. Sci World J 2014:*1*

Jamil S, Ali Q, Iqbal M, Javed MT, Iftikhar W, Shahzad F, Perveen R (2015) Modulations in plant water relations and tissue-specific osmoregulation by foliar-applied ascorbic acid and the induction of salt tolerance in maize plants. Rev Bras Bot 38(3):527–538

Jiménez E, Dorta F, Medina C, Ramírez A, Ramírez I, Peña-Cortés H (2011) Anti-phytopathogenic activities of macro-algae extracts. Mar Drugs 9(5):739–756

Kamanga RM, Mndala L (2019) Crop abiotic stresses and nutrition of harvested food crops: a review of impacts, interventions and their effectiveness. Afr J Agric Res 14(3):118–135

Kamel HM (2014) Impact of garlic oil, seaweed extract and imazalil on keeping quality of Valencia orange fruits during cold storage. J Hort Sci Ornam Plants 6:116–125

Kananont N, Pichyangkura R, Chanprame S, Chadchawan S, Limpanavech P (2010) Chitosan specificity for the in vitro seed germination of two Dendrobium orchids (*Asparagales Orchidaceae*). Sci Hortic 124(2):239–247

Karimi M, Avci P, Mobasseri R, Hamblin MR, Naderi-Manesh H (2013) The novel albumin–chitosan core–shell nanoparticles for gene delivery: preparation, optimization and cell uptake investigation. J Nanopart Res 15(5):1651

Kasmani MB, Samavat S, Mostafavi M, Khalighi A (2013) The effect of application of humic acid foliar on biochemical parameters of pistachio under drought stress. N Y Sci J 6(12):26–31

Kauffman GL, Kneivel DP, Watschke TL (2007) Effects of a biostimulant on the heat tolerance associated with photosynthetic capacity, membrane thermostability, and polyphenol production of perennial ryegrass. Crop Sci 47(1):261–267

Kaya C, Akram NA, Ashraf M, Sonmez O (2018) Exogenous application of humic acid mitigates salinity stress in maize (*Zea mays* L.) plants by improving some key physico-biochemical attributes. Cereal Res Commun 46(1):67–78

Keča N, Tkaczyk M, E A, Stocki M, Kalaji H, Nowakowska J, Oszako T (2018) Survival of European ash seedlings treated with phosphite after infection with the *Hymenoscyphus fraxineus* and Phytophthora species. Forests 9(8):442

Khairy HM, El-Shafay SM (2013) Seasonal variations in the biochemical composition of some common seaweed species from the coast of Abu Qir Bay, Alexandria, Egypt. Oceanologia 55(2):435–452

Khaled H, Fawy HA (2011) Effect of different levels of humic acids on the nutrient content, plant growth, and soil properties under conditions of salinity. Soil and Water Research 6(1):21–29

Khan W, Rayirath UP, Subramanian S, Jithesh MN, Rayorath P, Hodges DM, Prithiviraj B (2009) Seaweed extracts as biostimulants of plant growth and development. J Plant Growth Regul 28(4):386–399

Khan AS, Ahmad B, Jaskani MJ, Ahmad R, Malik AU (2012) Foliar application of mixture of amino acids and seaweed (*Ascophyllum nodosum*) extract improve growth and physicochemical properties of grapes. Int J Agric Biol 14(3):383–388

Khang VT (2011) Fulvic foliar fertilizer impact on growth of rice and radish at first stage. Omonrice 18:144–148

Khoshvaghti H, Lotfi R (2013) Assessment of hydro-priming on overcoming the allelopathic effect of walnut leaves aqueous extract on seed germination and seedling growth. Int J Biosci 3(1):94–100

Kim HJ, Chen F, Wang X, Rajapakse NC (2005) Effect of chitosan on the biological properties of sweet basil (*Ocimum basilicum* L.). J Agric Food Chem 53(9):3696–3701

Kim HM, Wi SG, Jung S, Song Y, Bae HJ (2015) Efficient approach for bioethanol production from red seaweed *Gelidium amansii*. Bioresour Technol 175:128–134

Kumar S, Trivedi PK (2018) Glutathione S-transferases: role in combating abiotic stresses including arsenic detoxification in plants. Front Plant Sci 9

Kuri SK, Islam MR, Mondal U (2011) Antifungal potentiality of some botanical extracts against important seed borne fungal pathogen associated with brinjal seeds, Solanum melongena L. J Agricul Technol 7(4):1139–1153

Lata R, Chowdhury S, Gond SK, White JF Jr (2018) Induction of abiotic stress tolerance in plants by endophytic microbes. Lett Appl Microbiol 66(4):268–276

Latef AAHA, Miransari M (2014) The role of arbuscular mycorrhizal fungi in alleviation of salt stress. In: Use of microbes for the alleviation of soil stresses. Springer, New York, NY, pp 23–38

Latef A, Hamed AA, Abu Alhmad M, Ahmad S (2017) Foliar application of fresh moringa leaf extract overcomes salt stress in fenugreek (*Trigonella foenum-graecum*) plants. Egypt J Bot 57(1):157–179

Latif HH, Mohamed HI (2016) Exogenous applications of moringa leaf extract effect on retrotransposon, ultrastructural and biochemical contents of common bean plants under environmental stresses. S Afr J Bot 106:221–231

Li X, Xing Y, Jiang Y, Ding Y, Li W (2009) Antimicrobial activities of ZnO powder-coated PVC film to inactivate food pathogens. Int J Food Sci Technol 44(11):2161–2168

Limpanavech P, Chaiyasuta S, Vongpromek R, Pichyangkura R, Khunwasi C, Chadchawan S, Bangyeekhun T (2008) Chitosan effects on floral production, gene expression, and anatomical changes in the Dendrobium orchid. Sci Hortic 116(1):65–72

Liu J, Tian S, Meng X, Xu Y (2007) Effects of chitosan on control of postharvest diseases and physiological responses of tomato fruit. Postharvest Biol Technol 44(3):300–306

Liu TG, Peng YL, Chen WQ, Zhang ZY (2010) First detection of virulence in Puccinia striiformis f. sp. tritici in China to resistance genes Yr24 (= Yr26) present in wheat cultivar Chuanmai 42. Plant Dis 94(9):1163–1163

López-Arredondo DL, Leyva-González MA, González-Morales SI, López-Bucio J, Herrera-Estrella L (2014) Phosphate nutrition: improving low-phosphate tolerance in crops. Annu Rev Plant Biol 65:95–123

Lotfi R, Gharavi-Kouchebagh P, Khoshvaghti H (2015) Biochemical and physiological responses of *Brassica napus* plants to humic acid under water stress. Russ J Plant Physiol 62(4):480–486

Lovatt CJ, Mikkelsen RL (2006) Phosphite fertilizers: what are they? Can you use them? What can they do? Better Crops 90(4):11–13

MacKinnon SL, Hiltz D, Ugarte R, Craft CA (2010) Improved methods of analysis for betaines in Ascophyllum nodosum and its commercial seaweed extracts. J Appl Phycol 22(4):489–494

Mahmoudi M, Aryee P (2015) Study the effect of fluvic acid on physiological traits of *Citrus unshu* under salt stress. Int J Chem Environ Biol Sci 3(3):2320–4087

Makkar HP, Siddhuraju P, Becker K (2007) Plant secondary metabolites. Humana Press, Totowa, NJ, pp 101–106

Malan M, Müller F, Cyster L, Raitt L, Aalbers J (2015) Heavy metals in the irrigation water, soils and vegetables in the Philippi horticultural area in the Western Cape Province of South Africa. Environ Monit Assess 187(1):4085

Malekpoor F, Pirbalouti AG, Salimi A (2016) Effect of foliar application of chitosan on morphological and physiological characteristics of basil under reduced irrigation. Res Crops 17(2):354–359

Malekzadeh P (2015) Influence of exogenous application of glycinebetaine on antioxidative system and growth of salt-stressed soybean seedlings (*Glycine max* L.). Physiol Mol Biol Plants 21(2):225–232

Malerba M, Cerana R (2015) Reactive oxygen and nitrogen species in defense/stress responses activated by chitosan in sycamore cultured cells. Int J Mol Sci 16(2):3019–3034

Maqbool M, Ali A, Ramachandran S, Smith DR, Alderson PG (2010) Control of postharvest anthracnose of banana using a new edible composite coating. Crop Prot 29(10):1136–1141

Matuszak-Slamani R, Bejger R, Cieśla J, Bieganowski A, Koczańska M, Gawlik A, Gołębiowska D (2017) Influence of humic acid molecular fractions on growth and development of soybean seedlings under salt stress. Plant Growth Regul 83(3):465–477

McDonald G, Bovill W, Taylor J, Wheeler R (2015) Responses to phosphorus among wheat genotypes. Crop and Pasture Science 66(5):430–444

Meganid AS, Al-Zahrani HS, El-Metwally MS (2015) Effect of humic acid application on growth and chlorophyll contents of common bean plants (Phaseolus vulgaris L.) under salinity stress conditions. Int J Innov Res Sci Eng Technol 4(5):2651–2660

Mejía-Teniente L, Durán-Flores FDD, Chapa-Oliver A, Torres-Pacheco I, Cruz-Hernández A, González-Chavira M, Guevara-González R (2013) Oxidative and molecular responses in *Capsicum annuum* L. after hydrogen peroxide, salicylic acid and chitosan foliar applications. Int J Mol Sci 14(5):10178–10196

Meng X, Tian S (2009) Effects of preharvest application of antagonistic yeast combined with chitosan on decay and quality of harvested table grape fruit. J Sci Food Agric 89(11):1838–1842

Michalak I, Chojnacka K (2015) Production of seaweed extracts by biological and chemical methods. In: Marine algae extracts: processes, products, and applications, pp 121–144

Michalak I, Chojnacka K (2016) The potential usefulness of a new generation of agro-products based on raw materials of biological origin. *Acta scientiarum Polonorum*. Hortorum cultus = Ogrodnictwo 15:97–120

Moghadam HRT, Khamene MK, Zahedi H (2014) Effect of humic acid foliar application on growth and quantity of corn in irrigation withholding at different growth stages. Maydica 59(2):124–128

Moradi P, Pasari B, Fayyaz F (2017) The effects of fulvic acid application on seed and oil yield of safflower cultivars. J Cent Eur Agric 18(3):584–597

Morsomme P, Boutry M (2000) The plant plasma membrane H+-ATPase: structure, function and regulation. Biochimica et Biophysica Acta (BBA)-Biomembranes 1465(1–2):1–16

Mukhtar I, Bajwa R (2011) Effect of aqueous extracts of some weeds on germination and seedling growth of tomato (Lycopersicon esculentum Mill.). Pak J Phytopathol 23:138–143

Nagahama H, Maeda H, Kashiki T, Jayakumar R, Furuike T, Tamura H (2009) Preparation and characterization of novel chitosan/gelatin membranes using chitosan hydrogel. Carbohydr Polym 76(2):255–260

Nardi S, Concheri G, Pizzeghello D, Sturaro A, Rella R, Parvoli G (2000) Soil organic matter mobilization by root exudates. Chemosphere 41(5):653–658

Nardi S, Pizzeghello D, Muscolo A, Vianello A (2002) Physiological effects of humic substances on higher plants. Soil Biol Biochem 34(11):1527–1536

Nardi S, Carletti P, Pizzeghello D, Muscolo A (2009) Biological activities of humic substances. Biophysico-Chemical Processes Involving Natural Nonliving Organic Matter In Environmental Systems 2(part 1):305–339

Nigania S, Sharma Y, Kumar B (2017) Role of humic acid and salicylic acid on quality parameters and K/Na ratio of groundnut (*Arachis hypogaea* L.) under salt and water stress. IJCS 5(6):278–283

Noman A, Ali Q, Maqsood J, Iqbal N, Javed MT, Rasool N, Naseem J (2018a) Deciphering physio-biochemical, yield, and nutritional quality attributes of water-stressed radish (*Raphanus sativus* L.) plants grown from Zn-Lys primed seeds. Chemosphere 195:175–189

Noman A, Ali Q, Naseem J, Javed MT, Kanwal H, Islam W, Aqeel M, Khalid N, Zafar S, Tayyeb M, Iqbal N, Buriro M, Maqsood J, Shahid S (2018b) Sugar beet extract acts as a natural biostimulant for physio-biochemical attributes in water stressed wheat (*Triticum aestivum* L.). Acta Physiol Plant 40(6):110

Nwangburuka CC, Oyekale K1, Ezekiel CN, Anokwuru PC, Badaru O (2012) Effects of Moringa oleifera leaf extract and sodium hypochlorite seed pre-treatment on seed germination, seedling growth rate and fungal abundance in two accessions of Abelmoschus esculentus (L) Moench. Arch Appl Sci Res 4(2):875–881

Oancea F, Velea S, Fãtu V, Mincea C, Ilie L (2013) Micro-algae based plant biostimulant and its effect on water stressed tomato plants. Roman J Plant Prot 6:104–117

Ohno H, Yoshizawa M, Ogihara W (2004) Development of new class of ion conductive polymers based on ionic liquids. Electrochim Acta 50(2–3):255–261

Osman HE, Salem OM (2011) Effect of seaweed extracts as foliar spray on sunflower yield and oil content. Egypt J Phycol 12(60):57–70

Pastor C, Sánchez-González L, Chiralt A, Cháfer M, González-Martínez C (2013) Physical and antioxidant properties of chitosan and methylcellulose based films containing resveratrol. Food Hydrocoll 30(1):272–280

Phiri C, Mbewe DN (2010) Influence of Moringa oleifera leaf extracts on germination and seedling survival of three common legumes. Int J Agric Biol 12:315–317

Pongprayoon W, Roytrakul S, Pichayangkura R, Chadchawan S (2013) The role of hydrogen peroxide in chitosan-induced resistance to osmotic stress in rice (*Oryza sativa* L.). Plant Growth Regul 70(2):159–173

Pornpienpakdee P, Singhasurasak R, Chaiyasap P, Pichyangkura R, Bunjongrat R, Chadchawan S, Limpanavech P (2010) Improving the micropropagation efficiency of hybrid Dendrobium orchids with chitosan. Sci Hortic 124(4):490–499

Pourhadi M, Badi HN, Mehrafarin A, Omidi H, Hajiaghaee R (2018) Phytochemical and growth responses of Mentha piperita to foliar application of biostimulants under greenhouse and field conditions. Herba Polonica 64(2):1–12

Prapagdee B, Kotchadat K, Kumsopa A, Visarathanonth N (2007) The role of chitosan in protection of soybean from sudden death syndrome caused by *Fusarium solani* f. sp. glycines. Bioresour Technol 98(7):1353–1358

Puglisi E, Fragoulis G, Ricciuti P, Cappa F, Spaccini R, Piccolo A, Crecchio C (2009) Effects of a humic acid and its size-fractions on the bacterial community of soil rhizosphere under maize (*Zea mays* L.). Chemosphere 77(6):829–837

Rady MM, Mohamed GF (2015) Modulation of salt stress effects on the growth, physio-chemical attributes and yields of *Phaseolus vulgaris* L. plants by the combined application of salicylic acid and *Moringa oleifera* leaf extract. Sci Hortic 193:105–113

Raho N, Ramirez L, Lanteri ML, Gonorazky G, Lamattina L, Ten Have A, Laxalt AM (2011) Phosphatidic acid production in chitosan-elicited tomato cells, via both phospholipase D and phospholipase C/diacylglycerol kinase, requires nitric oxide. J Plant Physiol 168(6):534–539

Ranjbar H, Shahryari R, Mollasadeghi V (2012) Production of wheat seeds with presence of humic fertilizer after anthesis drought condition. Afr J Agric Res 7(2):307–310

Ray SR, Bhuiyan MJH, Anowar M, Hossain SM, Tahjib-Ul-Arif M (2015) Chitosan suppresses antioxidant enzyme activities for mitigating salt stress in mung bean varieties. OSR J Agri Veter Sci 9(9):36–41

Raza S, Aown M, Saleem MF, Ashraf MY, Ali A, Asghar HN (2012) Glycinebetaine applied under drought improved the physiological efficiency of wheat (*Triticum aestivum* L.) plant. *Soil and*. Environment 31(1):67–71

Rinez I, Ghezal N, Rinez A, Muhammad F, Dbara S, Saad I, Haouala R (2018) Improving salt tolerance in pepper by bio-priming with Padina pavonica and Jania rubens aqueous extracts. Int J Agric Biol 20(3):513–523

Rönnbäck P, Crona B, Ingwall L (2007) The return of ecosystem goods and services in replanted mangrove forests: perspectives from local communities in Kenya. Environ Conserv 34(4):313–324

Rose MT, Patti AF, Little KR, Brown AL, Jackson WR, Cavagnaro TR (2014) A meta-analysis and review of plant-growth response to humic substances: practical implications for agriculture. Adv Agron 124:37–89

Rouphael Y, Franken P, Schneider C, Schwarz D, Giovannetti M, Agnolucci M, Colla G (2015) Arbuscular mycorrhizal fungi act as biostimulants in horticultural crops. Sci Hortic 196:91–108

Rouphael Y, Giordano M, Cardarelli M, Cozzolino E, Mori M, Kyriacou M, Colla G (2018) Plant- and seaweed-based extracts increase yield but differentially modulate nutritional quality of greenhouse spinach through biostimulant action. Agronomy 8(7):126

Ruzzi M, Aroca R (2015) Plant growth-promoting rhizobacteria act as biostimulants in horticulture. Sci Hortic 196:124–134

Said-Al Ahl HAH, El Gendy AG, Omer EA (2016) Humic acid and indole acetic acid affect yield and essential oil of dill grown under two different locations in Egypt. J Pharm Sci Res 8(7):594

Santaniello A, Scartazza A, Gresta F, Loreti E, Biasone A, Di Tommaso D, Perata P (2017) *Ascophyllum nodosum* seaweed extract alleviates drought stress in Arabidopsis by affecting photosynthetic performance and related gene expression. Front Plant Sci 8:1362

Schäfer M, Brütting C, Meza-Canales ID, Großkinsky DK, Vankova R, Baldwin IT, Meldau S (2015) The role of cis-zeatin-type cytokinins in plant growth regulation and mediating responses to environmental interactions. J Exp Bot 66(16):4873–4884

Schroetter S, Angeles-Wedler D, Kreuzig R, Schnug E (2006) Effects of phosphite on phosphorus supply and growth of corn (*Zea mays*). Landbauforschung Völkenrode 56(3/4):87

Shaddad MAK, Farghl AAM, Galal HR, Hassan EA (2014) Influence of seaweed extracts (*Sargassum dentifolium* or *Padina gymnospora*) on the growth and physiological activities of faba bean and wheat plants under salt stress. Egypt J Bot 54(1):121–135

Shahid M, Dumat C, Silvestre J, Pinelli E (2012) Effect of fulvic acids on lead-induced oxidative stress to metal sensitive *Vicia faba* L. plant. Biol Fertil Soils 48(6):689–697

Shahryari R (2017) Economic and biological yield assessment of wheat genotypes under terminal drought in presence of humic acid using stress tolerance indices/Shahryari, Reza. IIOAB Journal 7:1–6

Shukla PS, Borza T, Critchley AT, Prithiviraj B (2016) Carrageenans from red seaweeds as promoters of growth and elicitors of defense response in plants. Front Mar Sci 3:81

Siddiqui S, Bhardwaj S, Saeed Khan S, Meghvanshi MK (2009) Allelopathic effect of different concentration of water extract of Prosopsis juliflora leaf on seed germination and radicle length of wheat (Triticum aestivum Var-Lok-1). Am-Euras J Sci Res 4(2):81–84

Stevenson FJ (1994) Humus chemistry: genesis, composition, reactions. Wiley

Tang WW, Zeng GM, Gong JL, Liang J, Xu P, Zhang C, Huang BB (2014) Impact of humic/fulvic acid on the removal of heavy metals from aqueous solutions using nanomaterials: a review. Sci Total Environ 468:1014–1027

Thao HTB, Yamakawa T (2009) Phosphite (phosphorous acid): fungicide, fertilizer or biostimulator? Soil Sci Plant Nutr 55(2):228–234

Thirusenduraselvi D, Jerlin R (2007) Effect of pre-germination treatments on the emergency percentage of bitter gourd cv Co1 seeds. Trop Agric Res Ext 10:88–90

Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci 108(50):20260–20264

Tomar NS, Agarwal RM (2013) Influence of treatment of *Jatropha curcas* L. leachates and potassium on growth and phytochemical constituents of wheat (*Triticum aestivum* L.). Am J Plant Sci 4(5):1134

Trevisan S, Francioso O, Quaggiotti S, Nardi S (2010) Humic substances biological activity at the plant-soil interface: from environmental aspects to molecular factors. Plant Signal Behav 5(6):635–643

Varadarajan DK, Karthikeyan AS, Matilda PD, Raghothama KG (2002) Phosphite, an analog of phosphate, suppresses the coordinated expression of genes under phosphate starvation. Plant Physiol 129(3):1232–1240

Verdi P, Cano M, Liem E (2015) Low concentrations of humic substances enhanced the growth of *Lactuca sativa* L. American Journal of Experimental Agriculture 5(6):555

Violante A, Cozzolino V, Perelomov L, Caporale AG, Pigna M (2010) Mobility and bioavailability of heavy metals and metalloids in soil environments. J Soil Sci Plant Nutr 10(3):268–292

Wahid A (2007) Physiological implications of metabolite biosynthesis for net assimilation and heat-stress tolerance of sugarcane (*Saccharum officinarum*) sprouts. J Plant Res 120(2):219–228

Wang B-G, Zhang W-W, Duan X-J, Li X-M (2009) In vitro antioxidative activities of extract and semi-purified fractions of the marine red alga, Rhodomela confervoides (Rhodomelaceae). Food Chem 113(4):1101–1105

Waqas MA, Khan I, Akhter MJ, Noor MA, Ashraf U (2017) Exogenous application of plant growth regulators (PGRs) induces chilling tolerance in short-duration hybrid maize. Environ Sci Pollut Res 24(12):11459–11471

Wells E, Wilkinson M, Wood P, Scanlan C (2007) The use of macroalgal species richness and composition on intertidal rocky seashores in the assessment of ecological quality under the European water framework directive. Mar Pollut Bull 55(1–6):151–161

Wieczorek PP, Lipok J, Górka B (2013) Biologically active compounds isolated from algae and their application as a plant growth regulators. Open Conf Proc J 3(Suppl 1-M4):20–28

Yasmeen A, Basra SMA, Farooq M, ur Rehman H, Hussain N (2013) Exogenous application of moringa leaf extract modulates the antioxidant enzyme system to improve wheat performance under saline conditions. Plant Growth Regul 69(3):225–233

Yu-ling CHEN, LiJian-hua SHEN (1999) Effects of FAon iPA and GAs levels in winter wheat seedlings. J Hebei Normal Univesity (Nat Sci) 4:37

Zeng D, Luo X (2012) Physiological effects of chitosan coating on wheat growth and activities of protective enzyme with drought tolerance. Open J Soil Sci 2(03):282

Zhang Y, Dubé MA, McLean DD, Kates M (2003) Biodiesel production from waste cooking oil: 2. Economic assessment and sensitivity analysis. Bioresour Technol 90(3):229–240

Zhang Y, Zhang J, Meng T, Zhu T, Müller C, Cai Z (2013) Heterotrophic nitrification is the predominant NO 3− production pathway in acid coniferous forest soil in subtropical China. Biol Fertil Soils 49(7):955–957

Zhang A, Zhou X, Li M, Wu H (2017) Impacts of biochar addition on soil dissolved organic matter characteristics in a wheat-maize rotation system in loess plateau of China. Chemosphere 186:986–993

Zhao D, Wang J, Zhou E (2007) Oxidative desulfurization of diesel fuel using a Brønsted acid room temperature ionic liquid in the presence of H2O2. Green Chem 9(11):1219–1222

Chapter 23
Transcription Factors and Plant Abiotic Stress Responses

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Contents

Abstract Plants are exposed to different environmental stresses like drought, salinity, extreme temperatures, UV radiations, and heavy metals. Crop productivity is reduced significantly due to these stresses. As these abiotic stresses affect multiple stages of plant growth and development, so achieving tolerance to these stresses is also a complex process. Thus, basic mechanism of adaption and tolerance to abiotic stresses has been an area of comprehensive research to understand the mechanism of stress tolerance. The adverse environmental conditions are encountered by an integrated and complex cascade of molecular events in plants that depends upon the

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intensity and time period of the stress. Plant stress tolerance encompasses modifications at whole-plant, tissue, molecular, cellular, and physiological levels. In plants, the adjustments at biochemical and physiological levels, like generation of reactive oxygen species (ROS), electrolytic leakage, relative water content, accumulation of free radicals, leaf wilting, leaf aging, and root growth stimulation, disturb the cellular homeostasis that results in inactivation of enzymes, lipid peroxidation, and membrane damage, thus influencing cell viability. Moreover, gene expression is an important molecular response controlled by various transcription factors which regulate the expression of stress-related genes. The gene expression is either negatively or positively controlled by transcription factors determining the plant survival. Therefore, it is necessary to study the transcription factors involved in regulating the gene expression so that the mechanism of stress tolerance may be understood. This chapter discusses various transcription factors regulating genes responsible for different abiotic stresses.

Keywords Transcription factors · Reactive oxygen species · Signaling molecules · abiotic stress

23.1 Introduction

The transcription factors (TFs) are associated with regulation of different abiotic stress-responsive genes like drought, reactive oxygen species (ROS), salinity, heavy metals, heat, cold, UV-radiation, and submergence (Amjad et al. 2018). The TFs act with *cis*-regulatory elements as molecular switches to regulate gene expression under stress. These TFs have the ability to bind with the promoter region of gene(s) and the expression of stress-responsive genes is upregulated or downregulated. The efficiency of plant adaptive responses is enhanced by inserting these TFs-encoding genes by different plant engineering methods. These metabolic processes in plants work on two approaches. First is regulation of stress response by reprogramming primary metabolism and second is change in regulatory pathways to the stress (Gujjar et al. 2014). Regulatory pathways consist of various signaling molecules, TFs, *cis*-regulatory elements, and associated genes. So, the second approach is more effective because signaling cascade is immediately initiated on exposure to stress mediated by the transcription of stress-responsive genes triggered by different transcription factors (Golldack et al. 2011).

There are several TFs and other regulatory elements present in different organisms and many of them have been identified up till now. Some important TF families found in plants are abscisic acid (ABA)-responsive element-binding factor (ABF; Kerr et al. 2018), dehydration-responsive element-binding factor (*DREB*; Erpen et al. 2017), zinc-finger proteins (*ZFPs*; Faraji et al. 2018), myeloblastosis (*MYB*; Sun et al. 2018), *WRKY* genes (Vannozzi et al. 2018), *N*-acetyl-L-cysteine (*NAC*;

Martı et al. 2018), basic-leucine-zipper-protein (*bZIP*; Liu et al. 2019), and basic helix-loop-helix (*bHLH*; Alessio et al. 2018). They have very important roles in gene expression regulation of abiotic stress-responsive genes in different plant species. The perception of the stress signal and initiating the expression of particular stress-responsive gene is a multifactorial phenomenon in plants (Mahmood-ur-Rahman et al. 2019). Drought, cold, heat, submergence, UV radiation, and heavy metal tolerance are achieved by overexpression of stress-responsive genes in plant species with the help of TFs, which made this approach more useful in comparison with engineering of functional genes. The TFs of one family can stimulate the expression of many genes having the same or different functions (Gujjar et al. 2014). In this chapter, the TFs activated under different abiotic stresses by activating stress-responsive genes are explained in detail.

23.2 Transcription Factors Associated With Drought Stress

Any factor that causes the shortage of yield, when it is absent/present, is called stress (Rauf 2016). Every year in many parts of the world, development and growth of plant is reduced due to drought stress. As compared to other abiotic stresses, drought does not occur sharply, but it is developed gradually and rises with the passage of time, resulting in the significant damage to crop. The nutrient and water supply to plant are affected by drought. Water is necessary for various plant metabolic activities, and its shortage affects different biochemical and physical processes in plants (Ahmad et al. 2014). Plants have modified themselves to combat with these stresses at cellular, biochemical, molecular, and physiological stages. The expression of multiple genes in several plant species is induced due to several hostile environmental conditions. By using the microarray experimentations, multiple stress-tolerant genes have been studied simultaneously (Kobayashi et al. 2005). The response of these genes is considered to regulate the expression of some other genes via signal transduction (Xiong and Fei 2006). The exogenic application of abscisic acid (ABA) influences numerous genes that react during water scarcity. Many reports have been categorized genes that are influenced via desiccation stress; nevertheless, in Arabidopsis these genes do not react to foreign application of ABA. This suggests two types of signal transduction pathways: (a) ABA-dependent and (b) ABA-independent (Yamaguchi-shinozaki and Shinozaki 2006).

TFs are efficient regulators which are involved in controlling different gene clusters when arranged in varying patterns. A single TF can regulate gene expression by its accurate and specific binding with *cis*-acting elements. This form of transcriptional controlling system is called “regulon.” In Arabidopsis, some major regulons have been identified, which are regulated under stress conditions. The ABRE-binding factor (*ABF*) or ABA-responsive element-binding protein (AREB) is ABA-dependent regulon and C-repeat-binding factor (*CBF*) or dehydration-responsive element-binding protein 1 (DREB1) and DREB2 are ABA-independent regulon

(Sunkar et al. 2007). DREB2A and DREB2B proteins of Arabidopsis are important TFs involved in gene expression induced by drought (Nakashima et al. 2009). The core sequence "A/GCCGAC" of dehydration-responsive element (*DRE*) was identified in Arabidopsis. The ABA-independent *cis*-acting element is essential for controlling the gene expression in response to water deficiency and other environmental stresses (Nakashima et al. 2009).

Many ABA-dependent and drought-inducible genes encode several TFs that have been reported in past years. Although signaling pathways liable for functional analysis of these genes are highly indefinite, but transcriptional initiation of stress-responsive genes is effectively understood with the help of studies on *COR78/LTI78/RD29A* gene. Its promoter has both *DRE/CRT* (dehydration response element/C-repeat and ABA-responsive elements (*ABRE*); Yamaguchi-Shinozaki and Shinozaki 1994). The drought tolerance can be achieved by increasing the expression of *DREB1* or *CBF* in transgenic plants, proposing that the system is significant for improvement of stress tolerance in crops. In *Arabidopsis thaliana,* the overexpression of *ABF3/4* has resulted in slow transpiration rate and increased tolerance against drought and ABA hypersensitivity. The *RD22* is an ABA-dependent gene that is responsible for drought tolerance. In response to cold stress, *DREB1* or *CBF* cascades have a major role in improving ABA-independent expression of genes (Yamaguchi-shinozaki and Shinozaki 2006). *DREB1/DRE* regulon presents in several grasses and has capacity to develop drought stress tolerance via gene transfer in commercially essential grains.

Similarly, TFs (*DREB2A/2B*) show their response in desiccation stress and stimulate expression of several drought-responsive genes (Heo et al. 2018). *MYB* TFs are identified via presence of MYB-domain which is involved in binding with DNA (Dubos et al. 2010). *MYB/MYC* and *NAC* are some other regulons that are expressed in response to different environmental stimulus (Sunkar et al. 2007). The MYB proteins have been classified on the basis of different sequence repeats. Fifty-one percent of *AtMYB* genes are upregulated and 41% are downregulated by drought in *A. thaliana* (Katiyar et al. 2012). Moreover, various MYB-TFs have been functionally identified for the participation in other drought responses. Earlier, some other MYB-TFs have been characterized for their function to control specific developmental activity (Zimmermann et al. 2004) (see Table 23.1 for examples of TFs associated with drought stress).

23.3 Transcription Factors Associated With Salt Stress

The growth, development, and productivity of the plant are compromised by the excessive salt accumulation in the soil (Kronzucker and Britto 2011; Deinlein et al. 2014), inducing ion toxicity, alteration of metabolic processes, genotoxicity, osmotic stress, reduction of cell expansion and cell division, oxidative stress, membrane disorganization, and nutrient deficiency (Mahmood-ur-Rahman et al. 2019). It can also speed up the aging process in older leaves and lessen the growth of new shoots

Table 23.1 Various families of transcription factors involved in abiotic stress tolerance in plants

Family name	Transcription factor	Response to stress	Species in which studied
bZIP	*ABF1*	Cold	*Arabidopsis thaliana*
	ABF2	Drought and salt	*A. thaliana*
	ABF3	Salt	*A. thaliana*
	GmbZIP132	Drought, cold, and salt	*Glycine max*
	GmbZIP78	Salt and drought	*G. max*
	GmbZIP62	Salt, cold, and drought	*G. max*
	GmbZIP44	Salt and drought	*G. max*
	Wlip19	Drought and cold	*Triticum aestivum*
	ZmbZIP17	Heat, drought, and salt	*Zea mays*
	ABF1	WDS, salt, cold, oxidative, ROS, and ABA	*Oryza sativa*
	ABF2	Salt, WDS, cold oxidative, ROS, and ABA	*O. sativa*
	OsAREB1	Heat and drought	*O. sativa*
	OsAB15	Salt, ABA, cold, and WDS	*O. sativa*
	OsbZIP16	Salt, WDS, and ABA	*O. sativa*
	OsbZIP23	PEG, ABA, salt, and WDS	*O. sativa*
	OsbZIP46	Heat, WDS, H_2O_2, and ABA	*O. sativa*
	OsbZIP52	Cold stress (not induced in other stresses)	*O. sativa*
	OsbZIP71	PEG, WDS, salt, and ABA	*O. sativa*
	OsbZIP72	Cold, salt, PEG, and ABA	*O. sativa*
MYC	*AtMYC2*	Salt, drought, and cold	*A. thaliana*
MYB	*AtMYB2*	Salt and drought	*A. thaliana*
	AtMYB4	Ethylene, SA, JA, and salt	*A. thaliana*
	AtMYB6	Ethylene, SA, JA, and salt	*A. thaliana*
	AtMYB7	Ethylene, SA, JA, and salt	*A. thaliana*
	AtMYB44	Ethylene, SA, JA, and salt	*A. thaliana*
	AtMYB73	Ethylene, SA, JA, and salt	*A. thaliana*
	MYB15	Salt, cold, and drought	*A. thaliana*
	OsMYB2	Salt, cold, and WDS	*O. sativa*
	OsMYB55	Heat	*O. sativa*
	OsMYB91	Salt, PEG, WDS, and heat shock	*O. sativa*
	OsMYB3R-2	Salt, cold, and drought	*O. sativa*
	GmMYB76	Salt	*G. max*
	GmMYB92	Salt and cold	*G. max*
	GmMYB177	Salt and drought	*G. max*
	OsMYB3R-2	Cold, drought, and salt	*O. sativa*

(continued)

Table 23.1 (continued)

Family name	Transcription factor	Response to stress	Species in which studied
CBF/ DREB	*DREB1A*	Cold	*A. thaliana*
	DREB2A	Salt and drought	*A. thaliana*
	DREB2C	Mannitol, salt, and cold	*A. thaliana*
	CBF1	Cold	*A. thaliana*
	CBF2	Cold	*A. thaliana*
	CBF3	Cold	*A. thaliana*
	CBF4	Drought	*A. thaliana*
	OsDREB1A	Salt, wounding, and cold	*O. sativa*
	OsDREB1B	Cold	*O. sativa*
	OsDREB1C	Salt, wounding, cold, and drought	*O. sativa*
	OsDREB1F	Drought, cold, and salt	*O. sativa*
	OsDREB2A	Salt, drought, and cold	*O. sativa*
	OsDREB2B	Cold and heat	*O. sativa*
	DREB1	Cold	*O. sativa*
	OsEREBP1	Cold	*O. sativa*
	OsERF109	WDS, salt, ABA, and ACC (ethylene precursor)	*O. sativa*
	OsERF922	ABA and salt	*O. sativa*
	Sub1A-1	ABA and salt	*O. sativa*
	ZmDREB2A	Salt, heat, cold, and drought	*Z. mays*
	PgDREB2A	Salt, cold, and drought	*Pennisetum glaucum*
	SbDREB2	Drought	*Sorghum bicolor*
	SiDREB2	Salt and drought	*Setaria italica*
	CaDREBLP1	Salt, wounding, and drought	*Capsicum annum*
	AhDREB1	Salt	*Atriplex hortensis*
	GmDREBa	Drought, salt, and cold	*G. max*
	GmDREBb	Drought, salt, and cold	*G. max*
	GmDREBc	Salt and drought	*G. max*
	GmDREB2	Salt and drought	*G. max*
	DmDREBa	Cold	*Dendranthema x morifolium*
	DmDREBb	Cold	*Dendranthema x morifolium*
	PNDREB1	Cold and drought	*Arachis hypogea*
	CAP2	Salt, drought, and auxin	*Cicer arietinum*
	DvDREB2A	Heat, drought, and cold	*Dendranthema grandiflorum*
	SbDREB2A	Salt, heat, and drought	*Salicornia brachiate*

(continued)

Table 23.1 (continued)

Family name	Transcription factor	Response to stress	Species in which studied
NAC	*ATAF1*	Drought	*A. thaliana*
	AtNAC2	Salt	*A. thaliana*
	AtNAC019	Salt and drought	*A. thaliana*
	AtNAC055	Salt and drought	*A. thaliana*
	AtNAC072	Salt and drought	*A. thaliana*
	OsNAC6	Salt, drought, and cold	*O. sativa*
	SNAC1	WDS, salt, cold, and ABA	*O. sativa*
	SNAC2	WDS, salt, cold, wounding, and ABA	*O. sativa*
	SNAC3	WDS, heat, salt, and ABA	*O. sativa*
	OsNAC5	WDS, cold, high salt, ABA	*O. sativa*
	OsNAC6	Cold, WDS, and high-salt	*O. sativa*
	OsNAC9	High-salt, WDS, and ABA	*O. sativa*
	OsNAC10	High-salt, WDS, and ABA	*O. sativa*
	OsNAC045	High-salt, low temperature, WDS, and ABA	*O. sativa*
	OsNAP	Salt, PEG, cold, ABA, and H_2O_2	*O. sativa*
	CarNAC5	Heat and drought	*C. arietinum*
	TaNAC4	Wounding, ethylene, salt, and cold	*T. aestivum*
	GhNAC2	Drought and cold	
	GhNAC3	Cold	
	GhNAC4	Drought, cold, and salt	*G. hirsutum*
	GhNAC5	Drought and cold	
	GhNAC6	Drought, cold, and salt	*G. hirsutum*
	SiNAC	Salt, drought, and ethephon	*S. italica*
WRKY	*OsWRKY 11*	Heat shock and WDS	*O. sativa*
	OsWRKY 30	WDS and ABA	
	OsWRKY 76	Low-temperature and ABA	*O. sativa*
	GmWRKY21	Low-temperature and ABA	*G. max*
	GmWRKY54	Low-temperature and ABA	*G. max*
	GmWRKY13	Low-temperature and ABA	*G. max*
	NbWRKY	Low-temperature and ABA	*Nicotiana benthamiana*

(continued)

Table 23.1 (continued)

Family name	Transcription factor	Response to stress	Species in which studied
ZFP	*ZPT2–3*	Low-temperature and ABA	*Petunia spp.*
	CaZF	Low-temperature and ABA	*C. arietinum*
	OSISAP1	Low-temperature and ABA	*O. sativa*
	ZFP36	H_2O_2 and ABA	
	ZFP179	PEG, salt, and ABA	*O. sativa*
	ZFP182	Salt, cold, and ABA	*O. sativa*
	ZFP252	Salt stress and PEG	*O. sativa*
	OsTZF1	Methyl jasmonate, salicylic acid, and ABA	*O. sativa*
	OsDi19–4	High salt and WDS	*O. sativa*
	OsDIS1	WDS	*O. sativa*
	OsDSG1	WDS	*O. sativa*
	OsRDCP1	Cold and WDS	*O. sativa*
	OsSDIR1	WDS and salt	*O. sativa*
	OsSRFP1	Cold, salt, WDS, H_2O_2, and ABA	*O. sativa*

bZIP basic leucine zipper, MYB myeloblastosis, ZFP zinc finger protein, NAC *N*-acetyl-L-cysteine, ACC 1-aminocyclopropane-1-carboxylic acid, WDS water and dehydration stress, ABA abscisic acid, PEG polyethylene glycol, H_2O_2 hydrogen peroxide
Source: Plant TFD (http://planttfdb.cbi.pku.edu.cn/)

(Munns and Tester 2008). So, it is significant to increase the salinity tolerance in plants for enough food production leading towards sustainable agriculture. The stress tolerance in plants against abiotic stresses is increased by prior treatments with suboptimal conditions that improve survival capacity of the plants. For example, seedlings and seeds are pretreated with NaCl to improve salt tolerance. After the short-term acquaintance to the nonlethal levels of salinity, some glycophytic plant species temporarily attain tolerance against the lethal levels of salt stress, this process is called acclimation of salt (Xie et al. 2011). It is used for cultivating different crops like wheat (Janda et al. 2016), peas (Pandolfi et al. 2012), and maize (Pandolfi et al. 2016). It allows plant species to develop and grow in elevated salt concentrations.

Variations in meditations of phytohormones, organic solutes (glucose, fructose, sucrose, and proline), and inorganic solutes (chlorine ions, potassium ions, and sodium ions) have been detected usually during salt acclimation or adaptation (Li et al. 2016). Though, these physiological studies have been carried out for a long time, but there is still a need to decipher the molecular mechanism, particularly memory maintenance of past salinity exposures by plants. The issue has been illustrated in some studies by applying higher levels of salt stress immediately after the exposure to low salt stress (Garcia et al. 2015; Moyano et al. 2018). This method was not enough to predict the information stored during low salt stress to improve tolerance level of plant against high salt stress. It was interesting to study that plant memorizes the acclimation of salt after exposure to low salinity stress for a short time and improves its tolerance against high salinity stress applied for long time, even after stimulus removal from environment, which is a quite similar finding when the heat acclimation achieved after applying a mild heat shock for very short time (Wu et al. 2013).

To maintain plant memory, two mechanisms might be involved (Crisp et al. 2016). First mechanism is to maintain TFs, signaling molecules and key metabolic components. Second mechanism is the change in the state of chromatin combined with modifications in memory-responsive genes expression like alteration in DNA methylation patterns and histone modifications. In salt-acclimated cells, elevated levels of proline and ABA have been reported and excessive production of reactive-oxygen species in mitochondria may serve as a signal of salinity acclimation. Beside the fact, response of unfolded proteins also exists in salinity-acclimated cells. In Arabidopsis, salinity and other environmental stresses enhance accumulation of unfolded proteins and initiate the stress response of endoplasmic reticulum (ER) (Tian et al. 2018). These abnormal proteins persist there until ER chaperones fold or degrade them by ER-associated degradation. In addition, the unfolded protein response is initiated by ER and its signals are transferred with the help of membrane bound TFs like *bZIP17* and *bZIP18* to trigger the genes expression encoding the ER associated with degradation or protein-folding machinery (Tian et al. 2018). Another example of the transcription factor involved in salinity stress is *R2R3*-type myeloblastosis (MYB) transcription factor *OsMPS* in rice, which triggers the genes in the biosynthesis of cell wall and phytohormones (Schmidt et al. 2013). In plants, salt and drought tolerance is achieved by biosynthesis of plant cuticle polymers as many stress-responsive TFs are involved in the activation of the genes that belong to the development and biosynthesis of the plant cuticle and extracellular biomatrix (Golldack et al. 2014).

To maintain growth and development like circadian clock, floral organ morphogenesis, shoot branching, gametophyte development, and leaf growth, an important proteins regulator, TEOSINTE-BRANCHED1/CYCLOIDEA/PCF (TCP), is involved (Zhou et al. 2016). Domain TCP is significantly important for protein-protein interactions and gene expression regulation (Manassero et al. 2013). The *bHLH* (basic-helix-loop-helix) is present in some TCP domains. This bHLH structure is different from the *bHLH* family of TFs that serve as a DNA-binding motif in plants in terms of their structure. *TCPs* contain TEOSINTE BRANCHED (TB) from maize 1, CYCLOIDEA (CYC) region from *Antirrhinum majus,* and PROLIFERATING CELL FACTORS (*PCFs*) from rice. *TCPs* are found in different plants like Arabidopsis (23), rice (22), sorghum (20), tomato (30), strawberry (19), and *Gossypium raimondii* (38). *CYC* and *TB1* served as negative regulators of floral development and lateral-branching, respectively (Ilhan et al. 2018). Other important feature of the *TCPs* has been triggered by miR319, which is basically involved in leaf morphogenesis regulation. The genes like *TCP24*, *TCP10*, *TCP4*, *TCP3,* and *TCP2* are triggered by miR319 in Arabidopsis (Xu et al. 2014).

New proteins and genes are identified by using different bioinformatics approaches. The expression studies of some selected *TCP* genes by using *Phaseolus vulgaris* genotypes Zulbiye and Yakutiye under salinity stress have revealed the important functions of *TCP* in salt stress (Ilhan et al. 2018). Different families of TFs like *NAC*, *bZIP*, *MYB,* and *bHLH* have important roles to tolerate the salinity stress in various plant species. These TFs activate the genes that are responsible to tolerate salt stress by binding on the promoter region of the genes. The genes responsible for encoding these TFs can be bred in other plant species to make them tolerant to the severe salinity stress. This is necessary to meet the food demands and making agriculture sustainable (Golldack et al. 2014) (see Table 23.1 for examples of TFs associated with salt stress).

23.4 Transcription Factors Associated With Heat Stress

Heat stress is a universal stress which affects almost all organisms. The cellular components are damaged by heat stress due to membrane destabilization, generation of ROS, and protein denaturation (Hasanuzzaman et al. 2013). So, it is necessary for the living organisms to initiate their protection mechanism rapidly after the exposure to heat stress by maintaining cellular homeostasis. The eukaryotic cells respond to heat stress in a well-organized manner and have more chances to survive upon exposure to stress. The heat stress response (HSR) is mainly controlled by TFs that are called heat shock TFs (HSFs). The HSFs are evolutionary conserved elements present in eukaryotes and are chief regulatory factors of HSR. During high-temperature stress, the HSFs are responsible for activation of the genes and enhance the expression of many heat shock proteins (HSPs) encoding genes. The HSPs act as molecular chaperones to protect the cellular components by inhibiting protein aggregation and denaturation. The structure of HSFs is modular (Scharf et al. 2012) and among HSFs their N-terminal sequence is conserved, which is involved in DNA binding and oligomerization while their C-terminal sequence is divergent. The transactivation domains and nuclear localization signals are present in most HSFs. In Arabidopsis, HSFs form trimers during heat stress because it is necessary to bind with *cis*-regulatory elements (heat shock elements (HSEs); nTTCnnGAAn or nGAAnnTTCn) (Ohama et al. 2016). In eukaryotes, the HSEs are commonly found in promoter region of heat stress-responsive genes. Plants had developed an HSR mechanism that is further refined during evolution. A complex transcriptional network and large HSF families are present in plants to combat with different forms of stress induced by high temperature (Scharf et al. 2012).

The HSF families have ten members in plants which have different functions and expression patterns in HSR. In Arabidopsis, 3 classes that consist of 14 classes (A1-A9, B1-B4, and C1) are present and 21 HSFs are assigned to them. The A1 group has four members, *HsfA1a*, *HsfA1b*, *HsfA1d*, and *HsfA1e*. In a study, a mutant that does not have three genes (*HsfA1a*, *HsfA1b,* and *HsfA1d*) was unable to regulate the expression of many heat shock-responsive genes and showed a significant deficiency to achieve thermotolerance. So, it was suggested that the genes (*HsfA1a*, *HsfA1b*, and *HsfA1d*) act as chief regulators in HSR (Liu et al. 2011; Yoshida et al. 2011). Upon exposure to heat stress, *HsfA1s* not only are responsible for inducing expression of HSPs but also activate a transcriptional cascade consisting of different TFs, which include *MBF1c*, *DREB2A*, and *HsfBs* genes (*HsfB1*, *HsfB2a*, and *HsfB2b*) and *HsfAs* (*HsfA7a*, *HsfA7b*, *HsfA3*, *HsfA2*, and *HsfA1e*). The HsfAs act as both activators and repressors in heat shock response. The *DREB2A*, *MBF1c*, and *HsfAs* positively regulate the gene expression in HSR (Nishizawa-yokoi et al. 2011). These TFs are responsible for enhancing and sustaining the expression of heat shock-responsive genes. Particularly, a multistep transcriptional cascade is activated by *DREB2A* because it activates *HsfA3* (Ohama et al. 2016).

This transcriptional cascade is composed of *DREB2A*, *HsfA3*, and *HsfA1*; this cascade can be helpful to tolerate long period (almost for 24 h) of heat shock. In contrast, the *HsfBs* act as a repressor for the HSFs and negatively regulates heat shock response. The involvement of various TFs may be variable in different plant species, and it is helpful for plants to survive in varying temperature conditions. The activation of HSFs performs a significant role in the initiation of HSR. The regulatory mechanisms of *HsfA1s* are analyzed by using tomato, Chlamydomonas, and Arabidopsis. Some posttranscriptional modifications like phosphorylation are also involved in regulating the *HsfA1* gene activity (Schmollinger et al. 2013). Because plants and animals are completely different organisms, while considering their differences, it can be stated that plants must have evolved some unique mechanism for the regulation of *HsfA1*. However, some primary factors and molecular basis are unknown, which are involved in the regulation of *HsfA1* and it is not yet clear that only the activation of *HsfA1* is enough for initiating the transcriptional cascade. So, further analyses are yet needed to perform to completely understand the procedure. But, one thing is clear from this information that HSFs have great importance in regulating the heat shock response (Ohama et al. 2016) (see Table 23.1 for examples of TFs associated with heat stress).

23.5 Transcription Factors Associated With Cold Stress

Different plant species, including Arabidopsis, develop cold tolerance in response to low temperature which is called as cold acclimation. The basic purpose to study cold acclimation process is to identify the plant mechanism of survival in cold stress. At the beginning, it was well known that several physiological and biochemical changes occur during cold acclimation process, for example, modification in lipid composition, rise in the level of protein molecules, and increase in full soluble protein content that can function as a cryo-protectant similar to proline and sugars (Chinnusamy et al. 2003). More lately, the role of gene expression variation was identified in the process of cold acclimation. From this observation it can be stated that physiological and biochemical changes were controlled by gene expression variation during cold stress and may intensify cold tolerance. The characterization of TFs responsible for cold acclimation was accomplished. Numerous genes present in Arabidopsis that can combat with cold stress are *KIN* (cold induced), *ERD* (early responsive to dehydration), *RD* (responsive to dehydration), and *LTI* (low temperature induced) genes.

Upon exposure to cold stress, the transcript level for the genes responsible for cold tolerance starts to increase in few hours and it remained increasing over the time of cold exposure. Afterward, it quickly reduced to pretreatment points upon restoration of plants in hot weathers. *CBF1*, *CBF2*, and *CBF3* (relating to *DREB1a*, *DREB1b,* and *DREB1c*) are existing in tandem arrangement on chromosome 4 and are sudden expressed in response to cold stress and after exposure to stress, expression reaches at its peak within 2 hours (Kidokoro et al. 2017). Transcription activator proteins are encoded by these genes that can recognize *DRE/CRT* elements present in promoter regions of cold-responsive genes by ERF/AP2 DNA-binding domains. In the presence of cold stimuli, the transgenic Arabidopsis plants exhibit constitutive overexpression of *CBF1*, *CBF2,* and *CBF3* genes, which results in the cumulative expression of *COR* and *CRT/DRE* which help in enhancing freezing tolerance. Thus, it can be stated that *CBF* genes function like “master-switches” which trigger expression of gene groups (Van Buskirk and Thomashow 2006). Alike *cis*-acting elements, low-temperature responsive element and C-repeat (CRT) consisted of DRE core motifs and found in cold-inducible genes. The Arabidopsis cDNA coding CBF/DREB1 and DREB2 were separated by yeast via one-yeast hybrid screening method (Gehan et al. 2015). In different Arabidopsis varieties, these proteins consisted of ethylene-responsive element-binding factor (ERF)/APETALA2 (AP2) motifs that particularly bind with CRT/DRE sequences, thus regulating genes transcription driven through *CRT/DRE*. The Arabidopsis genome consists of six and eight *CBF/DREB* and *DREB2* genes, respectively, comprising of *DREB1A*, *DREB1B,* and *DREB1C*, which are greatly induced by cold. *DREB2A* and *DREB2B* influence by dehydration, not in cold stress (Singh and Laxmi 2015). For cold-inducible gene expression, *DREB1A*, *DREB1B*, and *DREB1C* are major TFs (Nakashima et al. 2009).

Cold stress-induced gene expression via *DRE/CRT* is highly increased through the signal produced from light. Phytochrome B is identified as a basic photo receptor responsible for the light signaling. *DREB1/DRE* regulon occurs in different grasses and has ability to improve cold stress tolerance through gene transfer in commercially significant grains (Yamaguchi-Shinozaki and Shinozaki 1994). Fascinatingly, *Fr-H2/Fe-AM2* gene locus was categorized as QTL against low-temperature stress. *DREB1/CBF* regulon has a role in stress tolerance without post-transcriptional alteration in several grasses and reacts to stress induced by low temperature (Nakashima et al. 2009). In many grasses like oat, wheat, barley, maize, rice, and sorghum, *DREB1/CBF*-homologous genes were characterized. Numerous *DREB1* genes are expressed as early response against low-temperature stress (see Table 23.1 for examples of TFs associated with cold stress).

23.6 Transcription Factors Associated With Ultraviolet Radiations

The solar energy in right dosage is essential to maintain life on the Earth. The ultraviolet (UV) radiations have wavelength 100–400 nm and have a small portion of electromagnetic radiations. A small fraction of UV radiation spectrum can reach to the earth surface because its composition is modified on its way to atmosphere. The ozone and atmospheric oxygen completely absorb the UV-C (200–280 nm). Some portions of UV-A (315–400 nm) and UV-B (280–315 nm) are absorbed by the stratospheric ozone layer. The levels of UV radiations in the environment can be changed depending upon weather, daytime, cloud coverage, latitude, and altitude; however, the progressive decrease in ozone layer from the last 50 years became a reason of increasing UV-rays level in the atmosphere, which has a great role in changing the plant ecosystem (Matus 2016). UV radiations can cause mutations in DNA when absorbed due to their high energy content. It has detrimental impacts on cellular functions like a decrease in membrane permeability and inhibits electron transport. Plants have developed mechanisms to respond to UV radiations that lead to biochemical and morphological changes. For example, UV-B radiations induce some physiological responses like cell expansion, altered growth patterns, thicker leaf blades, shorter petioles, and promotion of branching (Robson et al. 2015). UV-C radiation does not harm plants in terms of physiology, but in some plants, responses have been reported for the radiations of shorter wavelengths. In fact, the fruits are exposed to short UV-C treatments after harvesting to increase health-promoting metabolites (Crupi et al. 2013).

Gene expression is changed in response to UV radiations. It depends upon the interaction among different environmental factors, nature of the radiation, and degree of adaption of the plant. The main challenge in studying effects of UV is to recognize different types of radiations (for example, UV-A from UVB/C) and it is also tough to differentiate their signs from temperature and visible light. Plants initiate the formation of some defense-related phytochemicals and antioxidants in response to UV light that are basically secondary metabolites in response to UV radiations. Among secondary metabolites, some are involved in plant tissue coloring that is a source of attraction for seed dispersers and pollinators. Secondary metabolites are usually accumulated in the plant organs that are exposed to various UV radiations, but it depends upon the plant species, and they may also be composed of mixture of several compounds (Jenkins 2009). The TFs of various families are involved in the activation of phenylpropanoid-related genes. A great breakthrough is achieved by the combinatorial study of interactions among basic-helix-loop-helix (*bHLH*), aspartic acid and tryptophan rich repeat protein (*WDR*) and *R2R3-MYB*. The *R2R3-MYB* genes, member of the largest TFs family of plants known as myeloblastosis (MYB) superfamily that has two DNA-binding domains that are highly conserved, and their C-terminal motifs, are present in variable numbers. The phenylpropanoid regulation-related *R2R3-MYB* genes have been increased by duplication.

Many members of the MYB family had been characterized and some of them act as positive regulatory elements for the formation of flavonols (*MYBF1*), anthocyanins (*MYBA1/A2*, *MYB5B*), and PAS (*MYBPA1/PA2/PAR*). Many of the studies have reported that the *R2R3-MYB* genes of grapes are involved in response to UV radiations (Cavallini et al. 2015; Wong et al. 2016; Loyola et al. 2016). MYB activators enhance their expression on the exposure to radiations, while phenylpropanoid repressors show opposite behaviors. The different branches of the pathways have been fine-tuned by the repressor of *R2R3-MYB*, which belongs to a subgroup number (*MYB-c2*). Particularly, *VviMYB4A* is involved in the adaptation acclimation of propagative tissues to the UV-B radiation (Cavallini et al. 2015). *MYB13*, *MYB14,* and *MYB15* have been induced by applying UV-C treatments, but their response intensity is different, and their time response is different. One important candidate of this family is *MYB24* gene, and it is highly induced upon the exposure to UV (Carbonell-bejerano et al. 2014). Another function of this gene has been identified recently, which is its response in berries against water deficiency (Savoi et al. 2016).

In response to UV-B radiations, two common signaling pathways are present in Arabidopsis: The first is a photomorphogenic signaling pathway that is involved in regulating the response generated by low levels of UV-B radiation and the second is nonspecific pathway that is activated by high levels of UV radiation (release reactive oxygen species by causing direct DNA damage). The UVR8 (UV-resistance locus 8) is a UV-B receptor that perceives UV-B and in turn it activates a long cascade regulated by elongated hypocotyl5 (*HY5*) (Matus 2016). Several plant processes like in the dark growth of hypocotyl (Ulm et al. 2004), regulation of anthocyanin synthesis and flavanols (Ho et al. 2013), and nitrate uptake in roots (Chen et al. 2016b) in light and UV response are regulated by a master regulator *AtHY5*. The carotenoids are regulated by *LeHY5* genes in collaboration with PIF proteins in tomato. The depiction of *HY5* and *UVR8* orthologs in the grapes has demonstrated their functions in flavanols regulation in berries and leaves after the exposure to UV-B radiations. Direct activation of *R2R3-MYB* regulators can reprogram three secondary metabolites production, that is, terpenes, flavonoids, and stilbenes in response to UV radiation in grapes. The activation of *bZIP* genes initiates the adaptive mechanisms against the UV-B radiation high exposure in grape vines, combined with their photomorphogenic response on exposures to low radiation. The flavonoid pathway has some structural genes that are directly triggered via *bZIP* factors and it mediates *MYB* responses by regulating their expression as well. Thus, it can be stated that TFs have very important role in controlling the damage caused by UV radiations in plants where they may enhance the expression of those genes that produce beneficial compounds upon exposure to all types of UV radiations (Matus 2016) (see Table 23.1 for examples of TFs associated with UV stress).

23.7 Transcription Factors Associated With Heavy Metals Stress

The metals are needed in very minute quantities to maintain life while their excessive amounts can cause cellular damage. The various heavy metals that affect the growth of plants and other organisms which persist in the environment are mercury (Hg), chromium (Cr), iron (Fe), cadmium (Cd), copper (Cu), zinc (Zn), aluminum (Al), arsenite (AsIII), arsenate (AsV), manganese (Mn), molybdenum (Mo), and lead (Pb). These metals affect not only animals but also plants. They are necessary to maintain plant growth and development in trace amounts, and if these metals are not present in the minute amounts in the plant environment, plants cannot perform their functions properly. But, in excessive amounts they are very deleterious for the plants and other organisms consuming these plants. The damaging effects of metals on agriculture sustainability have been well understood (Jalmi et al. 2018). For example, Cd is a deleterious pollutant that is highly toxic for all living forms (Dias et al. 2013; Clemens et al. 2013). Cadmium binds to sulfhydryl groups to denature or inactivate proteins, which is a reason of cellular damage because of the displacement of cofactors from several proteins, including enzymes and TFs (Lin and Aarts 2012). Beside this, Cd toxicity initiates the oxidative stress in different animals and plants that mediate cellular damage (Gallego et al. 2012). Numerous mechanisms are involved in detoxifying the heavy metals and increasing tolerance against the stress caused by heavy metals in plant (Thapa and Sadhukhan 2012). Mechanisms of metals detoxification in plant species are metal sequestration, chelation, excretion from cell membrane, and their binding with different thiol compounds in cytosol (Chen et al. 2016a).

Some other molecules and signaling pathways might take part in this process (Singh et al. 2013). Additionally, several genes are also involved in heavy metal detoxification, which include *CAD2*, *APDR8*, *AtPDR12*, *MAN3*, *OsNRAMP5*, *OsHMA9*, *ZNT1*, *ZNTA*, *AtATM3*, *EIN2*, and *ACBP1* (Ishikawa et al. 2012; Sasaki et al. 2012; Lin and Aarts 2012; Chen et al. 2014, 2016a). It was also reported that *HsFA4a*, heat shock TF, is responsible for Cd tolerance in rice and wheat by triggering *MT* gene expression (Shim et al. 2009). TFs are majorly involved in regulating the genes responsible for heavy metals detoxification. It is reported that glutathione (*GSH*) is a very important factor in detoxifying Cd (Flores-C'aceres et al. 2015; Hernández et al. 2015; Jozefczak et al. 2015) and conjugated vacuolar sequestration of GSH and phytochelatin is involved in Cd tolerance and accumulation in plants. It is reported that 176 proteins are present in Arabidopsis, which have zinc finger domains and many of them perform significantly important functions in plant stress responses and development. *ZAT6*, an important zinc finger of *Arabidopsis thaliana,* has been identified first time. Its expression has been regulated by the regulation of phytohormones. *ZAT6* is also involved in regulating low Pi stress responses and root development. Recently, it was also reported that *ZAT6* is involved in multiple stress tolerance like freezing, salt, drought, and pathogen infection in Arabidopsis (Shi et al. 2014; Chen et al. 2016a). *ZAT6* has also very important roles in heavy metal detoxification. In Arabidopsis, the plants having high expression of *ZAT6* are found tolerant to the toxicity of Cd. *ZAT6* is directly involved in GSH synthesis and regulating the gene expression of phytochelatin-related genes that confer Cd tolerance in Arabidopsis (Chen et al. 2016a).

Heavy metals damage the organisms at cellular levels by several regulatory mechanisms. At the level of transcription, nongraminaceous plants accumulate Fe by the combinatorial action of FER-LIKE IRON DEFICIENCY-INDUCED TFs (*FIT*), *bHLH38,* and *bHLH39* TFs. The ethylene-insensitive3-like1 (*EIL1*) and enthylene-insensitive3 (*EIN3*) interact with *FIT* and enhance Fe accumulation mediated by *FIT* and these are like *bHLH38* and *bHLH39* transcription factors. The *IDF* (IRT1-degradation factor-1) regulates degradation of IRT1 proteins bounded with cell membrane (Shin et al. 2013). The Ferritin 1 (*FER1*) mediates intracellular availability of iron in the roots and it prevents iron-dependent oxidative stress by oxidizing and storing it. Fe allocation is triggered by the Popeye (*PYE*), *MYB10*, *MYB72*, *bHLH100,* and *bHLH101* transcription factors (Leskova et al. 2017). Although the mechanism of Fe-sensing is unclear, yet a group of hemerythrin motifs, Brutus (BTS) and ZFP from Arabidopsis and rice, respectively, has been identified as Fe sensors. The *PYE*-like TFs are regulated at the posttranslational level by an E3 ligase BTS (Selote et al. 2015). The ferric reductase defective 3 (*FRD3*), nicotianamine synthase 4 (*NAS4*), and ferric reduction oxidase 3 (*FRO3*) genes are involved in the intracellular transport of Fe in the root inner parts and are regulated by the TFs that interact with *PYE* (Selote et al. 2015). *MYB10* and *MYB72* are mutually controlled with the *NAS4* expression (Palmer et al. 2013).

The phenylpropanoid pathway is regulated by *MYB72,* which is combined with the coumarins synthesis, so it is linked by Fe allocation processes and Fe acquisition. The aforementioned genes are Fe deficiency-responsive genes that perform their functions on different regulatory stages (Wu et al. 2012). In Arabidopsis, two major genes, *FRO2* and *IRT1*, that are involved in Fe acquisition show their expression on exposure to Ni, Cd, or Zn, and the plant responds in the same way as in Fe deficiency. The *FRO2* and *IRT1* are also strongly repressed by applying the Cd stress in the same plant species. The expression of *MYB72*, *PYE*, *bHLH38*, *bHLH39*, *bHLH100*, and *bHLH101* genes is highly upregulated during Zn or Cd stress (Leskova et al. 2017). The various TFs are involved to tolerate the heavy metal stress-mediated responses like oxidative stresses because they are the key players in regulating the expression of those genes that take part in the synthesis of molecules like antioxidants and phytohormones that are used to combat with oxidative stress damages (see Table 23.1 for examples of TFs associated with heavy metal stress).

23.8 Transcription Factors Associated With Submergence

Though, only plant roots are exposed to soil flooding stress, but the complete plant functioning is disturbed in the nonappearance of proper perception of stress signals and initiating the proper feedback (Sauter 2013). As roots and soil microbes quickly utilize the O_2 in water-logged soils, so roots generate ATP for their appropriate functioning by switching to inefficient anaerobic fermentation. The root growth and functions are compromised because reserved carbohydrates are consumed, which creates an anoxia state in which phytotoxic compounds enter in the plant from water-logged soil, membrane integrity is disturbed, and plants suffer starvation. Water and nutrients transport to shoot is also affected resulting in aging or senescence, wilting, and even death. The adaptive mechanisms that prevent plants from anoxia are very crucial to sustain root functions and plant survival due to waterlogging. These mechanisms prevent the loss of oxygen to increase its excess to root tips by forming a lignin/suberin barrier (Shiono et al. 2011), and root aeration and organ porosity are increased by increasing the formation of air spaces (Sasidharan and Voesenek 2015) and formation of adventitious roots that are rich in aerenchyma (Sauter 2013).

In complete submergence, plants suffer more problems; for example, plant access is completely cut off to aboveground atmosphere and photosynthesis is extremely compromised (Voesenek and Bailey-serres 2015). The improved aeration can be beneficial to combat with submergence. The directed shoot growth outside of the flood water can restore the plant contact to the atmosphere (Van Veen et al. 2013). The aerenchymatous tissues facilitate the oxygenation of the whole plant after the oxygenation of shoots. The photosynthesis rate is improved in some species with the help of gas films and some specialized leaf traits. The plants strategy of energy-depleting escape is not beneficial if the floods are deep, because it will not lead to plant emergence, so plants switch to restricted growth strategy and preserve its reserved carbohydrates for postsubmergence growth establishment (Sasidharan et al. 2013).

A rice cultivar FR13A can survive for 2 weeks almost in complete submergence. The submergence 1 (Sub1) locus on the chromosome number 9 in rice is responsible for tolerating submergence (Xu et al. 2006). The Sub1 locus has three transcriptional regulators that are ethylene-responsive factors (ERF) A, B, and C (*Sub1A/B/C*). Submergence intolerant species of japonica cv M202 have two ERFs; *Sub1B-2* and *Sub1C-2* are made tolerant by integrating *FR13A* Sub1 locus (*Sub1A-1B-1/C-1*). Within 14 days of submergence, the presence and high expression of *Sub1A-1* are strongly associated with the submergence tolerance (Nakano et al. 2016). The mRNA of *Sub1C-1* accumulation is reduced due to submergence, in genotypes with *Sub1A-1* (Fukao et al. 2006). In semiaquatic plants, submergence is tolerated by elongation of aerial organs mediated by the phytohormones (Bailey-Serres and Voesenek 2008). The synthesis and signaling of ethylene and gibberellin (GA) are modulated by the quantitative trait locus Sub1 during submergence.

The leaf aging, carbohydrate metabolism, and shoot elongation are acclimation responses that are triggered by the submergence-responsive genes activated by increased levels of ethylene. The TFs having GRAS domain, Slender rice1 (*SLR1*), and slender rice1-like1 (*SLRL1*) are positively regulated by an increased level of ethylene upon exposure to submergence. The ethylene production is restricted by *Sub1A-1* stimulation. The biosynthesis of paclobutrazol, an inhibitor of GA, is involved in manipulating the leaf elongation during submergence and confirms the underwater shoot elongation that is mediated by GA. At the downstream of GA signaling, Sub1C performs its function and also plays roles in submergence intolerant rice in the process of shoot elongation (Jung et al. 2010).

Upon submergence, another important trait that is needed to be tolerated is detoxification of ROS that creates oxidative stress and causes cellular damage. The oxygen deprivation is caused by ROS, which is produced in response to various stresses. The plant faces a burst of ROS on exposure to air after a long anoxic condition. A wide range of enzymes known as antioxidants like glutathione peroxidase, ascorbate peroxidase, catalases, and superoxide dismutase and reductants like tocopherols, phenolic compounds, glutathione, and ascorbate can scavenge ROS to overcome the ROS stress. Various TFs are involved in regulating the genes responsible for ROS scavenging synthesis of antioxidants and regulating the other genes responsible for submergence tolerance (Loreti et al. 2016) (see Table 23.1 for examples of TFs associated with submergence stress).

23.9 Transcription Factors Associated With Reactive Oxygen Species

The adverse environmental conditions affect both plants and animals, but due to sessile in nature, plants cannot go away to protect themselves from stress. Hence, it is necessary for their survival to develop some mechanisms to combat with different stresses. It is needed for plants to synthesize some molecules that can bound the detrimental impacts of stresses on reproduction and growth (Formentin et al. 2018). Adversative environmental conditions can leads toward the production of various ROS like hydroxyl radical (OH^-), singlet oxygen ($^1O^2$), superoxide radical (O^{2-}), and hydrogen peroxide (H_2O_2) that can cause oxidative damage in different cell organelles (Singh et al. 2019). To avoid this oxidative damage, various TFs enhance the expression of stress-responsive genes. The TFs are involved in regulating the expression of many stress-responsive genes that have roles in adapting and tolerating the stress accompanied with *cis*-acting genes elements that participate in the ROS-induced modifications of transcription. The extensive expression studies have explained and confirmed that different genes have regulatory roles in abiotic stress tolerance and same roles have been identified after application of various ROS-forming compounds.

Different transcription factors are involved in various ROS-induced responses. For example, redox-responsive transcription factor 1 (*RRTF1*) and *AtERF6* bind with GCC box in response to ROS that brings transcriptional modifications (Wang et al. 2013; Matsuo et al. 2015). Oxidative damage downregulates some genes, for example, a transcription factor *AP2*/ *ERF*, cytokinin response factor 6, binds with GCC box to downregulate the genes related to cytokinin in damage produced by ROS (Zwack et al. 2016). Different TFs families like ZFNs, WRKY, MYB, GRAS, RAV, Zat, and NAC/NAM are also involved in ROS-mediated stress responses. Two

TFs *Zat6* and *Zat12* positively regulate *Apx1* gene expression that is an ROS-responsive gene while *Zat10* negatively regulates ROS-responsive genes. The oxygen and superoxide dismutase accumulation is negatively regulated by zinc finger paralogs *LSD1* and *LOL1* (Singh et al. 2019).

The TFs belong to NAC family and are also important in achieving tolerance in opposition to different environmental stresses via ABA-independent and ABA-dependent signal transduction pathways (Puranik et al. 2012). In Arabidopsis, a regulatory network is constituted by *NAC013*, *NAC032*, and *NAC053* along with *WRKY6* and *ERF6* in response to oxidative stress (Vermeirssen et al. 2014). The TFs, when these interact with *cis*-regulatory elements, can change the expression pattern to alter the response toward the stress induced by ROS. In response to some external stimuli, a plasma membrane localized kinase auto-phosphorylates to activate the TFs. Afterward, the phosphoryl group is transferred to transcription factors that have the potential to change the conformation of TFs, which is necessary for its binding with *cis*-regulatory elements of the promoter region and regulates the gene expression. One transcription factor can control the expression of many genes because diverse ROS forms interact with various cysteine residues. The hydrogen peroxide is responsible for the activation of protein-tyrosine phosphatase (PTP1) that is involved in the MAPK6 inactivation in Arabidopsis (Gupta and Luan 2003).

Some TFs can be activated by increasing with their binding affinity with *cis*-regulatory elements, transport, and proteolysis for achieving the tolerance against oxidative stress by changing the metabolome, transcriptome, and proteome. The NPR1 is present in cytoplasm as oligomer during normal condition, but after application of the oxidative stress, the reduction of disulfide occurs, which is mediated by thioredoxin and generated monomeric NPR1 is transported toward nucleus to modify the transcription process. Additionally, some posttranslational modifications like proteasome-mediated degradation and phosphorylation also regulate NPR1 activation. As well as, some heat shock factors are stimulated in response to hydrogen peroxide and transferred from cytoplasm to nucleus afterward the trimer formation (Liu et al. 2013; Giesguth et al. 2015). The activation of SAP12 is possible by changing its conformation by applying abiotic stress. During oxidative stress, Whirly1 is transported to nucleus from chloroplast and gets activated. The TFs like *ANAC013* and *ANAC089* are activated after their proteolysis in response to oxidative stress and these are translocated to nucleus from cytoplasm (Singh et al. 2019). The TFs along with *cis*-regulatory elements are responsible for differential expression of genes in response to ROS that help the plant to avoid oxidative damage (see Table 23.1 for examples of TFs associated with ROS).

References

Ahmad R, Waraich EA, Ashraf MY et al (2014) Does nitrogen fertilization enhance drought tolerance in sunflower? A review. J Plant Nutr 37:942–963. https://doi.org/10.1080/01904167.2013.868480

Alessio VM, Cavaçana N, de Dantas LL et al (2018) The FBH family of bHLH transcription factors controls ACC synthase expression in sugarcane (Saccharum spp.). J Exp Bot 69:2511–2525. https://doi.org/10.1093/jxb/ery083/4919670

Amjad M, Azeem F, Amjad M et al (2018) Transcription factors WRKY11 and WRKY17 are involved in abiotic stress responses in *Arabidopsis*. J Plant Physiol 226:12–21. https://doi.org/10.1016/j.jplph.2018.04.007

Bailey-Serres J, Voesenek LACJ (2008) Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol 59:313–339. https://doi.org/10.1146/annurev.arplant.59.032607.092752

Carbonell-bejerano P, Diago M, Martínez-abaigar J et al (2014) Solar ultraviolet radiation is necessary to enhance grapevine fruit ripening transcriptional and phenolic responses. BMC Plant Biol 14:183

Cavallini E, Matus JT, Finezzo L et al (2015) The Phenylpropanoid pathway is controlled at different branches by a set of R2R3-MYB C2 repressors in grapevine. Plant Physiol 167:1448–1470. https://doi.org/10.1104/pp.114.256172

Chen J, Yang L, Gu J et al (2014) MAN3 gene regulates cadmium tolerance through the glutathione-dependent pathway in *Arabidopsis thaliana*. New Phytol 205:570–582

Chen J, Yang L, Yan X et al (2016a) Zinc-finger transcription factor ZAT6 positively regulates cadmium tolerance through the glutathione-dependent pathway in *Arabidopsis*. Plant Physiol 171:707–719. https://doi.org/10.1104/pp.15.01882

Chen X, Yao Q, Gao X et al (2016b) Shoot-to-root Mobile transcription factor HY5 coordinates plant carbon and nitrogen acquisition. Curr Biol 26:640–646. https://doi.org/10.1016/j.cub.2015.12.066

Chinnusamy V, Ohta M, Kanrar S et al (2003) ICE1: a regulator of cold-induced transcriptome and freezing tolerance in *Arabidopsis*. Genes Dev 17:1043–1054. https://doi.org/10.1101/gad.1077503.CRT

Clemens S, Aarts MGM, Thomine S et al (2013) Plant science: the key to preventing slow cadmium poisoning. Trends Plant Sci 18:92–99. https://doi.org/10.1016/j.tplants.2012.08.003

Crisp PA, Ganguly D, Eichten SR et al (2016) Reconsidering plant memory: intersections between stress recovery, RNA turnover, and epigenetics. Sci Adv 2:e1501340

Crupi P, Pichierri A, Basile T, Antonacci D (2013) Postharvest stilbenes and flavonoids enrichment of table grape cv Redglobe (Vitis vinifera L.) as affected by interactive UV-C exposure and storage conditions. Food Chem 141:802–808. https://doi.org/10.1016/j.foodchem.2013.03.055

Deinlein U, Stephan AB, Horie T et al (2014) Plant salt-tolerance mechanisms. Trends Plant Sci 371:1–9. https://doi.org/10.1016/j.tplants.2014.02.001

Dias MC, Monteiro C, Jose MP et al (2013) Cadmium toxicity affects photosynthesis and plant growth at different levels. Acta Physiol Plant 35(4):1281–1289. https://doi.org/10.1007/s11738-012-1167-8

Dubos C, Stracke R, Grotewold E et al (2010) MYB transcription factors in *Arabidopsis*. Trends Plant Sci 15:573–581. https://doi.org/10.1016/j.tplants.2010.06.005

Erpen L, Devi HS, Grosser JW, Dutt M (2017) Potential use of the DREB/ERF, MYB, NAC and WRKY transcription factors to improve abiotic and biotic stress in transgenic plants. Plant Cell Tissue Organ Cult 132:1–25. https://doi.org/10.1007/s11240-017-1320-6

Faraji S, Hamidreza S, Seyyed R, Kazemitabar K (2018) Genome-wide exploration of C2H2 zinc finger family in durum wheat (Triticum turgidum ssp. Durum): insights into the roles in biological processes especially stress response. Biometals 31:1019–1042. https://doi.org/10.1007/s10534-018-0146-y

Flores-C'aceres ML, Hattab S, Hattab S et al (2015) Specific mechanisms of tolerance to copper and cadmium are compromised by a limited concentration of glutathione in alfalfa plants. Plant Sci 233:165–173. https://doi.org/10.1016/j.plantsci.2015.01.013

Formentin E, Sudiro C, Perin G et al (2018) Transcriptome and cell physiological analyses in different Rice cultivars provide new insights into adaptive and salinity stress responses. Front Plant Sci 9:204. https://doi.org/10.3389/fpls.2018.00204

Fukao T, Xu K, Ronald PC, Bailey-serres J (2006) A variable cluster of ethylene response factor—like genes regulates metabolic and developmental acclimation responses to submergence in Rice. Plant Cell 18:2021–2034

Gallego SM, Pena LB, Barcia RA et al (2012) Unravelling cadmium toxicity and tolerance in plants: insight into regulatory mechanisms. Environ Exp Bot 83:33–46. https://doi.org/10.1016/j.envexpbot.2012.04.006

Garcia J, Garma D, Fernandez-garcia N et al (2015) New insights into plant salt acclimation: the roles of vesicle trafficking and reactive oxygen species signalling in mitochondria and the endomembrane system. New Phytol 205:216–239

Gehan MA, Park S, Gilmour SJ et al (2015) Natural variation in the C-repeat binding factor cold response pathway correlates with local adaptation of *Arabidopsis* ecotypes. Plant J 84:682–693. https://doi.org/10.1111/tpj.13027

Giesguth M, Sahm A, Simon S, Dietz K (2015) Redox-dependent translocation of the heat shock transcription factor AtHSFA8 from the cytosol to the nucleus in *Arabidopsis thaliana*. FEBS Lett 589:718–725. https://doi.org/10.1016/j.febslet.2015.01.039

Golldack D, Lüking I, Yang O (2011) Plant tolerance to drought and salinity: stress regulating transcription factors and their functional significance in the cellular transcriptional network. Plant Cell Rep 30:1383–1391. https://doi.org/10.1007/s00299-011-1068-0

Golldack D, Li C, Mohan H, Probst N (2014) Tolerance to drought and salt stress in plants: unraveling the signaling networks. Front Plant Sci 5:151. https://doi.org/10.3389/fpls.2014.00151

Gujjar RS, Akhtar M, Singh M (2014) Transcription factors in abiotic stress tolerance. Indian J Plant Physiol 19:306–316. https://doi.org/10.1007/s40502-014-0121-8

Gupta R, Luan S (2003) Redox control of protein tyrosine phosphatases and mitogen-activated protein kinases in plants. Plant Physiol 132:1149–1152. https://doi.org/10.1104/pp.103.020792

Hasanuzzaman M, Nahar K, Alam MM et al (2013) Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci 14:9643–9684. https://doi.org/10.3390/ijms14059643

Heo J, Tienderen PV, Schranz E et al (2018) Cloning and functional analysis of three cold regulated CBF genes in the overwintering crucifer Boechera stricta. Int J Agric Biol 20:594–600. https://doi.org/10.17957/IJAB/15.0528

Hernández LE, Sobrino-plata J, Montero-palmero MB et al (2015) Contribution of glutathione to the control of cellular redox homeostasis under toxic metal and metalloid stress. J Exp Bot 66:2901–2911. https://doi.org/10.1093/jxb/erv063

Ho D, Choi M, Kim K et al (2013) HY5 regulates anthocyanin biosynthesis by inducing the transcriptional activation of the MYB75 / PAP1 transcription factor in *Arabidopsis*. FEBS Lett 587:1543–1547. https://doi.org/10.1016/j.febslet.2013.03.037

Ilhan E, Büyük İ, Inal B (2018) Transcriptome—scale characterization of salt responsive bean TCP transcription factors. Gene 642:64–73. https://doi.org/10.1016/j.gene.2017.11.021

Ishikawa S, Ishimaru Y, Igura M et al (2012) Ion-beam irradiation, gene identification, and marker-assisted breeding in the development of low-cadmium rice. Proc Natl Acad Sci U S A 109:19166–19171. https://doi.org/10.1073/pnas.1211132109

Jalmi SK, Bhagat PK, Verma D et al (2018) Traversing the links between heavy metal stress and plant signaling. Front Plant Sci 9:12. https://doi.org/10.3389/fpls.2018.00012

Janda T, Darko E, Shehata S et al (2016) Salt acclimation processes in wheat. Plant Physiol Biochem 101:68–75. https://doi.org/10.1016/j.plaphy.2016.01.025

Jenkins GI (2009) Signal transduction in responses to UV-B radiation. Annu Rev Plant Biol 60:407–431. https://doi.org/10.1146/annurev.arplant.59.032607.092953

Jozefczak M, Bohler S, Schat H et al (2015) Both the concentration and redox state of glutathione and ascorbate influence the sensitivity of *Arabidopsis* to cadmium. Ann Bot 116:601–612. https://doi.org/10.1093/aob/mcv075

Jung K, Seo Y, Walia H et al (2010) The submergence tolerance regulator sub1A mediates stress-responsive expression of AP2/ERF transcription factors 1. Plant Physiol 152:1674–1692. https://doi.org/10.1104/pp.109.152157

Katiyar A, Smita S, Lenka SK et al (2012) Genome-wide classification and expression analysis of MYB transcription factor families in rice and *Arabidopsis*. BMC Genomics 13:544

Kerr TCC, Abdel-Mageed H, Aleman L et al (2018) Ectopic expression of two AREB/ABF orthologs increases drought tolerance in cotton (*Gossypium hirsutum*). Plant Cell Environ 41:898–907. https://doi.org/10.1111/pce.12906

Kidokoro S, Yoneda K, Takasaki H et al (2017) Different cold-signaling pathways function in the responses to rapid and gradual decreases in temperature. Plant Cell 29:760–774. https://doi.org/10.1105/tpc.16.00669

Kobayashi Y, Murata M, Minami H et al (2005) Abscisic acid-activated SNRK2 protein kinases function in the gene-regulation pathway of ABA signal transduction by phosphorylating ABA response element-binding factors. Plant J 44:939–949. https://doi.org/10.1111/j.1365-313X.2005.02583.x

Kronzucker HJ, Britto DT (2011) Sodium transport in plants: a critical review. New Phytol 189:54–81

Leskova A, Giehl RFH, Hartmann A et al (2017) Heavy metals induce Iron deficiency responses at different hierarchic and regulatory levels. Plant Physiol 174:1648–1668. https://doi.org/10.1104/pp.16.01916

Li B, Byrt C, Qiu J et al (2016) Identification of a Stelar-localized transport protein that facilitates root-to-shoot transfer of chloride in *Arabidopsis*. Plant Physiol 170:1014–1029. https://doi.org/10.1104/pp.15.01163

Lin Y, Aarts MGM (2012) The molecular mechanism of zinc and cadmium stress response in plants. Cell Mol Life Sci 69:3187–3206. https://doi.org/10.1007/s00018-012-1089-z

Liu H, Liao H, Charng Y (2011) The role of class A1 heat shock factors (HSFA1s) in response to heat and other stresses in *Arabidopsis*. Plant Cell Environ 34:738–751. https://doi.org/10.1111/j.1365-3040.2011.02278.x

Liu Y, Zhang C, Chen J et al (2013) Plant physiology and biochemistry Arabidopsis heat shock factor HsfA1a directly senses heat stress, pH changes, and hydrogen peroxide via the engagement of redox state. Plant Physiol Biochem 64:92–98. https://doi.org/10.1016/j.plaphy.2012.12.013

Liu J, Chu J, Ma C et al (2019) Overexpression of an ABA-dependent grapevine bZIP transcription factor, VvABF2, enhances osmotic stress in Arabidopsis. Plant Cell Rep 38:587–596. https://doi.org/10.1007/s00299-019-02389-y

Loreti E, Van Veen H, Perata P (2016) Plant responses to flooding stress. Curr Opin Plant Biol 33:64–71. https://doi.org/10.1016/j.pbi.2016.06.005

Loyola R, Herrera D, Mas A et al (2016) The photomorphogenic factors UV-B RECEPTOR 1, ELONGATED HYPOCOTYL 5, and HY5 HOMOLOGUE are part of the UV-B signalling pathway in grapevine and mediate flavonol accumulation in response to the environment. J Exp Bot 67:5429–5445. https://doi.org/10.1093/jxb/erw307

Mahmood-ur-Rahman, Ijaz M, Qamar S et al (2019) Abiotic stress signaling in rice crop. In: Hasanuzzaman M, Fujita M, Nahar K (eds) Advances in rice research for abiotic stress tolerance. Elsevier, San Diego, pp 551–569. https://doi.org/10.1016/B978-0-12-814332-2.00027-7

Manassero NGU, Viola IL, Welchen E et al (2013) TCP transcription factors: architectures of plant form. Biomol Concepts 4:111–127. https://doi.org/10.1515/bmc-2012-0051

Matsuo M, Johnson JM, Hieno A et al (2015) High redox responsive transcription factor1 levels result in accumulation of reactive oxygen species in *Arabidopsis thaliana* shoots and roots. Mol Plant 8:1253–1273. https://doi.org/10.1016/j.molp.2015.03.011

Matus JT (2016) Transcriptomic and Metabolomic networks in the grape berry illustrate that it takes more than flavonoids to fight against ultraviolet radiation. Front Plant Sci 7:1337. https://doi.org/10.3389/fpls.2016.01337

Moyano E, Martinez-Rivaz FJ, Blanco-Portales R et al (2018) Genome-wide analysis of the NAC transcription factor family and their expression during the development and ripening of the Fragaria × ananassa fruits. PlosOne 13:e0196953

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911

Nakano T, Suzuki K, Fujimura T et al (2016) Genome-wide analysis of the ERF gene family in Arabidopsis and Rice. Plant Physiol 140:411–432. https://doi.org/10.1104/pp.105.073783.

Nakashima K, Ito Y, Yamaguchi-shinozaki K (2009) Transcriptional regulatory networks in response to abiotic stresses in Arabidopsis and grasses. Plant Physiol 149:88–95. https://doi.org/10.1104/pp.108.129791

Nishizawa-yokoi A, Nosaka R, Hayashi H et al (2011) HsfA1d and HsfA1e involved in the transcriptional regulation of HsfA2 function as key regulators for the Hsf signaling network in response to environmental stress. Plant Cell Physiol 52:933–945. https://doi.org/10.1093/pcp/pcr045

Ohama N, Kusakabe K, Mizoi J et al (2016) The transcriptional Cascade in the heat stress response of Arabidopsis is strictly regulated at the level of transcription factor expression. Plant Cell 28:181–201. https://doi.org/10.1105/tpc.15.00435

Palmer CM, Hindt MN, Schmidt H et al (2013) MYB10 and MYB72 are required for growth under Iron-limiting conditions. PLoS Genet 9:e1003953. https://doi.org/10.1371/journal.pgen.1003953

Pandolfi C, Mancuso S, Shabala S (2012) Physiology of acclimation to salinity stress in pea (*Pisum sativum*). Environ Exp Bot 84:44–51. https://doi.org/10.1016/j.envexpbot.2012.04.015

Pandolfi C, Azzarello E, Mancuso S et al (2016) Acclimation improves salt stress tolerance in *Zea mays* plants. J Plant Physiol 201:1–8. https://doi.org/10.1016/j.jplph.2016.06.010

Puranik S, Sahu PP, Srivastava PS et al (2012) NAC proteins: regulation and role in stress tolerance. Trends Plant Sci 17:369–381. https://doi.org/10.1016/j.tplants.2012.02.004

Rauf S (2016) Breeding sunflower (*Helianthus annuus L.*) for drought tolerance. Commun biom. Crop Sci 3:29–44

Robson M, Klem K, Urban O et al (2015) Re-interpreting plant morphological responses to UV-B radiation. Plant Cell Environ 38:856–866. https://doi.org/10.1111/pce.12374

Sasaki A, Yamaji N, Yokosho K (2012) Nramp5 is a major transporter responsible for manganese and cadmium uptake in rice. Plant Cell 24:2155–2167. https://doi.org/10.1105/tpc.112.096925

Sasidharan R, Voesenek LACJ (2015) Ethylene-mediated acclimations to flooding stress. Plant Physiol 169:3–12. https://doi.org/10.1104/pp.15.00387

Sasidharan R, Mustroph A, Boonman A et al (2013) Root transcript pro fi ling of two Rorippa species reveals gene clusters associated with extreme. Plant Physiol 163:1277–1292. https://doi.org/10.1104/pp.113.222588

Sauter M (2013) Root responses to flooding. Curr Opin Plant Biol 16:282–286. https://doi.org/10.1016/j.pbi.2013.03.013

Savoi S, Wong DCJ, Arapitsas P et al (2016) Transcriptome and metabolite profiling reveals that prolonged drought modulates the phenylpropanoid and terpenoid pathway in white grapes (*Vitis vinifera L.*). BMC Plant Biol 16:67. https://doi.org/10.1186/s12870-016-0760-1

Scharf K, Berberich T, Ebersberger I et al (2012) The plant heat stress transcription factor (Hsf) family: structure, function and evolution. Biochim Biophys Acta 1819:104–119. https://doi.org/10.1016/j.bbagrm.2011.10.002

Schmidt R, Schippers JH, Mieulet D et al (2013) MULTIPASS, a rice R2R3-type MYB transcription factor, regulates adaptive growth by integrating multiple hormonal pathways. Plant J 76:258–273. https://doi.org/10.1111/tpj.12286

Schmollinger S, Schulz-raffelt M, Strenkert D et al (2013) Dissecting the heat stress response in Chlamydomonas by pharmaceutical and RNAi approaches reveals conserved and novel aspects. Mol Plant 6:1795–1813. https://doi.org/10.1093/mp/sst086

Selote D, Samira R, Matthiadis A et al (2015) Iron-binding E3 ligase mediates Iron response in plants by targeting basic helix-loop-helix transcription factors. Plant Physiol 167:273–286. https://doi.org/10.1104/pp.114.250837

Shi H, Wang X, Ye T et al (2014) The Cysteine2/Histidine2-type transcription factor zinc finger of *Arabidopsis thaliana*6 modulates biotic and abiotic stress responses by activating salicylic acid-related genes and C-REPEAT-BINDING FACTOR genes in *Arabidopsis*. Plant Physiol 165:1367–1379. https://doi.org/10.1104/pp.114.242404

Shim D, Hwang J, Lee J et al (2009) Orthologs of the class A4 heat shock transcription factor HsfA4a confer cadmium tolerance in wheat and Rice. Plant Cell 21:4031–4043. https://doi.org/10.1105/tpc.109.066902

Shin L, Lo J, Chen G et al (2013) IRT1 degradation factor1, a RING E3 ubiquitin ligase, regulates the degradation of IRON-REGULATED TRANSPORTER1 in *Arabidopsis*. Plant Cell 25:3039–3051. https://doi.org/10.1105/tpc.113.115212

Shiono K, Ogawa S, Yamazaki S et al (2011) Contrasting dynamics of radial O_2 -loss barrier induction and aerenchyma formation in rice roots of two lengths. Ann Bot 107:89–99. https://doi.org/10.1093/aob/mcq221

Singh D, Laxmi A (2015) Transcriptional regulation of drought response: a tortuous network of transcriptional factors. Front Plant Sci 6:895. https://doi.org/10.3389/fpls.2015.00895

Singh S, Hasanuzzaman M, Nahar K et al (2013) Plant physiology and biochemistry importance of nitric oxide in cadmium stress tolerance in crop plants. Plant Physiol Biochem 63:254–261. https://doi.org/10.1016/j.plaphy.2012.12.001

Singh A, Kumar A, Yadav S et al (2019) Reactive oxygen species-mediated signaling during abiotic stress. Plant Gene 18:100173. https://doi.org/10.1016/j.plgene.2019.100173

Sun X, Matus JT, Wong DCJ et al (2018) The GARP/MYB-related grape transcription factor AQUILO improves cold tolerance and promotes the accumulation of raffinose family oligosaccharides. J Exp Bot 69:1749–1764. https://doi.org/10.1093/jxb/ery020/4827969

Sunkar R, Chinnusamy V, Zhu J, Zhu J (2007) Small RNAs as big players in plant abiotic stress responses and nutrient deprivation. Trends Plant Sci 12:301–309. https://doi.org/10.1016/j.tplants.2007.05.001

Thapa G, Sadhukhan A (2012) Molecular mechanistic model of plant heavy metal tolerance. Biometals 25:489–505. https://doi.org/10.1007/s10534-012-9541-y

Tian L, Zhang Y, Kang E et al (2018) Basic-leucine zipper 17 and Hmg-CoA reductase degradation 3A are involved in salt acclimation memory in *Arabidopsis*. J Integr Plant Biol doi 61:1062. https://doi.org/10.1111/jipb.12744

Ulm R, Baumann A, Oravecz A (2004) Genome-wide analysis of gene expression reveals function of the bZIP transcription factor HY5 in the UV-B response of *Arabidopsis*. Proc Natl Acad Sci U S A 101:1397–1402

Van Buskirk HA, Thomashow MF (2006) Arabidopsis transcription factors regulating cold acclimation. Physiol Plant 126:72–80. https://doi.org/10.1111/j.1399-3054.2005.00625.x

Van Veen H, Mustroph A, Barding GA et al (2013) Two Rumex species from contrasting hydrological niches regulate flooding tolerance through distinct mechanisms. Plant Cell 25:4691–4707. https://doi.org/10.1105/tpc.113.119016

Vannozzi A, Wong DCJ, Holl J et al (2018) Combinatorial regulation of stilbene synthase genes by WRKY and MYB transcription factors in grapevine (*Vitis vinifera* L.). Plant Cell Physiol 59:1043–1059

Vermeirssen V, De Clercq I, Van Parys T et al (2014) *Arabidopsis* ensemble reverse-engineered gene regulatory network discloses interconnected transcription factors in oxidative stress. Plant Cell 26:4556–4579. https://doi.org/10.1105/tpc.114.131417

Voesenek LACJ, Bailey-serres J (2015) Flood adaptive traits and processes: an overview. New Phytol 206:57–73

Wang P, Du Y, Zhao X et al (2013) Environmental stress and adaptation. Plant Physiol 161:1392–1408. https://doi.org/10.1104/pp.112.210724

Wong DCJ, Schlechter R, Vannozzi A et al (2016) A systems-oriented analysis of the grapevine R2R3-MYB transcription factor family uncovers new insights into the regulation of stilbene accumulation. DNA Res 23(5):451–466. https://doi.org/10.1093/dnares/dsw028

Wu H, Chen C, Du J et al (2012) Co-overexpression FIT with AtbHLH38 or AtbHLH39 in *Arabidopsis*-enhanced cadmium tolerance via increased cadmium sequestration in roots and improved Iron homeostasis of shoots. Plant Physiol 158:790–800. https://doi.org/10.1104/pp.111.190983

Wu T, Juan Y, Hsu Y et al (2013) Interplay between heat shock proteins HSP101 and HSA32 prolongs heat acclimation memory. Plant Physiol 161:2075–2084. https://doi.org/10.1104/pp.112.212589

Xie Y, Xu S, Han B et al (2011) Evidence of *Arabidopsis* salt acclimation induced by up-regulation of HY1 and the regulatory role of RbohD-derived reactive oxygen species synthesis. 280–292. Plant J 66:280–292. https://doi.org/10.1111/j.1365-313X.2011.04488.x

Xiong Y, Fei S-Z (2006) Functional and phylogenetic analysis of a DREB / CBF-like gene in perennial ryegrass (Lolium perenne L.). Planta 224:878–888. https://doi.org/10.1007/s00425-006-0273-5

Xu K, Xu X, Fukao T et al (2006) Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. Nature 442:705–708. https://doi.org/10.1038/nature04920

Xu R, Sun P, Jia F et al (2014) Genomewide analysis of TCP transcription factor gene family in Malus domestica. J Genet 93:733–746

Yamaguchi-Shinozaki K, Shinozaki K (1994) A novel cis-acting element in an *Arabidopsis* gene is involved in responsiveness to drought. Plant Cell 6:251–264

Yamaguchi-shinozaki K, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. Annu Rev Plant Biol 57:781–803. https://doi.org/10.1146/annurev.arplant.57.032905.105444

Yoshida T, Ohama N, Nakajima J et al (2011) *Arabidopsis* HsfA1 transcription factors function as the main positive regulators in heat shock-responsive gene expression. Mol Gen Genomics 286:321–332. https://doi.org/10.1007/s00438-011-0647-7

Zhou Y, Xu Z, Zhao K et al (2016) Genome-wide identification, characterization and expression analysis of the TCP gene family in *Prunus mume*. Front Plant Sci 7:1301. https://doi.org/10.3389/fpls.2016.01301

Zimmermann P, Hirsch-hoffmann M, Hennig L et al (2004) GENEVESTIGATOR. *Arabidopsis* microarray database and analysis toolbox. Plant Physiol 136:2621–2632. https://doi.org/10.1104/pp.104.046367.1

Zwack PJ, De Clercq I, Howton TC et al (2016) Cytokinin response factor 6 represses Cytokinin-associated genes during. Plant Physiol 172:1249–1258. https://doi.org/10.1104/pp.16.00415

Chapter 24
Ecophysiological Adaptation of Soybeans to Latitudes Through Photoperiodic and Growth Habit Genes

Rachana Tripathi, Nisha Agrawal, Meeta Jain, and Sanjay Gupta

Contents

Abstract Photoperiodic genes in soybean affect latitudinal adaptation, plant growth, and overall productivity of the crop. Soybean adapts to large latitudinal zones from 50°N to 40°S, but its individual accessions adapt to a very narrow latitudinal band. For its worldwide production, major considerations are its photoperiodic and growth habit genes. Inheritance of the photoperiodic genes and role of these genes regulate early or late flowering and also regulate early or late maturity of the crop. In this chapter, we have summarized the photoperiodic and growth habit genes and their role in soybean flowering and maturity. We have also discussed their mapping, mechanism, quantitative trait loci (QTL) study, and linked markers. Major photoperiodic genes include *E1* gene, *E2* gene, *E3* gene, *E4* gene, *E5* gene, *E7* gene, *E8* gene, and *E10* gene, and genes responsible for growth habit, *Dt1* and *Dt2*, interact with each other and are involved in the functions of flowering, maturity, and plant architecture. Specific combinations of these genes have been found to confer adaptation to specific zones of the world. Therefore, such study will be useful in the development of varieties adapted in adverse conditions of photoperiod in different

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zones of the country. Plant photoperiodic response provides the synchronization of their growth pattern with the seasonal events and, therefore, their better adaptation. At the same time, high photoperiodic sensitivity can retard the dispersal of important agricultural crops. These problems are solved with various breeding strategies.

Keywords Soybean · Flowering · Photoperiodic · Growth habit · Maturity · Markers

24.1 Introduction

Soybean (*Glycine max* (L.) Merrill) is a species of the legume, native of East Asia region (China), but now widely grown as edible bean all over the world. In different regions, this crop has its own unique production cycles of planting, growing, and harvesting. Soybean is a member of large family known as Leguminosae, and subfamily Papilionoideae, which is known for economically important plants, legumes, peas, and beans; it has a complex genome and is a paleopolyploid species. Galegoid and Phaseoloid are the two clades of the subfamily Papilionoideae (Goldblatt 1981). Soybean is a participant of the Phaseoloid clade and shares the same place with common bean (*Phaseolus vulgaris*) and mung bean (*Vigna radiata*), whereas the other clade, the Galegoid, comprises pea (*Pisum sativum*), alfalfa (*Medicago sativ*a), and two classical legumes, *Lotus japonicas* and *Medicago truncatula*. Warm and moist climate of the monsoon season is the basic need of soybean crop. Temperature between 15 and 32°C is required for its germination while optimum temperature required for its growth and yield ranges from 30 to 33°C. Temperature below 10 °C and above 38 °C affects the growth and yield. Day temperatures of 25 °C are good for flowering. The crop can be grown in areas that receive rainfall between 600 and 650 mm. Rainfall during maturity deteriorates the quality of grain. Cloudy weather prolongs the vegetative phase. The crop is generally cultivated at an altitude of 1200–2000 m. In most of the soybean varieties, day length is the key factor as they are sensitive to photoperiods and short-day plant duration. Most of the varieties of soybean flowers mature rapidly if grown under short-day conditions, where day length is less than 14 h. Hence, if longer-day conditions are present, flowering is affected by remaining in prolonged vegetative stage. Whereas, in very short-day conditions, flowering occur too early, which also ultimately affects the yield of the crop. So, in the adverse conditions of environment, photoperiodic duration can be controlled by studying the effects of various photoperiodic and growth habit genes and by understanding their mechanism to control flowering and maturity.

The interactions between environmental factors and various endogenous cycle are responsible for the control of the flowering of the plant species (Levy and Dean 1998). Various environmental factors like duration of light, intensity of light, and temperature are the major favorable circumstances to control the reproductive development of the plant species. It is the environmental cues mainly that give the competence to the plant species for their development. The day length limits the adaptation of soybean varieties and accessions to a small range of latitudes and date of sowing by disturbing vegetative and reproductive growth and development (Parvez and Gardner 1987). The time of flowering and maturity is an important trait for adaptation to specific latitudes. Here we have discussed the various genes involved in flowering under long-day conditions, which promotes early flowering in the same.

24.2 Eco-Physiology and Adaptation of Soybean Worldwide

Soybean was introduced in the historical background from Eastern part of China in 2510 BP, which leads to the revolt in the field of agriculture of the Eastern Zhou dynasty (Ho 1975). Landraces of soybean crop with the uppermost range in the genetic makeup were found around the Huang He/Yellow River region (Dong et al. 2004: Li et al. 2010). Many studies based on the phylogeny found that soybean originated in the Southern China region of the Yangtze basin (Guo et al. 2010). However, the study by Shimamoto et al. (2000) supports the Southern origin of soybean, but no phylogenetic evidence supports these (Lee et al. 2011). Further, the study by Han et al. (2016), of the genetic differentiation and gene flow in semi-wild soybean, classified soybean as the landraces or wild type of soybean. According to Fukuda (1933) and Hymowitz (1970), *Glycine gracilis* is a derivative of the process of evolution and product of the hybridization between wild type *Glycine soja* and the *Glycine max* species of domesticated soybean. They also observed that there was no gene flow from *Glycine max* species to domesticated *Glycine gracilis* or wild *Glycine soja*, but a considerable gene flow was observed between species *Glycine max* and domesticated *Glycine gracilis*, which supports wild *Glycine soja* as the progenitor of both *Glycine gracilis* and *Glycine max*. Secondly, the region called the Valley of Huang-Huai, located in the central region of China that lies in the middle of Yellow River and the Huai River, is the main probable location for the domestication of soybean. Divergence showed that wild types of *Glycine soja* and *Glycine max* species interacted and formed *Glycine gracilis* intermediate (Kim et al. 2010; Li et al. 2014). Several genetic bottlenecks appeared during the evolution of the soybean domestication and its diversification, markedly in the beginning of landraces in Asian and North American zones (Hyten et al. 2006). Valliyodan et al. (2016) and Li et al. (2013) stated about the nucleotide diversity found in soybean landraces. Also, there was introgression of different *G. soja* landraces genomes to increase the diversity in the modern breeding efforts between elite cultivars. During the study of selection for adaptation in wide range of latitudes of North America for photoperiodic gradient, founder effect was observed, which shows moderate level of diversity.

There are various hypotheses to explain evolutionary adaptation of soybean. Single origin hypothesis indicated that *G. soja* wild type of soybean form the domesticated soybeans ensuing from a distinct cluster explained by Zhou et al. (2015b). In contrast to this hypothesis, the phylogenetic studies by Xu et al. (2002) and also Abe et al. (2003), carried out by using nuclear or chloroplast markers (SSR) in soybean of wild cultivated soybeans, provide another hypothesis in East Asian zones. Studies by Lee and Park (2006) reported soybeans' high genetic diversity in the Korean peninsula. Furthermore, archaeologists trace larger amounts of seeds of soybean in the regions of Japan and Korea as compared to the amount of seeds dispersed in Yellow River in China during the period 5000–3000 BP (Lee et al. 2011). The complex hypothesis in Central Japan with larger amounts of seeds shows that *G. max* and *G. soja* and their complex take long divergence time, at various locations in East Asia region, to domesticate soybean.

The earliest mention of soybean in Japanese text dates back to 712 AD. Introduction of soybean into neighboring countries of China dates around the first century (Wang and Wang 1992; Gai 1996), while its introduction to the Indian subcontinent begins through the Himalayan and North-Eastern areas dating back to 1000 AD (Hymowitz and Kaizuma 1981). In India, soybean cultivation began from Assam and North-East zones, and from there they became adapted to grow in different zones and responded according to their photoperiodic conditions, that is, long- and short-day conditions; its diversification took long years to take place. However, different adapted varieties of particular zones do not perform well in another zone, due to different photoperiods. India is divided into six zones: Northern hill zone, Northern plain part of zone (28.7° average latitude), North-Eastern hill zone, Eastern zone, zone of Central part (22.61° average latitude), and Southern part of zones (16.13° average latitude).

Adaptation of soybean from its origin to different parts of the world through evolution at various latitudes explains the eco-physiological adaptation of this crop.

24.3 Photoperiodic Response

Photoperiodism is the plant response to the relative timespan of dark and light periods within the 24-h cycle. Growth and development of the plants, mainly flowering and vegetative growth, are affected by photoperiodism, which further affects the crop yield. Length of light duration is defined as critical day length when plant starts to bloom. It helps plant to change its phase from vegetative growth to reproductive phase, that is, flowering. Depending upon the photoperiod, day-length response plants is further classified as: (1) plants that bear flower under short duration of light, or short-day plant (SDP), like soybean, (2) plants that start flowering in longer duration of light phase, or long-day plant (LDP), like lettuce, spinach, etc., and (3) day-neutral plants (DNP). Soybean is a well-known photoperiod-sensitive leguminous crop species that flowers when light duration becomes shorter than the day length required of an accession. Genotypic constitution at major photoperiodic loci plays a significant role in defining the critical day length of an accession. Photoperiodic genes also control maturity and interact with growth habit genes in determining the plant architecture. Such a systematic effect of photoperiodic genes and light duration on plant architecture calls for basic studies to identify suitable combinations of these genes for different regions.

The interaction between the photo-morphogenic effects and CO_2 assimilation is a complicated one. For example, plant species in early short-day conditions flowered early, and improper development of plants reduced the height of plants, vegetative areas that ultimately affect the yield. Hence, maturation comes earlier and grain yield is affected also, decreased photosynthesis and shorter vegetative parts than average observed, to overcome the above-mentioned problems, along with latitudinal adaptation, combination of dominant and recessive alleles can be studied. Allelic variations at each of the loci have a significant effect on flowering and maturity. These genes have been cloned and characterized recently and used for deciphering the role of these genes on plant architecture and for identification of suitable multiallelic combinations for different regions. In soybean, major photoperiodic genes like gene *E1*, gene *E2*, gene *E3*, and gene *E4*, and growth habit *Dt1* genes were identified and characterized for their phenotypic effect long back in the 1970s. Dominant photoperiodic alleles confer photosensitivity, late flowering, and maturity. Recessive *dt1* confers determinate growth habit. This chapter summarizes the understanding of the role of photoperiodic genes, their alleles, and their effect on maturity and days to flower. These different genes have a major effect on the crop yield.

24.3.1 Photoperiodic Adaptation of Soybean Crop at Latitudes

The size and condition of the crop are determined by weather. Weather conditions are determined by atmospheric pressure, temperature, solar energy, wind, precipitation, humidity, and topography of the geographical zones. Due to the combination of these genes that controls flowering, individual soybean accessions are adapted to narrow latitudinal zones (Tsubokura et al. 2013). According to Watanabe et al. (2011), soybeans are grown worldwide ranging from the Equator to 50° N to 35° S latitudinal zones. Precision breeding is required for the development of the varieties with gene combinations that specify particular region and production, that are not comprising by early or late flowering and maturity due to the adaptation (Saindon et al. 1989b; Tsubokura et al. 2014). Fehr (1987)) declines the critical duration of photoperiod of cultivars successively moving from high to low latitudes. The development of short-day soybean crop under long-day conditions with early maturity gene in Canadian and Northern regions is the best example of latitudinal adaptation. Consequently, cultivar adaptable in Northern Hemisphere sown in south of its adaptation area will flower and mature prior because the duration of critical light is increased and the opposite happens with the Southern Hemisphere (Miyasaka et al. 1981). Soybean cultivation and production started from China and can be traced from the beginning era of China's agriculture. The key soybean producing countries are the USA, Brazil, Argentina, China, and India, ranking from first to fifth in the order. However, the crop is not cultivated in the entire country or state but in some specific zones of these countries due to the latitudinal adaptation. In higher latitudes, long-day conditions prevail, which needs early maturity gene combination to reduce prolonged vegetative phase to increase the crop production. The diversity of soybean in latitudinal adaptation is associated with particular photoperiod of the latitudinal zone. As soybean is SDP, it requires the sensitivity toward photoperiod for the expansion of its latitudinal adaptation.

24.3.2 Inheritance of Photoperiodism in Soybean

The crop is adaptive to a broader range due to major variation in the quantitative trait loci (QTL) and genes responsible for flowering time, maturity, and growth habit. To date, eight major genes governing flowering time under long-day conditions and maturity and two major genes controlling growth habit in soybean have been identified: *E1* and *E2* genes were identified by Bernard (1971), *E3* gene by Buzzell (1971), gene *E4* by Buzzell and Voldeng (1980), *E5* gene by McBlain and Bernard (1987), gene *E7* by Cober and Voldeng (2001)), gene *E8* by Cober et al. (2010)), gene *E10* by Samanfar et al. (2017)), *Dt1* by Woodworth (1932)), and *Dt2* by Bernard (1972)). *E1*, *E2* confer late flowering while e1, e2 early flowering, and recessive e3, e4 genes are for photo-insensitivity. Likewise, *Dt1Dt1* shows indeterminate stem growth and dt1dt1 determinate stem growth. *Dt1* and *Dt2* both reduce plant height but the effect of *Dt1* is higher. The most important maturity genes, *E1* to *E4*, postpone blooming in long-day conditions; however, they do not have major effects on flowering and maturity in short-day conditions (Cober and Tanner 1996).

Based on the latitudes and agro-climatic conditions, varietal adaptation to different zones is very specific and varieties suiting for more than one zone are rare. Since flowering, maturity, and growth habits are governed by many genes, the incorporation of specific combination during varietal development would require the help of molecular markers for these genes. For the ten flowering, maturity, and growth habit genes characterized—*E1*, *E2*, *E3*, *E4* (main genes), *E5*, *E7*, *E8*, *E10* (latest reported), *Dt1*, and *Dt2*—many markers have been developed. Jung and Müller (2009) reported several regulatory pathways linked with flowering in various plant species, like model plant *Arabidopsis thaliana* and *Oryza sativa.* Using simple sequence repeats (SSR) molecular markers, the photoperiodic and maturity genes (such as *E1* gene, *E2* gene, *E3* gene, *E4* gene, *E7* gene, and *E8* gene) loci were mapped correspondingly with various chromosomes (such as 06, 10, 19, 20, and 03) in soybean (Cregan et al. 1999; Cober and Voldeng 2001; Abe et al. 2003; Molnar et al. 2003; Cober et al. 2010).

24.3.3 Genetics of the Photoperiodic Genes

Genetics of photoperiodic genes involves the study, their interaction with each other, and inheritance of these genes in controlling plant vegetative and reproductive phases of growth and development. Genetics also deals with the relationship between phenotypic and dominant, recessive genotypic correlation of photoperiodic genes. Gene *E1* has been characterized that encodes a transcription factor conserved for domain B3, that is, putative nuclear localization signal, studied by Xia et al. (2012). At this locus, *E1* has been reported with three mutations: e1-as (recessive condition), e1-nl (lacking 130 bp region), and e1-fs (frame-shift mutation). Decrease in activity has been observed as a result of loss of nuclear localization domain in *E1* protein, which explains e1-as as a hypoactive allele. The GIGANTEA gene (GI) ortholog in *Arabidopsis* is referred as *E2* gene (Watanabe et al. 2011). *E3* gene and *E4* gene have been recognized as phytochrome A3 and phytochrome A2 genes, respectively, orthologous to *Arabidopsis* (Liu et al. 2008; Watanabe et al. 2009). Watanabe et al. (2009) and Xu et al. (2013) reported three mutations in *E3* gene, e3-tr, e3-fs, and e3-ns, of which allele e3-tr is a mutation that causes deletion in exon 4 whereas e3-fs (frame-shift) mutation causes stop codon in exon 1, and e3-ns mutation is SNP in exon 3 that introduces stop codon. *E4* gene reported has four types of mutations, e4-kes, e4-kam, e4-tsu, and e4-oto, that result in premature stop codons (Tsubokura et al. 2013). For these genes, allele-specific markers have been developed for ge in soybean by different researchers (Liu et al. 2008; Watanabe et al. 2009; Tsubokura et al. 2013; Xu et al. 2013). In *E10*, recessive conditions cause maturity earlier, by 5–10 days, than in dominant condition.

24.3.3.1 *E1* Gene

E1 and *E2*, two independent gene pairs identified by Bernard (1971), function in flowering response and maturity in soybeans (*Glycine max* (L.) Merrill) in the same genetic background that was developed as commercial variety (Clark) by backcrossing. *E1*, a gene for lateness linked to pubescence color (Tt), was transferred from strain T175, and *E2*, a gene responsible for earliness, from T245. *E1* locus near-isogenic lines (NILs) was prepared and selected for the study because it has shown dramatic variations in flowering time than other soybean *E* genes (Cober et al. 1996). Identification of molecular markers linked to photoperiodic genes enables breeders to establish the presence or absence of the gene in seedling without exposing the plants to required photoperiods and such molecular markers have been identified in soybean (Li and Niwa 1996). Earlier, it was implicit that gene *E1* would be a PHY gene as thought by Cober and Voldeng (2001) and Cober and Tanner (1996)). Stewart et al. (2003) found that *E1* locus has major impact on the time of flowering under the conditions of field. The overexpression of FT-like genes of many species like *Arabidopsis* governs flowering earlier (Lifschitz et al. 2006; Hsu et al. 2006; Hayama et al. 2007; Igasaki et al. 2008). The loci *E1*, *E3*, and *E4*

(Saindon et al. 1989; Cober and Tanner 1996; Abe et al. 2003) are deliberate and sensitive toward photoperiod on various light durations. Satt 489, Satt 134, Satt 100, and Satt 460 SSR markers as linked to *E1* gene on linkage group C2 (Abe et al. 2003). *E1* gene has been mapped on C2 linkage group between SSR marker Satt 277 and Satt 557 in 2.1 cM distance with the diagnostic Satt 365 marker (Molnar et al. 2003). The map position and SSR markers for *E1* gene was identified (Molnar et al. 2003) and has been confirmed by Liu and Abe (2010). A major QTL was present on linkage group C2 at SSR marker position Satt 557 (Liu and Abe 2010). Thakare et al. (2011) evaluated *E1* NILs (near-isogenic lines) to check the transcription of GmFT-like genes in *Arabidopsis* and determined the relationship between time of flowering and FT gene expression. Previously in 2010, they developed NILs to characterize flowering in the model plant species like *Arabidopsis thaliana* and *O. sativa* L. at *E1* locus in both short- and longer-day conditions to detect the expression of putative gene. Thakare et al. (2011) also noted that short days are inductive to flowering rather than longer days, by comparing flowering days in both recessive and dominant *E1* alleles; hence, they stated that plants are responsive to photoperiod differences. Soybean genes complement the *Arabidopsis* FT functions and *E1* locus affects time to flower by regulating the soybean FT expression. The allele that is responsible for lateness at each locus was partially dominant in most of the combinations. *E1* allele does not lengthen the reproductive duration but delays days to flowering. Using positional cloning approach, the *E1* gene has been cloned (Xia et al. 2012). In soybean, out of ten, only two of the FT-like genes are expressive while other FT-like gene functions are unknown. By positional cloning of the *E1* gene, it is reported that they contain highly conserved region of B3 transcription factors and encode a protein that has putative nuclear localization signal, explained by Xia et al. (2012). They reported that in *E1* alleles, one is lacking 130kbp portion from the *E1* gene and named it as *E1*-nl. Another one named as *E1*-fs, due to frameshift mutation caused by a single bp deletion, leads to premature proteins that have stop codon. The *E1* gene in recessive condition (e1-as) is because of single substitution of amino acid in protein, which leads to putative proteins that suppress nuclear localization signal. Allele-specific markers for these alleles are developed by Xu et al. (2013). According to Zhai et al. 2014a, b), mechanism of *E1* gene regulates flowering by controlling GmFT2a and GmFT5a to delay flowering under long-day conditions. *E3* and *E4* genes' function loss could also suppress the *E1* expression and congruently elevate the expression of GmFT, which leads to comparatively early flowering condition. However, longer-day conditions are essential for *E1* expression.

24.3.3.2 *E2* Gene

E2 allele is also known as photoperiodic gene responsible for blooming and maturity condition in soybean, and McBlain and Bernard (1987) suggested that *E5* is similar to *E2* in flowering. Further, it is explained (Bernard 1971; Watanabe et al. 2004; Yamanaka et al. 2001) that the effect of allele *E2* is weakened by recessive *E1* allele. It has been determined that *E2* gene locus is a GI ortholog (Koornneef et al. 1998; Fowler et al. 1999; Mizoguchi et al. 2005; Hayama et al. 2007). GI ortholog controls mRNA expression of CO and FT gene in many plant species and hence play an important role in flowering. Earlier, *E2* gene was mapped in a cross among the Misuzudaizu and Moshidou Gong 503 by Akkaya et al. (1995) and Cregan et al. (1999). *E2* candidate gene was identified in the linkage group O (Gm 10) with the help of map-based cloning of qFT2 in soybean, which is an identified QTL for flowering. In soybean, a flowering QTL, *E2* gene was identified in recombinant inbred lines (RILs) population that develops with the cultivar "Misuzudaizu" (ft2/ft2; JP28856) and "Moshidou Gong 503" (FT2/FT2; JP27603). Recessive genotype (*e2e2*) at the *E2* locus causes early flowering by the induction of FT2a, a homologue in soybean, whereas dominant genotype (*E2E2*) remains constant under a range of ecological conditions studied by Watanabe et al. (2011). Later researchers (Watanabe et al. 2009, 2011) identified genes *E2* and *E3* through positional cloning. *E2* gene (GmGIa, Glyma10 g36600) is the ortholog of *Arabidopsis* flowering time gene GIGANTEA. By using "Misuzudaizu" and "Moshidou Gong 503" recombinant hybrid lines fine mapping, which shows qFT2 within a region of 94 kilobase pair by preparing a single BAC clone harboring a genomic region of Williams 82, nine annotated genes were presumed. From the predicted genes, Glyma10g36600 shows very high similarity with *Arabidopsis GIGANTEA* (GI) gene. Through sequence analysis, it is found that glyma10g36600 in Misuzudaizu and cv. Harosoy NILs with dominant condition lack truncated GI, but in recessive Harosoy contains truncated GI due to SNP that causes premature termination codon in tenth exon of GI protein to make it dysfunctional. Whereas, Moshidou Gong 503 has donor for the late blooming qFT2 allele and this is further supported by the investigation having mutant of GI due to TILLING by EMS-mutagenesis population of cultivar Bay. Dominant conditions without dysfunctional protein cause early flowering and recessive conditions cause late flowering (Watanabe et al. 2011).

24.3.3.3 *E3* Gene

The flowering time inheritance in the short-day soybean was studied by Buzzel under long-day conditions with the artificial white fluorescent light (20 h) in the greenhouse (Buzzel 1971). One major gene with two alleles is responsible for controlling the flowering response. Through the study of various photosensitivity responses of different soybean NILs, the relationship between some of the photoreceptor genes and *E3* gene was recommended (Cober et al. 1996). Whereas, linkage relationship between *Dt1* and *E3* loci has also been reported later (Cober and Tanner 1996). *E3* gene has been mapped on the linkage group L with 32.4 cM distance in SSR marker Satt 099, with Satt 229 as a diagnostic marker (Molnar et al. 2003). Yamanaka et al. (2005) developed residual heterozygous line (RHL), which is derived from RILs, for evaluating QTLs (Haley et al. 1994). In the midst of these QTLs, many associations are reported with the *E3* gene (Orf et al. 1999; Mansur et al. 1993; Funatsuki et al. 2005). Salvi and Tuberosa (2005) explained the use of

NILs that must differ at a single QTL for fine mapping, and description of an individual locus is detected according to soyGD (Shultz et al. 2006; Shultz et al. 2007), the Soybean Genome Database (http://soybeangenome.siu.edu/), and the Legume Information System (LIS; http://www.comparative-legumes.org/). Many QTLs, over the range of 60 loci, are associated with traits related to agriculture in the region of approximately 30–40 cM between *Dt1* and Satt 373. Such tremendously huge number of QTLs in any way have effects, and the relation between the *Dt1* and *E3* loci can also have an effect on many aspects of plant morphology. The dominant allele *E3*, which gave a fluorescent-sensitive response of delayed flowering, also resulted in later field maturity while the recessive allele *e3* that gave an insensitive response resulted in earlier maturity. Using map-based cloning approach, this gene has been cloned (Watanabe et al. 2009). *E3* has been cloned and allele-specific primers have been identified by Watanabe et al. (2009). These researchers recognized the *E3* locus (PhyA) homologues GmPHYA3, and also reported that it lacks 13.33 kb region including exon 4, which formed incomplete histidine–kinase domain. These researchers designed three allele-specific primers in which forward primer is the same for both *E3* and e3 alleles but the reverse primer is from the normal gene in *E3* allele and from the deleted region in e3 allele. Watanabe et al. (2009) and Xu et al. (2013) both reported three types of mutations designated as *E3*-tr, *E3*-fs, and *E3*-ns for *E3* gene. As mentioned above, *E3*-tr mutation is due to lacking of the three regions in the gene including exon 4 of *E3*. Also, *E3*-fs (frame-shift) mutation creates a stop codon in exon 1 and, lastly, the mutation that introduces SNP in exon 3 causes glutamine amino acid change to stop codon known as *E3*-ns. Allele-specific amplification produces a band of 1904 bp in photosensitive genotype and 829 bp in photo-insensitive genotype. Gene responsible for *E3* locus is identified by map-based cloning using RHL lines.

24.3.3.4 *E4* Gene

E4 gene was identified by Buzzell (1971) studying the flowering time inheritance in soybean, under long-day conditions using natural day length (extended 20 h) with incandescent light (ILD). Buzzel identified that dominant allele of a gene *E4* responds to ILD and delays maturity whereas the recessive allele *E4* gives an insensitive response and early maturity. Later, the complete inheritance of ILD response was established and it was found that for a plant to be insensitive to ILD, it was necessary that both *E3* and *E4* alleles should be present (Saindon et al. 1989). *E4* gene has been mapped on linkage group I (Molnar et al. 2003), close to the diagnostic marker Satt 354. Satt 239 and Satt 496 SSR markers, as linked to *E4* gene on linkage group I (Liu et al. 2008), assigned this gene to linkage group I and could clone it. *E4* gene has been cloned by Liu et al. (2008) as one of homologue of PhyA, GmphyA2. These authors reported that insertion of 6238 bp long Ty1/copia-like retrotransposon found on exon 1 of functional *E4* results in its inactivation. Three allele-specific primers were developed in which forward primer is the same for photosensitive and photo-insensitive genotypes but a reverse primer is from retroposon in *E4* (*E4*-SORE) and normal gene in *E4*. Allele-specific amplification produces a band of 1229 bp in photosensitive genotypes and 837 bp in photo-insensitive genotypes. Later, Tsubokura et al. (2013) identified four more recessive alleles named as *E4*-kam, allele *E4*-oto, allele *E4*-tsu, and allele *E4*-kes, and developed allele-specific CAPS markers for them.

24.3.3.5 *E5* Gene

E5 gene was reported using a cross: Harosoy × L64–4830 (McBlain and Bernard 1987); segregation study for late maturity was noted later (Watanabe et al. 2011) and a new gene was reported designated as *E5* for allele in L64–4830 and recessive e5 in Harosoy. "Clark" variety performs major function for the maturity gene isolines; it is having *E2* (dominant allele) instead of recessive e2 present in Harosoy. It is thought that it also has e5 allele. In the cross between the above-mentioned lines (Harosoy-*E5* × Clark-e5), QTL analysis was performed and high LOD score was obtained between markers qDF_01 and qDM_01, which indicated *E2* is close to it (Watanabe et al. 2011). Their result indicates that probably *E5* is located close to *E2* or it may be an allele of *E2* locus. Harosoy-*E5* may be the result of astonishing outcrossing with the plant containing *E2*-dl allele pollen, which results in lateness in Harosoy-*E5*. So, they predicted that *E5* is a separate gene. Study of the gene further would be helpful in knowing the mechanism responsible for flowering and maturity response in soybean plants. Dissanayaka et al. (2016) mapped this new locus and found a crossover between Satt 365 SSR marker, while Watanabe et al. (2009) found *E5* in heterozygous condition in F2 plants with Satt 557 marker.

24.3.3.6 *E7* Gene

Cober and Voldeng (2001a) identified *E7* locus; in its response to ILD, Cober and Voldeng (2001b)) found that *E7* allele confers early maturity and weakens the sensitivity to ILD only under the genotype of *E1E1E3E3E4E4*. *E7E7* gene has been mapped on LG C2 to a 22.2 cM distance between SSR markers Satt 100 and Satt 460 that have Satt 319 as a diagnostic marker (Molnar et al. 2003). Recently, Liu and Abe (2010) reported that *E7* may confer the photosensitivity even under the genotype *E1E1E3E3E4E4*.

24.3.3.7 *E8* Gene

The *E8* gene is also found in the linkage group C1 flanked by Sat_404 and Satt 136 SSR markers. Till now, in this linkage region no other maturity gene is reported. Soybean Genetics Committee gave the symbol *E8E8* to this gene flanking in C1 linkage group. Dominant *E8E8* condition is responsible for late maturity, whereas recessive *e8e8* is responsible for early maturity. Similarly, recessive *E6* alleles hasten flowering in short-day conditions and are mainly found in tropical region, so it is doubtful that *E8* allele is *E6* or similar to this (Bonato and Vello 1999).

24.3.3.8 *E10* Gene

E10 has been identified very recently (Samanfar et al. 2017), and linked SSR markers were developed for the locus. Isoline derived from Maple Presto OT98–17 and that derived from Harosoy isoline OT02–18, both are having the same genotypic constituents at the main known photoperiodic and maturity loci in condition *e1e1* (recessive) *e2e2* (recessive) *e3e3* (recessive) *e4e4* (recessive) *e7e7* (recessive) *e8e8* (recessive). Then also the isoline OT98–17 matured 6 days before in comparison to the OT02–18 isoline in open (field) conditions. Early maturity could be introgressed into OT02–18 and OT98–17 and late maturity by merely choosing unreplicated progeny of F3 as parents, and this explained OT98–17 having an extra, unknown maturity gene with earliness. Through genetic analyses, *E10* was identified and FT4 was identified as the candidate gene for *E10*. *E1* gene controls flowering by regulating the expression of flowering locus, but day length is the factor that is important in regulation of this gene. FT4 is expressed in parallel with *E1*. When long-day conditions are prevailing, it results in later flowering and when shorter-day conditions are present, downregulation of FT4 results in flowering with earliness (Zhai et al. 2014a, b). *E1* functions downstream and acts as a repressor in flowering time of soybean (Xu et al. 2015). At chromosome 08, gene *E10* is located. Recessive *E10* results in earlier maturity, 5–10 days earlier than dominant *E10*. FT4 is the likely candidate gene for the *E10* locus by the analysis of protein:protein interaction.

24.4 Growth Habit

Growth habit genes in soybean are determined as *Dt1* and *Dt2*. Plant height is mainly controlled by *Dt1* gene. Recessive *dt1* confers determinate growth habit. However, information as well as knowledge on these genes in our literature is not available. Therefore, in this chapter, we have attempted to provide knowledge of photoperiodic and growth habit genes, especially in the soybean crop. The recessive *dt1* allele at growth habit locus expresses determinate growth habit and *Dt1* confers indeterminate growth habit with late or an early flowering combination. Soybean is a quantitative short-day crop (SDP) that means the night length will facilitate and control the initiation of flowering. This signal starts from the leaf and moves via phloem toward the whole plant. In addition to growth, the photoperiod is also responsible for controlling the mechanism of plant maturity, its height, seed weight, pod number, number of branches, node number, etc. In the USA, 13 different maturity groups (from 000 to X) have been distinguished according to their maturity and adaptation. Cultivars belonging to the same group may not compulsorily be the same; they may mature in different periods and can have different development rates. A high latitude with a long-day photoperiod and temperature range significantly affect the maturity rates of soybeans.

Soybean yield depends indirectly on stem growth habit as it is an important adaptation and agronomic trait that directly affects many phenotypic traits like height of a plant, days to flower, duration of the maturity, number of nodes, several abiotic stress tolerance, agronomic traits (Specht et al. 2001; Bernard 1972; Heatherly and Smith 2004). There are two types of classification on the basis of duration of the termination of apical stem growth, which are: determinate and indeterminate. Determinate stem is the thick stem and its growth stops when flowering is initiated. The thickness of this type of stem is more due to latitudinal growth in stem girth, which continues even after the apical growth of the stem length comes to an end. Most of the soybean cultivar of the USA and China are indeterminate and grow in the North region while in contrast the cultivars growing in the South are determinate types. The indeterminate types discussed above are better adapted to a shorter growing season because of proper vegetative and reproductive growth. On the other hand, vegetative and reproductive stages are separated in determinate type of growth habit, as explained by Heatherly and Elmore (2004). Semi-determinate types find the North more valuable, like determinate types, which do not need a compact seeding rate to achieve higher yield, in comparison to indeterminate types. They generally turn out lesser number of stem nodes. Moreover, some degree of lodging resistance is observed in the indeterminate one, which is overcome in the semi-determinate cultivars as they are shorter in height than the previous one (Chang et al. 1982). In “green revolution,” Peng et al. (1999) took into account similar cereal genes in their study.

According to conventional genetic analysis, epistatic interaction between two genes, *Dt1* and *Dt2*, controls growth habit of the stem in various genotypes of soybean (Bernard 1972). Semi-determinate phenotypes are obtained when dominant *Dt2/Dt2* is present in the genetic background of *Dt1/Dt1*, whereas indeterminate phenotypes are produced in presence of *dt2/dt2*. However, epistatic effect of *dt1* allele is confirmed when determinate phenotype is obtained in the presence of *dt1/dt1* genetic backgrounds on the transcription of *Dt2/dt2* locus. *Dt1* gene is the plant ortholog of *Arabidopsis thaliana TERMINAL FLOWER1* with functionally conserved domain, which is a floral suppressor gene (Tian et al. 2010; Liu et al. 2010). Expression (Shannon and Meeks-Wagner 1991; Bradley et al. 1997) in shoot apical meristems (SAMs) was explained, which cause transformation of indeterminate phenotype growth habit to the determinate phenotype growth habit. Tian et al. (2010) noticed four independent mutations caused in soybean during its domestication. *Dt1* locus is positioned on chromosome 19 (Liu et al. 2007; Tian et al. 2010), whereas chromosome 18, at which the *Dt2* gene is located, has been identified as MADS domain factor gene (Ping et al. 2014). Since determinate and semi-determinate growth habits are not seen in *G. soja*, and *Dt2* confers semi-determinacy, it is regarded as a gain of function mutation.

Woodworth (1932) first reported in soybean the *Dtdt* gene pair, now known as *Dt1*dt1. They are commonly categorized as determinate (*Dt1Dt1*) or indeterminate (*Dt1*d1) because their major effects are in stem growth termination. Gene *Dt1* was cloned by Liu et al. (2010) as TFL gene. Four dysfunctional alleles are reported in this locus (*Dt1*-ab, *Dt1*-bb, *Dt1*-tb, and *Dt1*-ta); these mutant alleles code for the protein single amino acid substitutions. Xu et al. (2013) reported three dysfunctional allele-specific primers except for *dt1-ta*. Bernard (1972) found the strain T 117 in the USDA Genetic type core collection, which has character of the intermediate stem type called semi-determinate, where *Dt2* is controlled by a dominant gene at a diverse locus. Bernard also found it phenotypically similar to the heterozygote *Dtldt1* gene. *Dt1* and *Dt2* are epistatic loci. *Dt2* locus is only expressed in the presence of *Dtl*, and *Dt1*dt1 homozygous genotype causes its suppression.

24.5 Conclusion

Our knowledge about photoperiodic and growth habit genes in soybean crop has greatly facilitated our understanding of their mechanisms in eco-physiological and latitudinal adaptation of the crop. Study of and understanding photoperiod are important because day length is a reliable indicator of plant development, its flowering schedule, and circadian rhythms. Shedding light on genes is directly related with plant photoperiodism and growth habit. We have summarized the traits that can be combined together and screened phenotypically for genetic improvement in the crop. Moreover, in the past, large amounts of genetic resources are available for the development of better-adapted plant species. But the usage of these resources is limited due to unavailable gene sequences, which might be possible nowadays for identification of quantitative traits of soybean. Plant breeding gives the opportunity to study and bring changes in the previously unfamiliar areas of plant sciences, and also brings together physiology and genetics to disclose the several agricultural bases of molecular breeding.

References

Abe J, Xu D, Miyano A, Komatsu K, Kanazawa A, Shimamoto Y (2003) Photoperiod insensitive Japanese soybean landracesdiffer at two maturity loci. Crop Sci 43:1300–1304

Akkaya MS, Shoemaker RC, Specht JE, Bhagwat AA, Cregan PB (1995) Integration of simple sequence repeat DNA markers into a soybean linkage map. Crop Sci 35:1439–1445

Bernard RL (1971) Two genes for time of flowering in soybeans. Crop Sci 11:242–244

Bernard RL (1972) Two genes affecting stem termination in soybeans. Crop Sci 12:235–239

Bonato ER, Vello NA (1999) E6, a dominant gene conditioning early flowering and maturity in soybeans. Genet Mol Biol 22:229–232

Bradley D, Ratcliffe O, Vincent C, Carpenter R, Coen E (1997) Inflorescence commitment and architecture in Arabidopsis. Science 275:80–83

Buzzell RI (1971) Inheritance of a soybean flowering response to fluorescent-daylength conditions. Can J Genet Cytol 13:703

Buzzell RI, Voldeng HD (1980) Inheritance of insensitivity to long day length. Soybean Genet Newsl 7:26–29

Chang JF, Green DE, Shibles R (1982) Yield and agronomic performance of semi-determinate and indeterminate soybean stem types. Crop Sci 22:97–101

Cober ER, Tanner JW (1996) Performance of related indeterminate and tall determinate soybean lines in short-season areas. Crop Sci 35:361–364

Cober ER, Voldeng HD (2001) A new soybean maturity and photoperiod-sensitivity locus linked to *E1* and. T Crop Sci 41:698–701

Cober ER, Voldeng HD (2001a) A new soybean maturity andphotoperiod-sensitivity locus linked to *E1* and. T Crop Sci 41:698–701

Cober ER, Voldeng HD (2001b) Low R: FR light quality delaysflowering of *E7E7* soybean lines. Crop Sci 41:1823–1826

Cober ER, Tanner JW, Voldeng HD (1996) Genetic control of photoperiod response in early-maturing, near-isogenic soybean lines. Crop Sci 36:601–605

Cober ER, Molnar SJ, Charette M, Voldeng HD (2010) A new locus for early maturity in soybean. Crop Sci 50:524–527

Cregan PB, Jarvik T, Bush AL, Shoemaker RC, Lark KG, Kahler AL, Kaya N, Van Toai TT, Lohnes DG, Chung J, Spetch JE (1999) An integrated genetic linkage map of the soybean genome. Crop Sci 39:1464–1490

Dissanayaka A, Rodriguez TO, Di S, Yan F, Githiri SM, Rodas FR, Abe J, Takahashi R (2016) Quantitative trait locus mapping of soybean maturity gene *E5*. Breed Sci 66(3):407–415

Dong Y, Zhao L, Liu B, Wang Z, Jin Z, Sun H (2004) The genetic diversity of cultivated soybean grown in China. Theor Appl Genet 108:931–936

Fehr WR (1987) Breeding methods for cultivar. Development:249–293

Fowler S, Lee K, Onouchi H, Samach A, Richardson K, Morris B, Coupland G, Putterill J (1999) GIGANTEA: a circadian clock controlled gene that regulates photoperiodic flowering in Arabidopsis and encodes a protein with several possible membrane-spanning domains. EMBO J 18:4679–4688

Fukuda Y (1933) Cytogenetical studies on the wild and cultivated Manchurian soybeans (*Glycine* L.). Jpn J Bot 6:489–506

Funatsuki H, Kawaguchi K, Matsuba S, Sato Y, Ishimoto M (2005) Mapping of QTL associated with chilling tolerance during reproductive growth in soybean. Theor Appl Genet 111:851–861

Gai J (1996) Soybean breeding. In: Gai J (ed) Plant breeding-crop science. China Agriculture Press, Beijing, China

Goldblatt P (1981) Cytology and the phylogeny of Leguminosae. In: Polhill RM, Raven PH (eds) Advances in legume systematics, part 2. Royal Botanic Gardens, Kew, United Kingdom, pp 427–463

Guo J, Wang Y, Song C, Zhou J, Qiu L, Huang H, Wang Y (2010) A single origin and moderate bottleneck during domestication of soybean (*Glycine max*): implications from microsatellites and nucleotide sequences. Ann Bot 106:505–514

Haley SD, Afanador LK, Miklas PN, Stavely JR, Kelly JD (1994) Heterogeneous inbred populations are useful as sources of near isogenic lines for RAPD marker localization. Theor Appl Genet 88:337–342

Han YP, Zhao X, Liu DY, Li YH, Lightfoot DA, Yang ZJ, Zhao L, Zhou G, Wang ZK, Huang L, Zhang Z, Qiu L, Zheng H, Li W (2016) Domestication footprints anchor genomic regions of agronomic importance in soybeans. New Phytol 209:871–884

Hayama R, Agashe B, Luley E, King R, Coupland G (2007) A circadian rhythm set by dusk determines the expression of FT homologs and the short-day photoperiodic flowering response in Pharbitis. Plant Cell 19:2988–3000

Heatherly LG, Elmore RW (2004) Managing inputs for peak production. In: Soybeans: improvement, production and uses eds by Boerma HR and Specht JE. 3rd Agronomy N-16, ASA, CSSA, SSSA, Madison, 451–536

Heatherly LG, Smith JR (2004) Effect of soybean stem growth habit on height and node number after beginning bloom in the midSouthern USA. Crop Sci 44:1855–1858

Ho P-T (1975) Cradle of the East: an enquiry into the indigenous origins of techniques and ideas of neolithic and early historic China, 5000–1000 B.C. Chinese University of Hong Kong, Hong Kong, China

Hsu CY, Liu Y, Luthe DS, Yuceer C (2006) Poplar FT2 shortensthe juvenile phase and promotes seasonal flowering. Plant Cell 18:1846–1861

Hymowitz T (1970) On the domestication of the soybean. Econ Bot 24:408–421

Hymowitz T, Kaizuma N (1981) Soybean protein electrophoresis profiles from 15 Asian countries or rwegions: hypothesis on paths of dissemination of the soybean from China. Econ Bot 35:10–23

Hyten DL, Song Q, Zhu Y, Choi I-Y, Nelson RL, Costa JM, Specht JE, Shoemaker RC, Cregan PB (2006) Impacts of genetic bottlenecks on soybean genome diversity. Proc Nat Acad Sci U S A 103:16666–16671

Igasaki T, Watanabe Y, Nishiguchi M, Kotoda N (2008) The FLOWERING LOCUS T/TERMINAL FLOWER 1 family in Lombardy poplar. Plant Cell Physiol 49:291–300

Jung C, Müller AE (2009) Flowering time control and applications in plant breeding. Trends Plant Sci 14:563–573

Kim MY, Lee S, Van K, Kim T-H, Jeong S-C, Choi I-Y, Kim D-S, Lee Y-S, Park D, Ma J (2010) Whole-genome sequencing and intensive analysis of the undomesticated soybean (*Glycine soja* Sieb. And Zucc.) genome. Proc Nat Acad Sci U S A 107:22032–22037

Koornneef M, Alonso-Blanco C, Blankestijn-de Vries H, CHanhartand CJ, Peeters AJ (1998) Genetic interactions among late-flowering mutants of Arabidopsis. Genetics 148:885–892

Lee Y, Park T (2006) Origin of legumes cultivation in Korean peninsula by view point of excavated grain remains and genetic diversity of legumes. Korean Agric Hist Assoc 5:1–31

Lee G-A, Crawford GW, Liu L, Sasaki Y, Chen X (2011) Archaeological soybean (*Glycine max*) in East Asia. PLoS One 6:e26720

Levy YY, Dean C (1998) The transition to flowering. Plant Cell 10:1973–1989

Li J, Niwa M (1996) Microsatellite Dna markers linked to a gene controlling days to flowering in soybean (*Glycine max*) under short day conditions. Breed Sci 46:81–84

Li YH, Li W, Zhang C, Yang L, Chang RZ, Gaut BS, Qiu LJ (2010) Genetic diversity in domesticated soybean (*Glycine max*) and its wild progenitor (*Glycine soja*) for simple sequence repeat and single-nucleotide polymorphism loci. New Phytol 188:242–253

Li Y-h, Zhao S-c, Ma J-x, Li D, Yan L, Li J, Qi X-t, Guo X-s, Zhang L, He W-m (2013) Molecular footprints of domestication and improvement in soybean revealed by whole genome resequencing. BMC Genom 14:579

Li Y-h, Zhou G, Ma J, Jiang W, Jin L-g, Zhang Z, Guo Y, Zhang J, Sui Y, Zheng L (2014) De novo assembly of soybean wild relatives for pan-genome analysis of diversity and agronomic traits. Nat Biotechnol 32:1045–1052

Lifschitz E, Eviatar T, Rozman A, Shalit A, Goldshmidt A, Amsellem Z, Alvarez JP, Eshed Y (2006) The tomato FTortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli. Proc Natl Acad Sci U S A 103:6398–6403

Liu B, Abe J (2010) QTL mapping for photoperiod insensitivity of a Japanese soybean landrace Sakamotowase. J Hered 101:251–256

Liu B, Fujita T, Yan ZH, Sakamoto S, Xu DH, Abe J (2007) QTL mapping of domestication related traits in soybean (*Glycine max*). Ann Bot (Lond) 100:1027–1038

Liu B, Kanazawa A, Matsumura H, Takahash R, Harada K, Abe J (2008) Genetic redundancy in soybean photo responses associated with duplication of the phytochrome a gene. Genetics 180:995–1007

Liu B, Watanabe S, Uchiyama T, Kong F, Kanazawa A, Xia Z, Nagamatsu A, Arai M, Yamada T, Kitamura K, Masuta C, Harada K, Abe J (2010) The soybean stem growth habit gene *Dt1* is an ortholog of Arabidopsis TERMINAL FLOWER1. Plant Physiol 153:198–210

Mansur LM, Lark KG, Kross H, Oliveira A (1993) Interval mapping of quantitative trait loci for reproductive, morphological, and seed traits of soybean (*Glycine max* L.). Theor Appl Genet 86:907–913

McBlain BA, Bernard RL (1987) A new gene affecting the timeof flowering and maturity in soybean. J Hered 78:160–162

Miyasaka S, Vernetti FJ, Sediyama T, Medina JC (1981) Titulo do capitulo? A Soja no Brasil. ITAL, Campinas, pp 261–278

Mizoguchi T, Wright L, Fujiwara S, Cremer F, Lee K, Onouchi H, Mouradov A, Fowler S, Kamada H, Putterill J, Coupland G (2005) Distinctroles of GIGANTEA in promoting flowering and regulatingcircadian rhythms in Arabidopsis. Plant Cell 17:2255–2270

Molnar SJ, Rai S, Charette M, Cober ER (2003) Simple sequence repeat (SSR) markers linked to *E1*, *E3*, *E4*, and *E7* maturity genes in soybean. Genome 46:1024–1036

Orf JH, Chase K, Jarvik T, Mansur LM, Cregan PB, Adler FR, Lark KG (1999) Genetics of soybean agronomic traits: I Comparison of three related recombinant inbred populations. Crop Sci 39:1642–1651

Parvez AQ, Gardner FP (1987) Daylength and sowing date responses of soybean lines with "juvenile" trait. Crop Sci 27:305–310

Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, Flintham JE, Beales J, Fish LJ, Worland AJ, Pelica F, Sudhakar D, Christou P, Snape JW, Gale MD, Harberd NP (1999) Green revolution' genes encode mutant gibberellin response modulators. Nature 400:256–261

Ping J, Liu Y, Sun L, Zhao M, Li Y, She M, Sui Y, Lin F, Liu X, Tang Z, Nguyen H, Tian Z, Qiu L, Nelson RL, Clemente TE, Specht JE, Ma J (2014) *Dt2* is a gain-of-function MADS-domain factor gene that specifies semi determinacy in soybean. Plant Cell 26:2831–2842

Saindon G, Voldeng HD, Beversdorf WD, Buzzell RI (1989) Genetic control of long daylength response in soybean. Crop Sci 29:1436–1439

Saindon G, Voldeng HD, Beversdorf WD, Buzzell RI (1989b) Genetic control of long daylength response in soybean. Crop Sci 29:1436–1439

Salvi S, Tuberosa R (2005) To clone or not to clone plant QTLs: present and future challenges. Trends Plant Sci 10:297–304

Samanfar B, Molnar SJ, Charette M, Schoenrock A, Dehne F, Golshani A, Belzile F, Cober ER (2017) Mapping and identification of a potential candidate gene for a novel maturity locus, *E10*, in soybean Theor Appl genet. 2017. Feb 130(2):377–390

Shannon S, Meeks-Wagner DR (1991) A mutation in the Arabidopsis TFL1 gene affects inflorescence meristem development. Plant Cell 3:877–892

Shimamoto Y, Abe J, Gao Z, Gai JY, Thseng FS (2000) Characterizing the cytoplasmic diversity and phyletic relationship of Chinese landraces of soybean, *Glycine max*, based on RFLPs of chloroplast and mitochondrial DNA. Genet Resour Crop Evol 47:611–617

Shultz JL, Kurunam D, Shopinski K, Iqbal MJ, Kazi S, Zobrist K, Bashir R, Yaegashi S, Lavu N, Afzal AJ, Yesudas CR, Kassem MA, Wu C, Zhang HB, Town CD, Meksem K, Lightfood DA (2006) The soybean genome database (SoyGD): a browser for display of duplicated polyploid, regions and sequence tagged site on the integrated physical and genetic maps of *Glycine max*. Nucl Acids Res 34(Database iss):D758–D765

Shultz JL, Kazi S, Bashir R, Afzal AJ, Lightfood DA (2007) The development of BAC-end sequence based microsatellite markers and placement in the physical and genetic maps of soybean. Theor Appl Genet 114:1081–1090

Specht JE, Chase K, Macrander M, Graef GL, Chung J, Markwell JP, Germann M, Orf JH, Lark KG (2001) Soybean response to water: A QTL analysis of drought tolerance. Crop Sci 41:493–509

Stewart DW, Cober ER, Bernard RL (2003) Modeling genetic effects on the photothermal response of soybean phonological development. Agron J 95:65–70

Thakare D, Kumudini S, Dinkins RD (2011) The alleles at the *E1*locus impact the expression pattern of two soybean FT-like genesshown to induce flowering in Arabidopsis. Planta 234:933

Tian Z, Wang X, Lee R, Li Y, Specht JE, Nelson RL, McClean PE, Qiu L, Ma J (2010) Artificial selection for determinate growth habit in soybean. Proc Natl Acad Sci U S A 107:8563–8568

Tsubokura Y, Watanabe S, Xia Z, Kanamori H, Yamagata H, Kaga A, Harada K (2013) Natural variation in the genes responsible for maturity loci *E1*, *E2*, *E3* and *E4* in soybean. Ann Bot 113:429–441

Tsubokura Y, Watanabe S, Xia Z, Kanamori H, Yamagata H, Kaga A, Katayose Y, Abe J, Ishimoto M, Harada K (2014) Natural variation in the genes responsible for maturity loci *E1*, *E2*, *E3* and *E4* in soybean. Ann Bot (Lond) 113:429–441

Valliyodan B, Dan Q, Patil G, Zeng P, Huang J, Dai L, Chen C, Li Y, Joshi T, Song L, Vuong Tri D, Musket T, Xu D, Shannon G, Shifeng C, Liu X, Nguyen HT (2016) Landscape of genomic diversity and trait discovery in soybean. Sci Rep 6:23598

Wang L, Wang J (1992) Soybean genetics and breeding. Science press, Beijing, China

Watanabe S, Tajuddin T, Yamanaka N, Hayashi M, Harada K (2004) Analysis of QTLs for reproductive development and seed quality traits in soybean using recombinant inbred lines. Breed Sci 54:399–407

Watanabe S, Hideshima R, Xia Z, Tsubokura Y, Sato S, Nakamoto Y, Yamanaka N, Takahashi R, Ishimoto M, Anai T, Tabata S, Harada K (2009) Map-based cloning of the gene associated with the soybean maturity locus *E3*. Genetics 182:1251–1262

Watanabe S, Xia Z, Hideshima R, Tsubokura Y, Sato S, Yamanaka N, Takahashi R, Anai T, Tabata S, Kitamura K, Harada K (2011) A map based cloning strategy employing a residual heterozygous line reveals that the GIGANTEA gene is involved in soybean maturity and flowering. Genetics 188:395–407

Woodworth CM (1932) Genetics and breeding in the improvement of the soybean

Xia Z, Watanabe S, Yamada T, Tsubokura Y, Nakashima H, Zhai H, Anai T, Sato S, Yamazaki T, Lu S, Wu H, Tabata S, Harada K (2012) Positional cloning and characterization reveal the molecular basis for soybean maturity locus *E1* that regulates photoperiodic flowering. Proc Natl AcadSci USA 109:E2155

Xu D, Abe J, Gai J, Shimamoto Y (2002) Diversity of chloroplast DNASSRs in wild and cultivated soybeans: evidence for multiple origins of cultivated soybean. Theor Appl Genet 105:645–653

Xu M, Xu Z, Liu B, Kong F, Tsubokura Y, Watanabe S, Xia Z, Harada K, Kanazawa A, Yamada T, Abe J (2013) Genetic variation in four maturity genes affects. BMC Plant Biol 13:91. https://doi.org/10.1186/1471-2229-13-91

Xu M, Yamagishi N, Zhao C, Takeshima R, Kasai M, Watanabe S, Kanazawa A, Yoshikawa N, Liu B, Yamada T, Abe J (2015) The soybean-specific maturity gene *E1* family of floral repressors controls night-break responses through down-regulation of FLOWERING LOCUS Torthologs. Plant Physiol 168:1735–1746

Yamanaka N, Ninomiya S, Hoshi M, Tsubokura Y, Yano M, Nagamura Y, Sasaki T, Harada K (2001) An informative linkage map of soybean reveals QTLs for flowering time, leaflet morphology and regions of segregation distortion. DNA Res 8:61–72

Yamanaka N, Watanabe S, Toda K, Hayashi M, Fuchigami H, Takahashi R, Harada K (2005) Fine mapping of the FT1 locus for soybean flowering time using a residual heterozygous linederived from a recombinant inbred line. Theor Appl Genet 110:634–639

Zhai H, Lü S, Liang S, Wu H, Zhang X, Liu B, Kong F, Yuan X, Li J, Xia Z (2014a) GmFT4, a homolog of FLOWERING LOCUS T, is positively regulated by *E1* and functions as a flowering repressor in soybean. PLoS One 9:e89030

Zhai H, Lu S, Wang Y, Chen X, Ren H, Yang J, Cheng W, Zong C, Gu H, Qiu H, Wu H, Zhang X, Cui T, Xia Z (2014b) Allelic variations at four major maturity E genes and transcriptional abundance of the *E1* gene are associated with flowering time and maturity of soybean cultivars. PLoS One 9(5):e97636

Zhou Z, Jiang Y, Wang Z, Gou Z, Lyu J, Li W, Yu Y, Shu L, Zhao Y, Ma Y (2015) Resequencing 302 wild and cultivated accessions identifies genes related todomestication and improvement in soybean. Nat Biotechnol 33:408–414

Chapter 25
Arsenic Accumulation, Compartmentation, and Complexation in *Arthrocnemum indicum*

Dhouha Belhaj Sghaier, Sílvia Pedro, Bernardo Duarte, Mário Diniz, Isabel Caçador, and Noomene Sleimi

Contents

Abstract After the use by a wide range of activities and applications, and/or after making available by accidental sources, the trace metal elements remain as a major contaminant in the main environmental compartments including soils. Very complex systems were evolved by plants which offered a control of the adsorbed and the accumulated metals. Researches have been directed to upgrade the understanding of the plant tolerance process with high arsenic (As) accumulation outside consider-

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able metabolic deterioration. The review of the research results presented here may be helpful to figure out the detoxification mechanisms that point out tolerance in *Arthrocnemum indicum*.

Keywords Arsenic · Accumulation · Cellular compartmentation · Detoxification · *Arthrocnemum indicum*

25.1 Introduction

The arid zone of the developing countries needed the treatment facilities to avoid the wastewater charges containing salt and heavy metals in agricultural soil (Helal et al. 1999). Arsenic (As) toxifies humans, animals, and plants and as a result, contaminated soil by As is a worldwide problem. As appeared in the environment through human action (Vromman et al. 2016) and affects agricultural yield through disturbing the expansion, behavior, and living of the plants (Sghaier et al. 2015).

In fact, it was reported that metals have an effect to provoke phytotoxicity originates from their solid attraction to the thiol (S-H) groups of the proteins. Besides, the extent of the plant's response to As stress depends not only on its intensity but also its duration (Vromman et al. 2016). Thus, to mitigate their deleterious effects, the plants develop various physiological and biochemical mechanisms such as the extrusion of toxic ions, the reduced uptake of ions and the chelating harmful ions by proteins linking metals are the suitable tools adjusted by plants to reduce the adverse effects of the metal poisonous (Briat 2010). In fact, understanding how the plants accumulate and store the heavy metals, is basic to select the suitable species used for the phytomanagement (Montargès-Pelletier et al. 2008). In Zn and Ni hyperaccumulator plants, it has been demonstrated that the compartmentation at the cellular plays an important role for the detoxification of these metals (Frey et al. 2000; Küpper et al. 2001). Despite the harmful consequences of As, some species are disposed to resist in As contaminated site (Wenzel 2013). It is likely that the cellular/subcellular compartmentation level is a key factor in the detoxification of As in the plants species (Hall 2002; Leitenmaier and Küpper 2013). In our previous works, Tamarix gallica demonstrated that the As was distributed into the different component like the cell wall and the intracellular/soluble fraction reducing their toxic effect (Sghaier et al. 2016).

Arthrocnemum indicum L. is a succulent perennial shrub, from family Chenopodiaceae widely encountered in salt marshes (Rabhi et al. 2009). The halophyte *A. indicum* is particularly interesting because it is one of the rare species that has proved extremely well adapted to hypersaline and harsh environmental conditions (Redondo-Gómez et al. 2010). This chapter will be specifically focused on the mechanisms contributing to the As subcellular localization and the rate of accumulation inside this halophyte in the leaves and the roots.

25.2 Accumulation of As

An elevated metal dose was observed in the roots more than in the leaves among treatments (Table 25.1). The translocation factor (TF) is designated as metal transferring/moving from the roots to the leaves; it ranged from 0.26 ± 0.01to 0.45 ± 0.04, indicating that the treatment with the minimum As dose had the elevated TF. The adverse trend was detected for the combined stress, the highest TF present in the elevated dose of metal combined with salt (Table. 25.1).

In the present study, the translocation factor was below than 1. In fact, the translocation TF is considered as the mechanism whereby metal ions absorbed by the belowground part are directed to the aboveground part and to the intracellular compartment (Revathi and Subhashree 2013). Previous studies demonstrated that *Zea mays*, *Lolium perenne*, *Brassica napus*, and *Helianthus annuus* accumulated As in the roots and not in the aerial tissues resulting in a translocation factor below 1 (Gulz et al. 2005; Gupta et al. 2008; Wu et al. 2011).

Halophytes seem to have a process limiting the transferring of the captivated metals to the aboveground parts, and most trace metals are stored in the belowground parts (Yim and Tam 1999). A weak arsenic mobilization to the aerial parts of plants has been documented (Lizama et al. 2011); in our previous studies, *Tamarix gallica* showed also an As TF below 1 (Sghaier et al. 2016) implying a conservation of the metal in their lengthy range transfer, as a resistance mechanism adopted by As accumulator species. The As restriction translocations to the shoots by internal fence are controlled to preserve the aerial part (Quaghebeur and Rengel 2004). Arsenic is distinguished by a weak mobility concerning the translocation from the roots to the shoots; an arsenate-tolerant genotype revealed a weak rate of phosphate and arsenate absorption than the non-tolerant genotype and also exhibited a lack of the strong affinity absorption mechanism (Indriolo et al. 2010). The impaired anion uptake system was attributed to arsenate tolerance (Meharg and Hartley-Whitaker 2002). The arsenic restricted translocation might be induced as a consequence to the arsenic reduced to the arsenite in the roots, pursued by an association with thiols, and therefore will be confined in the root vacuoles (Zhao et al. 2009). Further, it was reported that *Holcus lanatus* tolerance to arsenate needed both adaptive elimination of the strong affinity transport mechanism and production of constitutive phytochelatin (PC) (Hartley-Whitaker et al. 2001).

Table 25.1 Translocation factors (TF) for metals within *Arthrocnemum indicum* (*n* = 3; average ± SD)

	Arsenic					
	200 µM	500 µM	800 µM	200 µM + NaCl	500 µM + NaCl	800 µM + NaCl
TF	0.43 ± 0.03	0.37 ± 0.03	0.45 ± 0.04	0.26 ± 0.01	0.36 ± 0.07	0.34 ± 0.02

25.3 Cellular Compartmentalization of As

Arsenic was mainly bound to the aqueous fraction in the leaves (Fig. 25.1a), varying from 50.97 ± 0.4% to 55.18 ± 0.9%, and identical doses were observed in the polysaccharides and the ethanolic fraction. In the roots, it was bound to the aqueous and the ethanolic fraction (Fig. 25.1b), with concentrations ranging from 31.77 ± 0.7% to 49.69 ± 1.2% and 33.61 ± 0.2% to 48.09 ± 0.4%, respectively; the variation of the

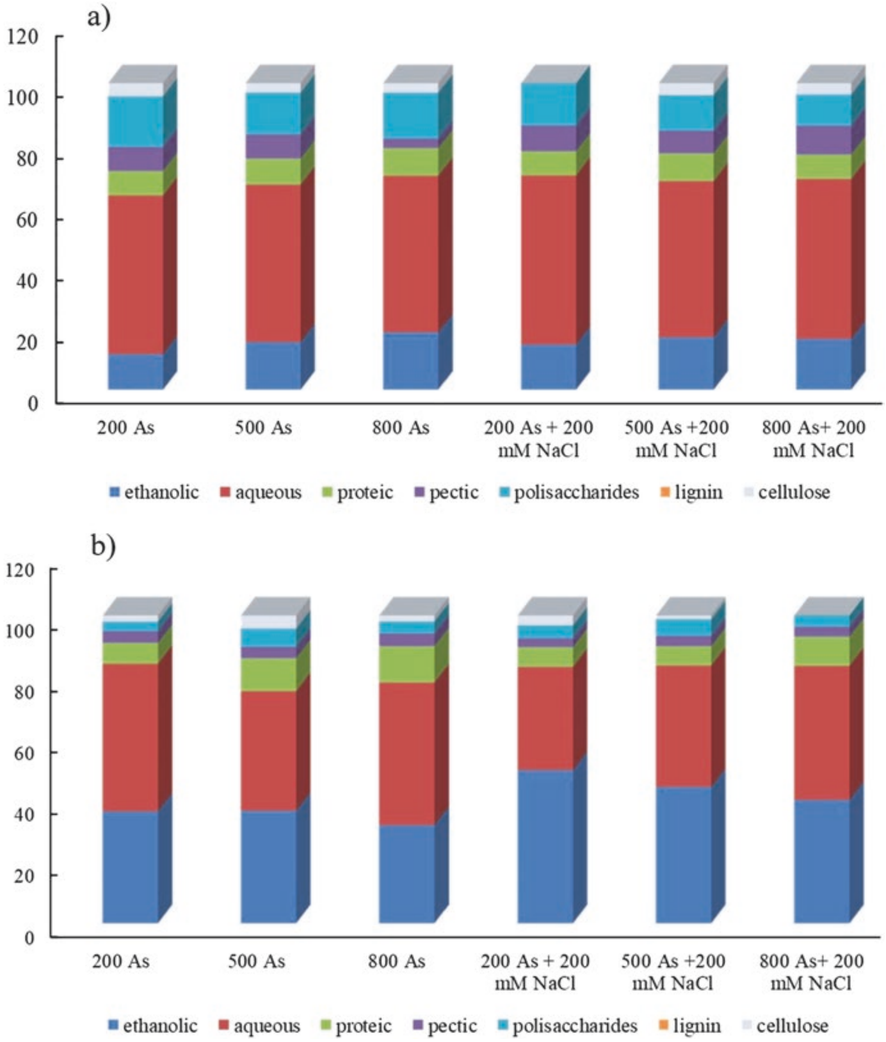

Fig. 25.1 Metal concentrations (average %; n = 3) in different fractions of *Arthrocnemum indicum*. Leaf (**a**) and root (**b**) fractions, from bottom to top, are ethanolic, aqueous, proteic, pectin, polysaccharides, lignin, and cellulose

fractions was less obvious (Fig. 25.1b) (with total miss in the lignin fraction in the roots and the leaves) (Fig. 25.1).

In the treatment without salt, the global of As in the leaves presented a different behavior in As compartmentation: the intracellular/soluble fraction showed powerful differences between treatments ($p < 0.05$), showing a rising accumulation with a pike below the 800 μM As dose. Inner the soluble fraction, the variation appeared in the ethanolic fraction when the elevated dose was tested. Otherwise, the As related to the proteins did not show a major difference (Fig. 25.2a). In the cell wall

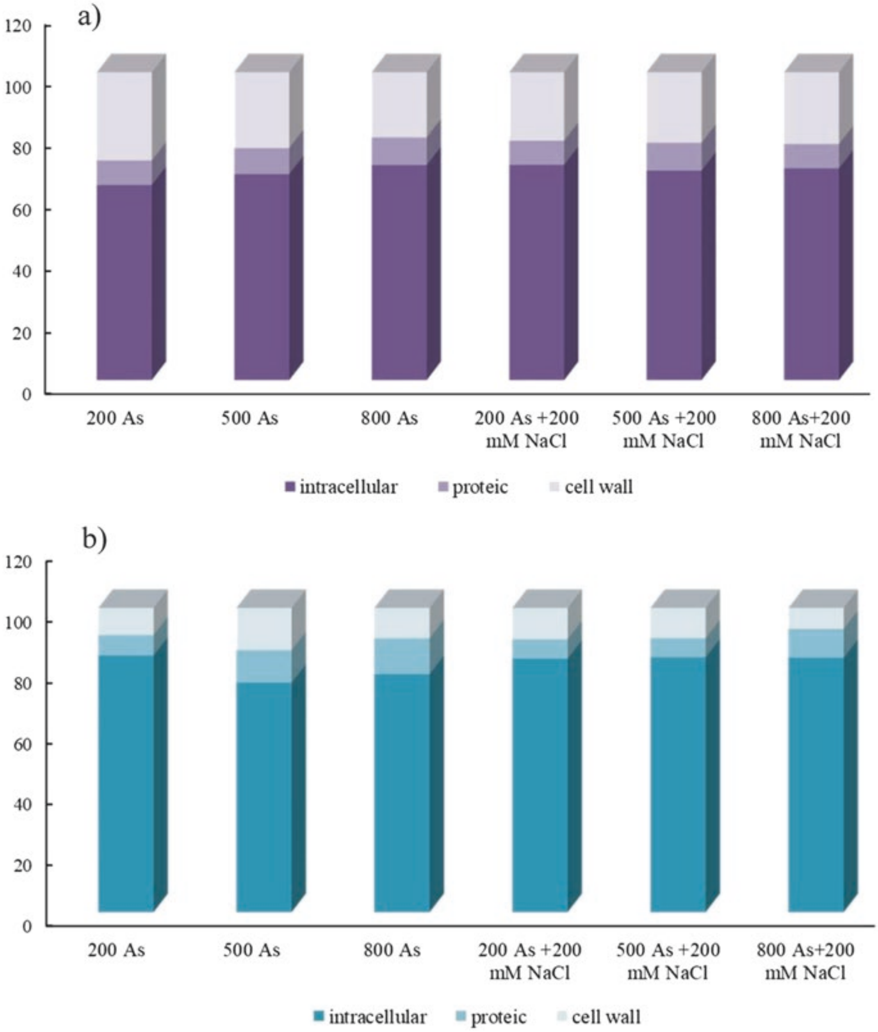

Fig. 25.2 Metal concentration (average %; n = 3) located intracellularly (ethanolic + aqueous fraction), on the proteic fraction and on the cell wall (pectin + polysaccharides + lignin + cellulose fractions) of *Arthrocnemum indicum*: leaves (**a**) and roots (**b**)

component, the change was noteworthy between extreme doses (Fig. 25.2a); it was clear to notice that when the elevated dose of As was applied in the medium (800 μM), a decline in the As accumulation in the pectin fraction was detectable. Contrary to what was detected in the leaves, the global As dose in the roots demonstrated a major difference with rising treatment doses: the elevated accumulation was observed when 500 μM As was provided in the medium and an expansion was detected in the As linked to cell wall components, but declined when the elevated dose was utilized. The highest As accumulation in the polysaccharides and the cellulose fraction was observed at 500 μM As (Fig. 25.2b). Contrarily, a decrease in As accumulation in the soluble/intracellular fraction was observed when 500 μM was applied in the medium followed by an augmentation at 800 μM As. A rise in Al accumulation across treatment was presented in the proteic fraction (Fig. 25.2b).

In the combined stress, the total As accumulation in the leaves was different to the observed above; no difference showed across treatments ($p > 0.05$). Nonetheless, some changes were observed in comparison to the treatments without NaCl: the As accumulation in the cellulose fraction was determinate in the highest doses (500 and 800 μM) and was absent at lowest concentration. Additionally, a decrease in As accumulation was detected in the polysaccharide fraction. There was too a rising in the ethanolic fraction with huge variation among the two extreme concentrations, 200 μM and 800 μM ($p < 0.05$) (Fig. 25.1a). In the roots, in the soluble fraction there was no difference marked with rising treatment concentrations; the only difference was observed between the extreme values in the ethanolic and the aqueous fraction ($p < 0.05$) (Fig. 25.1b). The cell wall components accumulated less As at the highest treatment (800 μM), particularly in the cellulose fraction where no As was found at 800 μM; the pectic fraction revealed a maximum amassing from 200 to 500 μM As, yet continued constant, while further metal was provided in the medium. Both with and without NaCl added, the proteic fraction retained more stable arsenic (Fig. 25.2b). In the treatment without salt, the changes were observed from one treatment to another, whereas with the addition of the salt the greatest increase was detected in 800 μM As (Fig. 25.2b).

The plant ability to withstand in spite of the accumulation of elevated metal doses in their tissues is largely overcame by metal chelation in nontoxic form and its compartmentation in the cell walls, the vacuoles, and the non-photosynthetic tissues (Ghnaya et al. 2013; Cappa and Pilon-Smits 2014). Using a sequential extraction and in different solvents, we obtain the various forms of accumulated As. The As speciation in the tissues indicated that the considerable form of metal accumulation in *A. indicum* was obtained by 80% ethanol and aqueous relative to the intracellular/soluble fraction containing the vacuole and the cytoplasm (Fourati et al. 2016). Similarly, a large fraction of As in *Pityrogramma calomelanos* was found as water extractable (up to 93%) (Francesconi et al. 2002). Overall, As compartmentation offered an outstanding difference among roots and leaves, with almost metal linked to the soluble fraction (up to 80% in the roots and up to 60% in the leaves) with or without NaCl. Further, more than 20% of As in the leaves was cell wall related with a slight decrease in the roots (10%). Arsenic compartmentation in the leaves was more shared; the protein and the soluble fractions together contained more than 30% of total As. In advanced researches, to decrease metal toxicity, the metals are stored in the plant in distinct cell compartments (Sousa et al. 2008; Reboreda and Caçador 2007) and confined in the vacuoles and in the cell wall (Sousa et al. 2008). The rate of the subcellular Ni compartmentalization has a crucial potency in the tolerance (Küpper et al. 2001).

Thus, this study revealed that As bound essentially to intracellular fraction. Since the soluble fraction includes the liquids from the cytoplasm and the vacuole, vacuolar sequestration was proposed as a prevention mechanism to build metal in the cytosol (Küpper et al. 2001). Vacuoles are recognized as a powerful location of trace metal amassing (Wu et al. 2005). It has been shown that free metal ion chelators in plant cells, such as phytochelatins, organic anions, and inorganic anions, allow cells to handle higher external metal concentrations (Zaier et al. 2010; Ghnaya et al. 2013). The synthesis of phytochelatins disabled the metal ion toxicity; then the production of the complexes metal phytochelatin is a common process where the homeostasis of trace metals is in plants (Zenk 1996).

Nonetheless, the compartmentation model is considered as species and metal specific. For example, Ni, Cd, and Zn are accumulated in the vacuoles of epidermis cells (Küpper et al. 2001; Psaras et al. 2000). In *A. indicum*, at elevated external doses, the proteic fraction has become important in the leaves and the roots, especially in the metal treatment. The same observation was obtained in *T. gallica*'s roots which demonstrated that the proteic fraction had a great importance in the compartmentation of As (Sghaier et al. 2016). The researches on Hybanthus floribundus demonstrated that the cell wall is treated as the early obstacle opposing the access of the harmful metals in the cell and could thus to cover the cytoplasm by blocking the cross-linking of the metal ions (Bidwell et al. 2004). Besides, it is demonstrated that 70–90% of trace metals were found in the cell walls and Cd was interrupted to access the cytoplasm in *Athyriumyo koscense* (Xiong et al. 2009), *Lactuca sativa* (Ramos et al. 2002), and *Bechmeria nivea* (Wang et al. 2008). This result was mentioned in the research relative of *Halimione portulacoides* which proved that the half of the total cellular Cd was bound to the cell wall (Sousa et al. 2008). Similarly, it is demonstrated that Cd^{2+} attached to the pectin and the cellulose which are the dominant elements of the wall (Reboreda and Caçador 2007; Qiu et al. 2011). Further, it was reported that the powerful capacity of *Sesuvium portulacastrum* to link Ni in the cell walls might reveal the tolerance to this metal faced to *Cakile maritima* (Fourati et al. 2016). Arsenic related to cell wall pectin could not be a fundamental tolerance process (Krzesłowska 2011). In this study, the As was not stored in the cellulose and in the pectin fraction in the leaves (less than 3% of total As), regardless of the treatment applied. While the polysaccharide fraction was the preferred attached location in the leaves.

25.4 Conclusion

The translocation restriction into the shoots and the metals linking to the cell wall are recognized as a process for non-hyperaccumulator plants (Wagner 1993; Grant et al. 1998).

As related to the soluble fraction and the cell wall can be an effective mechanism for blocking the amassing in the cytoplasm and also its toxicity to the metabolic reactions of the plants. According to these data, we conclude that the vacuoles and the cell wall are included in the As tolerance process to cover the active metabolic cellular compartment from harmful doses, and various approaches are distinctly implicated relying on the elements. This physiological study proposes the ability of *A. indicum* to be used for rehabilitation of As-contaminated soils.

References

Bidwell SD, Crawford SA, Sommer-Knudsen J et al (2004) Sub-cellular localization of Ni in the hyperaccumulator, *Hybanthus floribundus* (Lindley) F. Muell. Plant Cell Environ 27:705–716

Briat JF (2010) Arsenic tolerance in plants: "pas de deux" between phytochelatin synthesis and ABCC vacuolar transporters. PNAS 107:20853–20854

Cappa JJ, Pilon-Smits EA (2014) Evolutionary aspects of elemental hyperaccumulation. Planta 239:267–275

Fourati E, Wali M, Vogel-Mikuš K et al (2016) Nickel tolerance, accumulation and subcellular distribution in the halophytes *Sesuvium portulacastrum* and *Cakile maritima*. Plant Physiol Biochem 108:295–303

Francesconi K, Visootiviseth P, Sridokchan W et al (2002) Arsenic species in an arsenic hyperaccumulating fern, *Pityrogramma calomelanos*: potential phytoremediator of arsenic-contaminated soil. Sci Total Environ 284:27–35

Frey B, Zierold K, Brunner I (2000) Extracellular complexation of cd in the Hartig net and cytosolic Zn sequestration in the fungal mantle of Picea abies–*Hebeloma crustuliniforme* ectomycorrhizas. Plant Cell Environ 23:1257–1265

Ghnaya T, Zaier H, Baioui R et al (2013) Implication of organic acids in the long-distance transport and the accumulation of lead in *Sesuvium portulacastrum* and *Brassica juncea*. Chemosphere 90:1449–1454

Grant CA, Buckley WT, Bailey LD et al (1998) Cadmium accumulation in crops. Can J Plant Sci 78:1–17

Gulz PA, Gupta SK, Schulin R (2005) Arsenic accumulation of common plants from contaminated soils. Plant Soil 272:337–347

Gupta DK, Tripathi RD, Mishra S et al (2008) Arsenic accumulation in root and shoot Vis-a-Vis its effects on growth and level of phytochelatins in seedlings of *Cicer arietinum* L. J Environ Biol 29:281–286

Hall JL (2002) Cellular mechanisms for heavy metal detoxification and tolerance. J Exp Bot 53:1–11

Hartley-Whitaker J, Ainsworth G, Vooijs R et al (2001) Phytochelatins are involved in differential arsenate tolerance in *Holcus lanatus*. Plant Physiol 126:299–306

Helal HM, Upenov A, Issa GJ (1999) Growth and uptake of cd and Zn by *Leucaena leucocephala* in reclaimed soils as affected by NaCl salinity. J Plant Nutr Soil Sci 162:589–592

Indriolo E, Na G, Ellis D et al (2010) A vacuolar arsenite transporter necessary for arsenic tolerance in the arsenic hyperaccumulating fern *Pteris vittata* is missing in flowering plants. Plant Cell 22:2045–2057

Krzesłowska M (2011) The cell wall in plant cell response to trace metals: polysaccharide remodeling and its role in defense strategy. Acta Physiol Plant 33:35–51

Küpper H, Lombi E, Zhao F et al (2001) Cellular compartmentation of nickel in the hyperaccumulators *Alyssum lesbiacum, Alyssum bertolonii* and *Thlaspi goesingense*. J Exp Bot 52:2291–2300

Leitenmaier B, Küpper H (2013) Compartmentation and complexation of metals in hyperaccumulator plants. Front Plant Sci 4:374

Lizama K, Fletcher TD, Sun G (2011) Removal processes for arsenic in constructed wetlands. Chemosphere 84:1032–1043

Meharg AA, Hartley-Whitaker J (2002) Arsenic uptake and metabolism in arsenic resistant and non resistant plant species. New Phytol 154:29–44

Montargès-Pelletier E, Chardot V, Echevarria G et al (2008) Identification of nickel chelators in three hyperaccumulating plants: an X- ray spectroscopic study. Phytochemistry 69:1695–1709

Psaras GK, Constantinidis T, Cotsopoulos B et al (2000) Relative abundance of nickel in the leaf epidermis of eight hyperaccumulators: evidence that the metal is excluded from both guard cells and trichomes. Ann Bot 86:73–78

Qiu Q, Wang Y, Yang Z et al (2011) Effects of phosphorus supplied in soil on subcellular distribution and chemical forms of cadmium in two Chinese flowering cabbage (*Brassica parachinensis* L.) cultivars differing in cadmium accumulation. Food Chem Toxicol 49:2260–2267

Quaghebeur M, Rengel Z (2004) Arsenic uptake, translocation and speciation in pho1 and pho2 mutants of *Arabidopsis thaliana*. Physiol Plant 120:280–286

Rabhi M, Hafsi C, Lakhdar A et al (2009) Evaluation of the capacity of three halophytes to desalinize their rhizosphere as grown on saline soils under nonleaching conditions. Afr J Ecol 47:463–468

Ramos I, Esteban E, Lucena JJ et al (2002) Cadmium uptake and subcellular distribution in plants of *Lactuca* sp. Cd-Mn interaction. Plant Sci 162:761–767

Reboreda R, Caçador I (2007) Halophyte vegetation influences in salt marsh retention capacity for heavy metals. Environ Pollut 146:147–154

Redondo-Gómez S, Mateos-Naranjo E, Andrades-Moreno L (2010) Accumulation and tolerance characteristics of cadmium in a halophytic cd-hyperaccumulator, *Arthrocnemum macrostachyum*. J Hazard Mater 184:299–307

Revathi S, Subhashree V (2013) Physiological and biochemical mechanisms of heavy metal tolerance. Int J Environ Sci 3:1339–1354

Sghaier DB, Duarte B, Bankaji I et al (2015) Growth, chlorophyll fluorescence and mineral nutrition in the halophyte *Tamarix gallica* cultivated in combined stress conditions: arsenic and NaCl. J Photochem Photobiol B Biol 149:204–214

Sghaier DB, Pedro S, Diniz MS et al (2016) Tissue localization and distribution of as and Al in the halophyte *Tamarix gallica* under controlled conditions. Frontiers Mar Sci 3:274

Sousa AI, Caçador I, Lillebø AI et al (2008) Heavy metal accumulation in *Halimione portulacoides*: Intra- and extra-cellular metal binding. Chemosphere 70:850–857

Vromman D, Lefèvre I, Šlejkovec Z et al (2016) Salinity influences arsenic resistance in the xerohalophyte *Atriplex atacamensis* Phil. Environ Exp Bot 126:32–43

Wagner GJ (1993) Accumulation of cadmium in crop plants and its consequences to human health. Adv Agron 51:173–212

Wang X, Liu Y, Zeng G et al (2008) Subcellular distribution and chemical forms of cadmium in *Bechmeria nivea* (L.) gaud. Environ Exp Bot 62:389–395

Wenzel WW (2013) Arsenic. In: Heavy Metals in Soils. Trace Metals and Metalloids in Soils and their Bioavailability. Alloway, B. J. (3rd Eds.). Springer, Dordrecht. 613 p

Wu FB, Dong J, Qian QQ et al (2005) Subcellular distribution and chemical form of cd and cd–Zn interaction in different barley genotypes. Chemosphere 60:1437–1446

Wu Z, Ren H, McGrath SP et al (2011) Investigating the contribution of the phosphate transport pathway to arsenic accumulation in Rice. Plant Physiol 157:498–508

Xiong J, An L, Lu H, Zhu C (2009) Exogenous nitric oxide enhances cadmium tolerance of rice by increasing pectin and hemicellulose contents in root cell wall. Planta 230:755–765

Yim MW, Tam NFY (1999) Effects of wastewater-borne heavy metals on mangrove plants and soil microbial activities. Mar Pollut Bull 39:179–186

Zaier H, Mudarra A, Kutscher D et al (2010) Induced lead binding phytochelatins in *Brassica juncea* and *Sesuvium portulacastrum* investigated by orthogonal chromatography inductively coupled plasma-mass spectrometry and matrix assisted laser desorption ionisation-time of flight mass spectrometry. Anal Chim Acta 671:48–54

Zenk MH (1996) Heavy metal detoxification in higher plants. Gene 179:21–30

Zhao FJ, Ma JF, Meharg AA et al (2009) Arsenic uptake and metabolism in plants. New Phytol 181:777–794

Chapter 26
Plant-Microbe Interactions under Adverse Environment

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Abstract Plants face a number of environmental stresses that affect the crop productivities, food quality and food safety worldwide. The environmental adversities including biotic and abiotic stresses alter physiological aspects, biochemical traits and molecular mechanisms of plants. The employment of pesticides, fertilizers and herbicides during agricultural practices leads to reduced soil fertilities and addition of pollutants into the environment. It is therefore advisable to use economical and environmentally friendly methods for sustainable agriculture. Soil microorganisms are considered to be the important candidates that provide the economically fascinating mode for plant protection during stressed conditions. They modulate plant growth through plethora of mechanisms by regulation of phytohormone levels, nutrient uptake, nitrogen fixation, phosphate solubilization, antioxidative defence expression, production of different secondary metabolites and siderophores. Furthermore, they also provide tolerance towards biotic stresses such as pathogenic organisms through activation of induced systemic resistance (ISR) and systemic acquired resistance (SAR) mechanisms in plants. The microbe interactions with plants are, therefore, most crucial in sustainable agriculture practices that replace conventional methods by biological methods. They contribute to improve plant characteristics and control plant diseases under changing environmental conditions without interfering in the functioning of ecosystem. So, the inclusive use of the soil microorganisms proves to be the potential technology for sustainable agriculture globally. The present chapter highlights the interactions of beneficial microbes with plants under adverse conditions and their mechanism of action for improvement of plant health.

Keywords Abiotic stresses · Biotic stresses · Reactive oxygen species · Rhizosphere · Phytopathogens

26.1 Introduction

The rapid industrialization and urbanization and use of different chemical pesticides and fertilizers have caused considerable environmental adversities and affected the fertility of soil and microbes inhabiting within them (Battisti and Naylor 2009; Youssef and Eissa 2014). Moreover, the abrupt use of different chemicals, insecticides, weedicides, fungicides, etc., has led to reduce the beneficial microbial populations from the soil. Since, substantial use of fertilizers alters soil pH and makes the minerals and other nutrients unavailable to plants, thereby reducing their productivities (Gupta et al. 2015a, b). There are huge losses of crop productivities due to pathogenic organisms and pests as well (Berendsen et al. 2012; Venkateshwaran et al. 2013). The pathogenic attack is further augmented by different conditions such as temperature, drought, heavy metals, salinity, flooding, etc. (Borneman and Becker 2007). Therefore, abiotic and biotic stresses together contribute towards global loss of agricultural productivities. These environmental stresses disturb morphology, physiology, biochemical traits and genetic attributes of plants (Chodak et al. 2015). The abrupt utilization of chemical fertilizers is increased for replenishment of mineral components such as nitrogen and phosphorous in soil for obtaining higher yields of crops that possess environmental hazard as well as economically unfeasible for the farmers (Pii et al. 2015). To preclude this problem, and for sustainable agricultural practices, the most possible approach is exploiting microbial communities such as PGPB (plant growth-promoting bacteria) and arbuscular mycorrhizal (AM) fungi that aid growth promotion in plants under all conditions (Kumar and Verma 2018). Different microbial genera associated with plant growth-promoting characteristics are *Pseudomonas*, *Bacillus*, *Burkholderia*, *Azotobacter*, *Enterobacter*, *Azospirillum*, *Klebsiella*, *Serratia*, *Variovorax*, etc., that improve growth and development of plants (Hayat et al. 2010; Kaymak 2010; Ahemad and Khan 2012). Many of these microbial diversities are able to tolerate abiotic stresses and resist pathogenic attack because of which they have been commercialized as biofertilizers and biopesticides (Vimal et al. 2017; Banerjee et al. 2010; Finkel et al. 2017). There are a number of direct and indirect mechanisms of growth promotion in plants possessed by microbes during stressful conditions (Ortíz-Castro et al. 2009). The direct microbe-mediated stress tolerance mechanism in plants occurs through synthesis of different phytohormones (auxins, gibberellins, cytokinins), ACC deaminase, N_2 fixation, production of siderophores and different secondary metabolites (Glick 2010; Mayak et al. 2004; Kaymak 2010). They also induce systemic resistance in plants during pathogenic attack and enhance mineralization, enzyme synthesis and phosphorous solubilization under different stressed conditions (Trivedi et al. 2005). Other indirect mechanisms mainly comprise of microbial use as biocontrol agents, antibiotic synthesis and chelation of iron and its complexes in rhizospheric zone (van Loon 2007). Rhizobacterial strains, namely, *Pseudomonas fluorescens* and *Bacillus subtilis*, are considered to be the most effective indirect stimulants in mediating stress tolerance in plants (Damayanti et al. 2007; Spaepen et al. 2007). Other characteristics such as nitrogen assimilation, nutrient acquisition and secretion of different antibiotics and enzymes also provide plant protection against different plant pathogens, thereby implicating their role in improving agricultural crop quality (Damayanti et al. 2007; Hayat et al. 2010; Mishra et al. 2010). Studies have revealed that PGPR exhibited antagonistic relationship with different pathogens through producing Fe chelators, antibiotics, pigments, HCN, glucanases and chitinases (Pathma et al. 2011; Zahir et al. 2004; Farooq et al. 2009). The growth-promoting microorganisms use multiple methods to assist plant growth and these multiple stimulants can become active simultaneously during stressful conditions (Farooq et al. 2009; Martínez-Viveros et al. 2010). The advancement in metabolomic and transcriptomic techniques provides new insights for studying different biosynthetic pathways encompassing regulation and biological control (Gupta et al. 2013). However, to be active in rhizosphere, the microbes must sustain in a significant population in that zone for longer time in order to positively regulate plant growth and development (Bhattacharyya and Jha 2012; Joshi and Bhatt 2011). It has been suggested that inoculation with beneficial microorganisms regulated hormonal balance and induced plant growth resistance against different phytopathogens (Spence and Bais 2015). In addition, they secrete metabolites such as rhizobitoxine and exopolysaccharides which induce many developmental processes in plants through inhibition of ethylene levels during stressed conditions (Złoch et al. 2016; Spence and Bais 2015; Vardharajula et al. 2011). Some of the PGPR are comprised of sigma factors that regulate the gene expression during extremities in order to overcome the adverse effects in plants (Ahmad et al. 2011; Gupta et al. 2013). The role of arbuscular mycorrhizal fungi assisted with the roots of higher plants has also been explored in stimulating growth and development of plants. They play an essential role in sustainable agriculture because of cycling of nutrients, their absorption and translocation towards shoots. All these mechanisms enable the plant to maintain their normality under severe conditions and best suited to be substituted for different inorganic pesticides and fertilizers (Govindasamy et al. 2010). In particular, we will discuss the evidences highlighting the interactions of plants with microorganisms for promoting plant health during stressed conditions and their sustainable use for agricultural practices.

26.2 Microbial Communications in Rhizosphere

Zone in the soils that are adjacent to roots is recognized as the rhizosphere and the whole surface region of roots is termed as the rhizoplane (Fig. 26.1) (Coats and Rumpho 2014). This region is of chief significance for plant growth, development and productivity as it is the main fraction of interaction with a great diverse microbial neighbourhood, also referred as microbiome (Venturi and Keel 2016; Poole 2017). In nature, plants cohabit along with varied microorganism like archaea, bacteria, fungi and protists collectively called the plant microbiota (Hassani et al. 2018). Terrestrial plants intermingle with microbes largely at roots. Roots provide special niche at the interface that is comprised of rhizospheric soil, rhizoplane as well as endorhizosphere. Microbiome is enclosed with symbiotic microbes, commensals and few pathogens that form relation with roots and soils and give rise to root holobiont for determining biological and agricultural yield (Fig.26.1). There is an evidence to signify the meaning of root microbiome that is entangled with rhizosphere-associated microbiota, including their genetic elements for determination of plant health (Coats and Rumpho 2014; Philip Poole 2017).

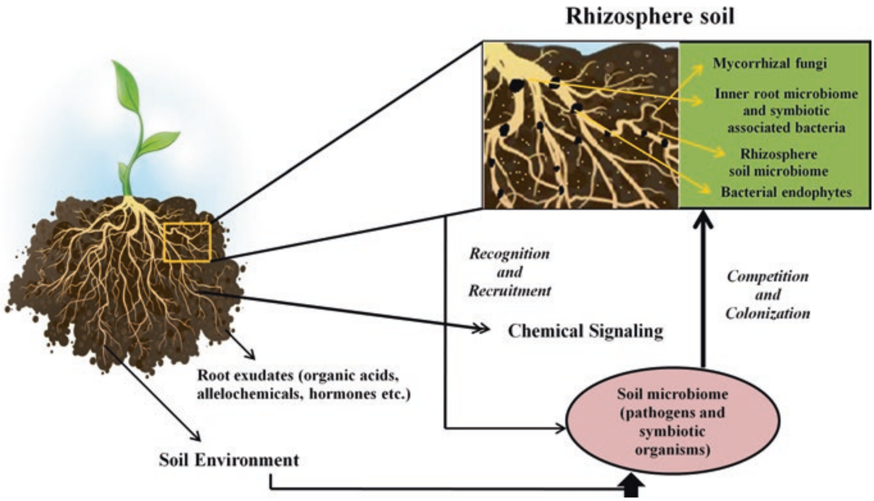


Fig. 26.1 Plant-microbe interactions in root, rhizosphere and bulk soil zones

Roots are also entitled for the production of chemical signals for promoting growth of microorganism predominantly for the zoospores (Gow et al. 1999). This generates a link between the plant and soil components to act as an intermediate. And this plant-microbe communication is mediated through root exudates generating chemotactic response of the microbes towards secreted products such as soluble sugars, organic acids and various amino acids for root colonization (Bais et al. 2006; Haldar and Sengupta 2015; Mhlongo et al. 2018).

26.2.1 Function of Root Exudates in Rhizosphere Microbial Interactions

The roots act as perfunctory support for transport of minerals and water in plants. In addition, the rhizospheric zone is a well-known hotspot for microorganisms (Kuzyakov and Blagodatskaya 2015). This is mainly attributed to the amount of compounds they secrete which act as key signals that enable them to either attract or repel towards the plants (Lakshmanan et al. 2014). It was further suggested that root exudation regulates the link between the roots and soil microbes (Mommer et al. 2016). Moreover, the shared machinery of signalling pathways in the rhizosphere persuades intensification of plant-microbe, microbe-microbe and plant-plant interaction for controlling various responses in the rhizosphere.

Olanrewaju et al. (2019) had reviewed that root exudates along with other components such as rhizodeposits synthesized by plants enable the determination of microbiota accumulated in the rhizobiome plane region adjoining the plants. It is not necessary that root exudation entirely help in plant nutrition and growth. Many of them play key signal molecules in developing associations at rhizobiome. Sugars, for instance, monosaccharides disaccharides, raffinoses, arabinose, polysaccharides and oligosaccharides; amino acids like leucine, aspartate, proline, asparagine, aspartic acid, glutamine, tryptophan, arginine, isoleucine and cysteine; organic acids (oxalic, tartaric, fumaric, maleic); metabolites; enzymes; and hormones are the main regulatory molecules associated with plants (Hayat et al. 2017; Olanrewaju et al. 2019). It is assumed that other antimicrobial metabolites and volatile organic compounds (VOCs) significantly play a positive role for long-distance linkage in the rhizobiome. For example, in maize (*Zea mays*), benzoxazinoids are a class of defensive molecules synthesized during the emergence of lateral and crown roots (Guo et al. 2016; Gunina and Kuzyakov 2015).

Plants possess unique machinery for the transport and secretion of compounds within the rhizosphere (Weston et al. 2012). To illustrate, Lorenz Hiltner described the term ‘rhizosphere’ as the soil cubicle and is effected by plant roots (Haldar and Sengupta 2015). The microorganisms are chemotactically attracted towards plant root exudates, volatile organic carbon and rhizodeposits and get activated in this carbon-rich environment (Fig.26.1) (Ho et al. 2017). Plant root exudates vary from species to species; therefore the differences among rhizosphere microbiomes are expected (Evangelisti et al. 2014).

In the last few decades, rhizospheric interactions mediated by root exudates have been extensively studied (Broeckling et al. 2008; Badri et al. 2013; Chaparro et al. 2013a, b). Moreover, the associations could be neutral or favourable or deadly (Hassani et al. 2018; Doornbos et al. 2012). In some cases, organisms display transitions from pathogenicity to symbiosis according to environmental conditions (Zhang et al. 2015; Newton et al. 2010; Wille et al. 2019). The PGPB interact among one another and, with plants in a refined mode, mediated through chemical communication recognized in rhizosphere. This leads to mutual affairs that are pivotal for effective root-root associations (Bertin et al. 2003; Mommer et al. 2016), mineral availability, microorganism accrual and biofilm construction in inhabiting communities (Sasse et al. 2017). Along with this, they are well inhibitors of pathogenic organisms (Rosier et al. 2016; Li et al. 2013). To elucidate, various metabolomic and metagenomic approaches are boon for researchers to discover and enumerate compounds released by microbes including their profiling. Among metabolite ‘blends’ nearby root exudates are substantial for mutual interaction. In addition, the term ‘signalomics’ also effectively explains these approaches for interpretation of chemical signal communications taking place within rhizosphere, roots and microbes (Mhlongo et al. 2018).

PGPB occurring at microbiome assemblages led to secrete an array of signalling metabolites affecting gene expression of host plants that has made these metabolites a hotspot for researchers. Here, VOCs are the crucial signalling molecules of bacterial communities as they are having low molecular weight firstly and secondly due to their lipophilic nature serve as chemical signals for effective microbial communication in contrast to non-volatile counterparts (Gonzalez and Marketon 2003; Tyc et al. 2015). This cell communication mediates quorum sensing (QS) signals to colonize plant roots with plant growth-promoting rhizobacteria (PGPR) (Kai et al.

2016; Kanchiswamy et al. 2015; Hong et al. 2012; Helman and Chernin 2015). These signals further act as autoinducers for intra- and inter-bacterial communication among different species (Gonzalez and Marketon 2003). With respect to microbial associations, the exudates also present antimicrobial activities and also regulate quorum systems (QS) (Zuniga et al. 2017; Hassan et al. 2016). Various microbes also partake in quorum sensing (QS) that defines the skill for detection and responsiveness towards microbial density, with the raised levels or response to small metabolic QS signal molecules (Garcia-Contreras et al. 2016).

A symbiotic relationship gets established between plants and rhizobacteria either through secreted or emitted molecules which are beneficial for plants. While plant hormones are growth inducers and defence regulators, PGPR also generate these metabolites such as auxins, cytokinins, gibberellins, ABA, SA and JA (Wei-wei et al. 2008; Fahad et al. 2015). The formation of VOCs in maintaining soil fertility, plant growth and resistance is well known (Kai et al. 2009; Rothballer et al. 2018).

The chemical convolution encompassing root exudation is linked to many external factors like photosynthesis, size and soil characteristics. These compounds can be modulated varying on their secreting source. The strong intricacy determines that root exudates have prospective to overlie more comprehensive information regarding communication events of rhizosphere (Mommer et al. 2016; Sasse et al. 2017). Furthermore, the chemical nature of root exudates directly affects rhizospheric communities that has been proved through implicating the use of secreted products affecting soil microbial communities. For instance, citric acid secreted from cucumber roots attracted *B. amyloliquefaciens* SQR9 and induced biofilm formation. Likewise in banana, fumaric acid magnetized *B. subtilis* N11 strain to form biofilm over the surface (Zhang et al. 2014). Another compound observed in the root exudates is flavonoids (i.e. 2-phenyl-1,4-benzopyrone derivatives) for the induction of nod genes in bacteria and for lipochitooligosaccharide (LCO) formation. This further triggers nodulation process in the roots. Captivatingly, LCO participates efficiently during interactions between arbuscular mycorrhizal fungi and plants. Besides, the flavonoids also mimic QS molecules of bacteria, to influence bacterial metabolism (Hassan and Mathesius 2012). QS considerably functions in regulating bacterial genotype and phenotype for victorious root colonizations (Rosier et al. 2016). Numerous low-carbon molecules are also present in the root exudates; and these molecules behave as precursors in hormonal profiles of PGPR. Tryptophan, for example, is a precursor for indole-3-acetic acid and is aggregated at root tips (Haichar et al. 2014). Additionally, aminocyclopropane-1-carboxylic acid (ACC), the precursor of ethylene, is exudated from plants as a source of nitrogen and carbon for PGPR (Haichar et al. 2014).

26.2.2 Plant-Rhizobiome Communication

The plant-microbe interactions involve a complex study to be comprehended. There is a multilevel connection among organisms, gene regulation, induction and repression of signals in different pathways along with their response elicitation. PGPB are tremendously imperative for maintaining plant health. Apart from this, for enrichment of nutrient availability, PGPB and AMF functionally persuade plant's defence to pathogens (Di Benedetto et al. 2017; Olanrewaju et al. 2017). Few basic mechanisms comprise of biofertilization, biostimulation, bioremediation and biocontrol (Babalola 2010; Olanrewaju et al. 2017). Biofertilization involves the use of PGPR for maintaining nutrient cycle of plants, thereby improving seed germination rate and seedling emergence. This further improves crop yield by microbes through processes such as N_2 fixation, phosphate uptake and release of plant hormones, while biocontrol means suppression of pathogens and controlling diseases via synthesis of siderophores, ACC deaminase, induced systemic resistance and acquired systemic resistance, respectively (Gupta et al. 2015a, b; Glick 2015).

26.2.2.1 Plant Growth-Promoting Microorganisms (PGPM)

PGPM was named by Joe Kloepper in the late 1970s that defined 'the soil bacteria communities' colonization in roots of various plants by inoculating them for stimulating plant growth'. Santoyoa et al. (2016) reviewed the capacity of assorted bacterial endophytes for plant growth stimulation occurs as an outcome of many mechanisms. Firstly, direct plant growth promotion takes place when a bacterium facilitates acquisition of minerals or triggers hormonal profiles of a plant. The mineral acquisition facilitated by PGPB comprises of nitrogen, phosphorus and iron. Further, the intonation of hormone levels may entail PGPB (plant growth-promoting bacteria) synthesizing one or more of the phytohormones, namely, auxins, cytokinins and gibberellins. Also, some PGPB reduce ethylene through enhanced production of 1-aminocyclopropane-1-carboxylate (ACC deaminase that cleaves the compound ACC). Secondly, the indirect growth promotion of plant occurs when a PGPB reduces plant damage from phytopathogen (fungi and bacteria). This is attributed to inhibition of the pathogen through PGPB.

The benefits of PGPM for plants in terms of growth and immunity are well reported for bacteria belonging to *Azospirillum*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Rhizobium*, *Serratia*, *Stenotrophomonas* and *Streptomyces* and fungal genera like *Ampelomyces*, *Coniothyrium*, *Glomus* and *Trichoderma*. Multiple strains of fluorescent *Pseudomonads* are well reported for improving plant growth from pathogens by P solubilization and regulation of plant growth stimulators (Ho et al. 2017; Wille et al. 2019). There is mounting record of reports depicting rhizosphere community and *B. cereus* UW85, *B. megaterium* B153–2-2 and *B. subtilis* GB03 exploitation in controlling damping-off disease in alfalfa and cotton and *Rhizoctonia* root rot disease in soybean (Gupta et al. 2015a, b). The count of bacterial species (PGPR) has augmented considerably from past decades owing to the plentiful studies conducted on plants in hunt of sustainability tools and advancements in molecular genetics progressing towards upgradation of bacterial taxonomy.

The studies on spectacular interactions among plants, rhizosphere and microbes in view of future agricultural aspect and plant breeding will ultimately give sustainable remedies for reduction of threat caused by pathogens.

26.3 Challenges of Different Stresses Faced by Plants

There are a wide number of stresses in the environment that act as global threats for future agricultural productivity. The different stresses are chief constraints for hampering crop yield, food quality and global food security. Stresses could be naturally caused or through human interference. A number of plant attributes are negatively affected; for instance, physiology, biochemical aspects and molecular nature of plants are hindered under stress conditions. The effects of various stresses upshot loss of soil microbiota, soil fertility and struggle for nutrient resources. The major abiotic stresses are freezing, flooding, temperature, drought, salinity and heavy metal stress that have been known to undergo a wide range of alterations in the normal functioning of the plants (Kumar and Verma 2018). On the other hand, pathogenic attack to different plants also disturbs various biochemical processes within them. Plants have adopted many resistance mechanisms against different environmental stresses (Fig. 26.2).

The different abiotic stresses have been known to cause huge impact on different mechanisms of plants. Effects of different abiotic stresses on morphological, biochemical and physiological attributes of different plants are given in tabulated form (Table 26.1).

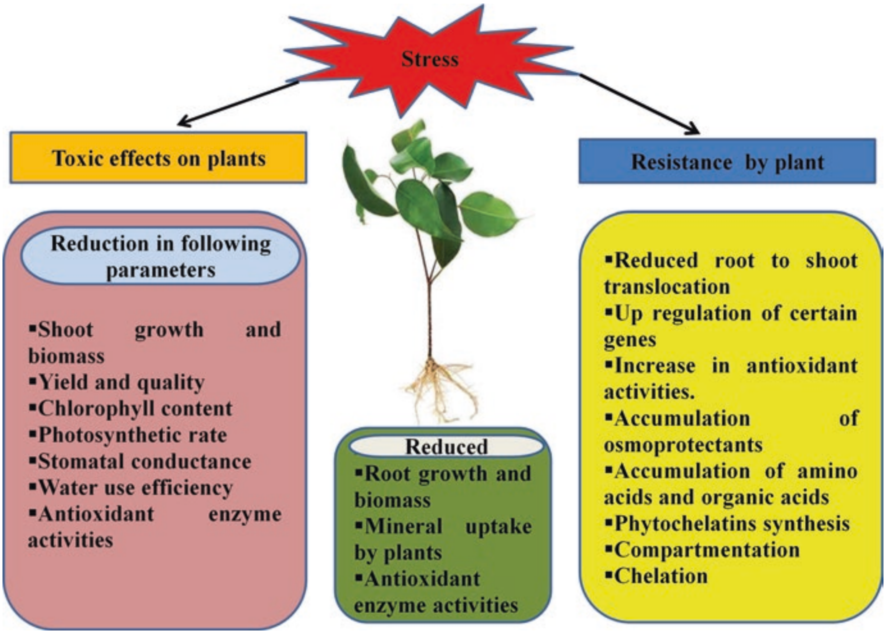


Fig. 26.2 Schematic representation of toxic effects and resistance mechanisms adopted by plants during stress conditions

Table 26.1 Effect of different abiotic stresses on plants

Abiotic stress	Plant species	Effect on plants	Reference
Drought	*Glycine max*	Retarded plant growth	Kang et al. (2014)
	Cicer arietinum	Reduced seed germination and membrane integrity and growth parameters along with enhanced osmolyte accumulation	Tiwari et al. (2016)
	Helianthus annuus	Declined chlorophyll a, chlorophyll b and total chlorophyll content	Kaur and Asthir (2017)
	Abelmoschus esculentus L.	Enhanced membrane damage and protein denaturation	Pravisya et al. (2019)
Salinity	*Vaccinium corymbosum*	Lowered leaf growth and increased leaf senescence, with reduced leaf/stem ratio	Machado et al. (2014)
	Brassica oleracea	Reduction in overall growth and yield	Giuffrida et al. (2016)
	Spinacia oleracea L.	Inhibition of photosynthesis, stomatal and mesophyll conductance, CO_2 diffusion rate and ribulose-1,5-bisphosphate carboxylase/oxygenase enzyme activity	Machado et al. (2017)
	Raphanus sativus	Reduction of leaf area expansion that limits light interception and growth reduction	Machado et al. (2017)
Temperature	*Vitis vinifera*	Reduced concentration of phenolic acids and decreased scavenging capacity in the leaves	Krol et al. (2015)
	Brassica oleracea	Decreased stomatal conductance and leaf water content as a result plant produces smaller and thicker leaves	Rodríguez et al. (2015)
	Saccharum officinarum	Distorted chloroplast structure and microtubules reorganization	Li et al. (2018)
	Vicia faba (L.)	Damaged reproductive organs and photosystem II	Zhou et al. (2018)
Heavy metal stress	*Brassica juncea*	Limited leaf, shoot and root growth	Goswami and Das (2015)
	Triticum aestivum	Impairment in ATPase activity of plasma membrane and enhanced lipid peroxidation in cell membrane	Verma et al. (2017)
	Brassica species	Oxidative stress generation by overproduction of reactive oxygen species and lipid peroxidation	Rizwan et al. (2018)
	Alternanthera bettzickiana	Decreased plant growth, biomass, photosynthetic pigments along with altered SOD, POD and CAT activities	Tauqeer et al. (2016)

26.4 Microbial Remediation to Environmental Adversities

Due to negative impact of toxic pollutants on human population (Raghunandan et al. 2014, 2018), contaminants degrade the human health along with the natural ecosystem. The studies are focusing to explore and modulate the natural capacity of PGPM to neutralize harmful compounds (Raghunandan et al. 2014, 2018).

Bioremediation is defined as application of microorganisms to degrade harmful environmental pollutants. In addition to regulate biogeochemical cycles (Griggs et al. 2013; Kumar et al. 2016), maintaining the balance between the ecosystem and environment, they also play a central role for cleaning environmental contaminants (Morris et al. 2011). The microbe-mediated remediation is of immense connotation because they are economical and environmentally friendly methods relative to many frequently employed non-biological remedial methods.

26.4.1 Potential Approaches for Bioremediation

Microbes are the most effective approach for the elimination of heavy metals from polluted environments due to their varied ability of interacting with heavy metals (Mosa et al. 2016). Microorganisms adopt different mechanisms to interact and survive in the presence of various pollutants (Fig.26.3). Several mechanisms of bioremediation used by microbes are biotransformation, biosorption, bioaccumulation, use of enzymes and metal-microbe interactions (Fig. 26.3). Bioremediation processes attempt to explore the naturally existing microbe catabolic diversity for transformation, accumulation and detoxification of hazardous compounds like hydrocarbons (e.g. oil), polychlorinated biphenyls (PCBs), polyaromatic hydrocarbons (PAHs), radionuclides and metals (Ojuederie and Babalola 2017). Several microorganisms, including bacteria, fungi, yeasts and other beneficial organisms, are involved in bioremediation process under environmental adverse conditions.

Unlike other organic pollutants, the heavy metals are difficult to detoxify, but are primarily necessary to be converted into stable form or completely removed. The bioremediation of metals is mediated through mechanisms, viz. biotransformation, enzyme-catalysed transformation (redox reactions), biosorption (metal ion sorption over cell surface by various physicochemical reactions), bioleaching (mobilization of ions via excretion of organic acids) or methylation reactions, intracellular accumulation, etc. The key microbial processes influencing bioremediation potential of metals are summarized in Fig. 26.1.

26.4.2 Significance of Systems Biology Approach Towards Bioremediation

Plant metagenomic is emerging field of science owing to the vital need to environmental remediation and ecological sustainable development (Gemperline et al. 2016). Plant-associated microbes can have various interactions (rhizospheric and endophytic). The interaction between these plants and microbes enhanced the growth traits by tolerance and survival techniques in polluted environments. Plants

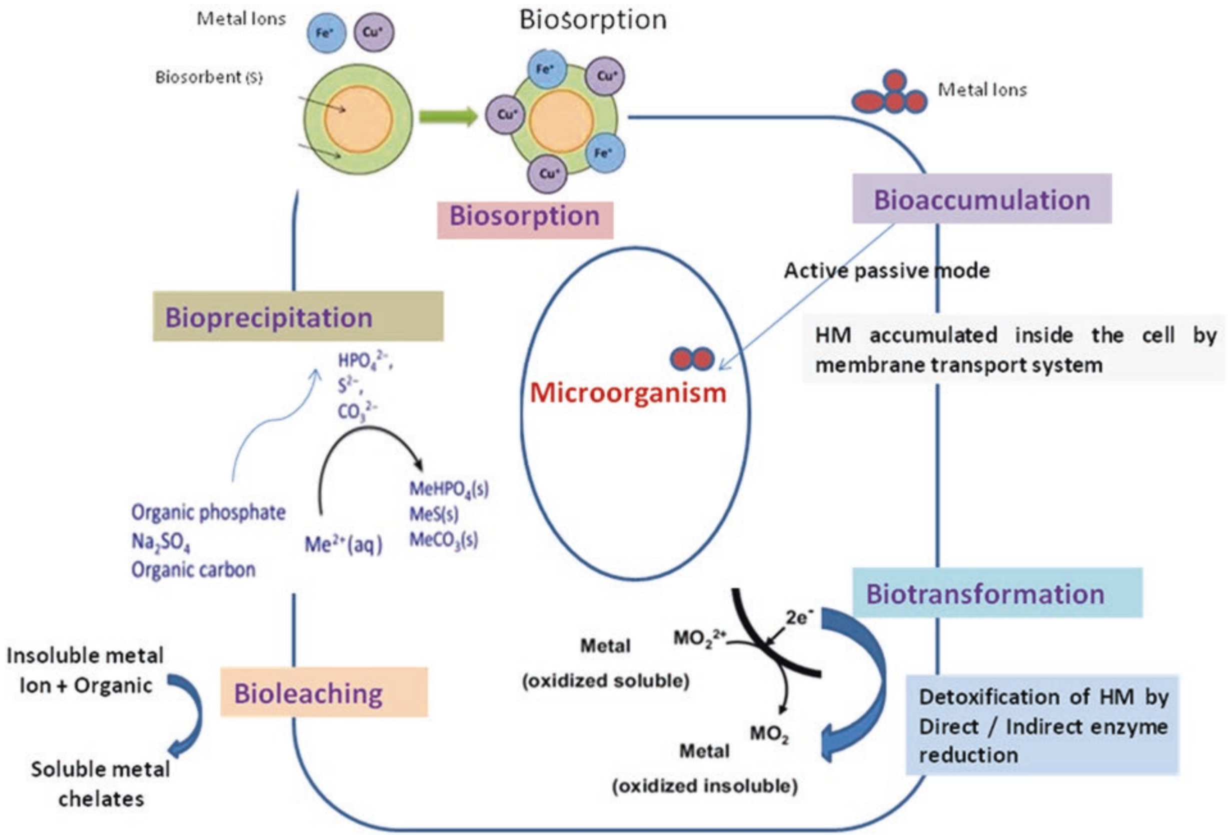


Fig. 26.3 Bioremediation mechanisms during metal-microbe interactions

and microbes can appreciably develop bioremediation potential in synchronic way, through the provision of habitat and nutrition along with the microbial counterparts, whereas the microbes induce plant efficiency by lowering the toxicity levels of contaminants in soil. Genome-enabled investigations unravel a pathway associated to plant microbial diversity of the polluted environments. This understanding lays a foundation to comprehend microbial communities that devise tools for the efficient remediation of toxic environments. Recently, an approach related to systems biology has been accepted to spot viable plant species, microbes and explicit genes encoding bioremediation and mechanisms behind these processes, namely, resistance, immobilization, tolerance, enzymatic transformation, accumulation, filtration, precipitation and metabolism of toxic metals in ecosystem for remediating or mitigating toxic products (Mani and Kumar 2014; Malla et al. 2018).

Bioremediation may be in situ or ex situ type. Many other distinguished methods have been employed for the confiscation of organic (e.g. explosives, pesticides, TCE, solvents, dyes, etc.) and inorganic (e.g. nitrates, chlorides, sulphides, uranium) pollutants (Nizzetto 2010; Ramos et al. 2018). But recent reports indicated that employment of biology alone will not entirely eradicate the pollution. Therefore, for the successful bioremediation application, an interdisciplinary approach is requisite (van der Meer and Belkin 2010; He and McMahon 2011). It has been visualized from past centuries that advancement in bioremediation potential has extensively achieved as of culturable microbes to well-defined catalytic activities. Currently, 'omics' technologies have been considered to discover the hidden microbial potential to explore the enzymatic activities associated with the degradation of environmental contaminants.

26.5 Plant-Microbe Interactions under Abiotic Stresses

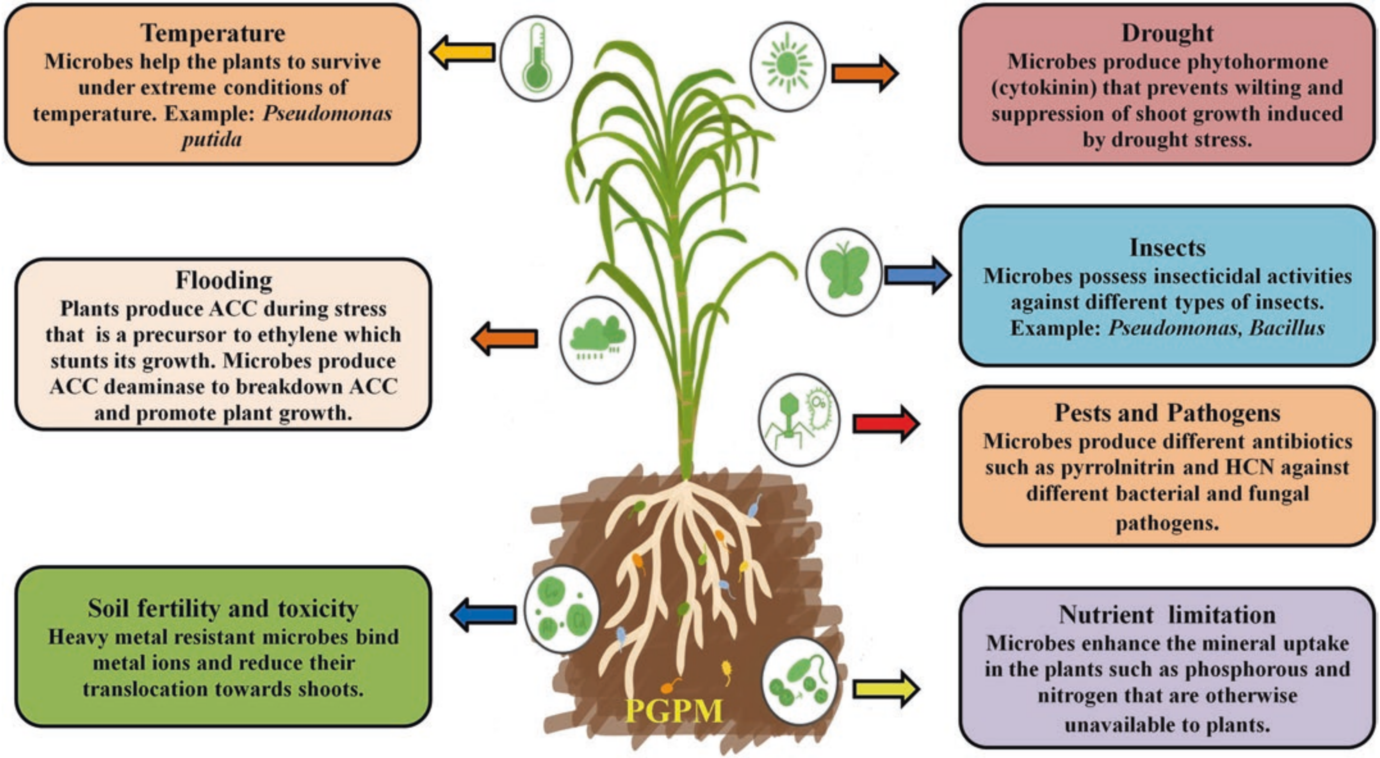
The association of microorganisms with plants has been proved to be effective for both plants and microbes during any kind of stressed conditions (Souza et al. 2015; de Zelicourt et al. 2013). The microbes have been observed to trigger resistance mechanisms in plants through induced systemic tolerance (IST) (Nadeem et al. 2014). In addition, they possess inner potential to alter intrinsic metabolic and genetic processes in order to cope up against different adversities (Gopalakrishnan et al. 2016). Several microbial genera aid plant growth and mitigate different stresses by modulating different genes associated with aquaporins, dehydrins and malondialdehyde (Pandey et al. 2016). Other microbe-mediated responses observed in plants include alterations in the levels of plant hormones, defensive proteins, enzymes, antioxidant levels and exopolysaccharides (Kaushal and Wani 2016). Furthermore, the systemic resistance induced in the plants via extracellular signals produced in the form of secondary metabolites activates the internal signalling processes. These signals are perceived by plant cells that in turn initiate or activate series of defence pathways (Macho and Zipfel 2014; Franken 2012). The prospective of microbial interactions with different plants, therefore, has a multifaceted role in alleviation of stresses along with maintaining their growth and development. These aspects make them strong and viable alternatives in stress amelioration during sustainable agriculture. Figure 26.4 shows the diagrammatic representation of microbe-mediated stress responses in plants.

26.5.1 Drought Stress

Rainfall is the main source of water for irrigation in most of the agricultural lands of the earth. The gradual delay or imbalanced precipitation as a result of climatic changes are affecting the ecosystem. Drought is considered as most harmful abiotic stress factor and major agriculture problem worldwide, which restricts plant growth and development. Water deficit conditions affect cell size, membrane integrity, photosynthetic machinery and generation of ROS (Tiwari et al. 2016; Lata and Prasad 2011) ultimately resulting in drop off in quality as well as productivity of a crop (Zandalinas et al. 2018). Various morphological, physio-biochemical and molecular strategies have been adopted by plants to thrive in drought conditions. Plant root system is inhabited by diverse array of microbial community (including bacteria and fungi) that can have positive, negative or neutral association with plants (Mendes et al. 2013). These microbial communities, known as plant growth-promoting rhizobacteria, interact with plants and influence plant growth and biomass (Schmidt et al. 2014). It was reported by Barnard et al. (2013) that period of drought changes the soil microbial flora which directly or indirectly influences nutrient cycle and production. However, changes in structure of microbial communities that are resistant to abiotic stress increase plant potential to tolerance and quick adaptation to withstand drought stress (Table 26.2, Mendes et al. 2013; Schmidt et al. 2014; Barnard et al. 2013; Cherif et al. 2015). These plant-associated microbes colonize around rhizosphere and improve morphological and developmental traits by producing plant hormones like IAA, CK, ABA, ACC deaminase and microbial exopolysaccharides and induced systemic tolerance. Microbes also enhance the osmoprotectant accumulation and maintain the membrane permeability in plants (Kumar and Verma 2018). Various reports of microbe-inoculated plants during stressed conditions have been summarized in Table 26.2.

26.5.2 Salinity Stress

Salinity is the main abiotic stresses that affects the crop productivities worldwide. It has been estimated that more than 6% of total land area which is used for agriculture purpose is severely affected by salt stress (Munns and Tester 2008). Salt stress reduces soil water potential and therefore limits plant water uptake and nutrient potential resulting in osmosis stress. A plethora of cations (Na^+, Ca^{2+}, K^+, etc.) and anions (Cl^-) existing in soil as electrically charged species (Shrivastava and Kumar 2015)



Temperature
Microbes help the plants to survive under extreme conditions of temperature. Example: *Pseudomonas putida*

Flooding
Plants produce ACC during stress that is a precursor to ethylene which stunts its growth. Microbes produce ACC deaminase to breakdown ACC and promote plant growth.

Soil fertility and toxicity
Heavy metal resistant microbes bind metal ions and reduce their translocation towards shoots.

Drought
Microbes produce phytohormone (cytokinin) that prevents wilting and suppression of shoot growth induced by drought stress.

Insects
Microbes possess insecticidal activities against different types of insects. Example: *Pseudomonas, Bacillus*

Pests and Pathogens
Microbes produce different antibiotics such as pyrrolnitrin and HCN against different bacterial and fungal pathogens.

Nutrient limitation
Microbes enhance the mineral uptake in the plants such as phosphorous and nitrogen that are otherwise unavailable to plants.

Fig. 26.4 Microbe-mediated stress responses in plants

Table 26.2 A list of plant and microbe interaction to withstand drought stress

S. No	Plants	Microbes	Effect of microbes on plants under drought conditions	References
1.	*Pisum sativum*	*Pseudomonas fluorescens* G	Increased water uptake and water potential	Zahir et al. (2008)
2.	*Arabidopsis thaliana*	*Bacillus subtilis*(GB03)	Elevated metabolic profile of choline along with glycine betaine in osmotically stressed plants and improved leaf RWC and dry DMW	Zhang et al. (2010)
3.	*Ocimum basilicum* L.	*Pseudomonades* sp., *Bacillus lentus* and *A. brasilense*	Peak activity of antioxidative defence enzymes (GPX and APX) was observed	Heidari and Golpayegani (2012)
4.	*Zea mays*	*Bacillus* sp.	Increased seed germination and accumulation of metabolites like proline, osmolytes, sugars, free amino acids and decrease electrolyte leakage	Vardharajula et al. (2011)
5.	*Oryza sativa* L.	*Trichoderma harzianum*	Promoted root growth and delayed drought response	Shukla et al. (2012)
6.	*Triticum aestivum* L.	*Azotobacter chrocoocum* (E1) and *Pseudomonas* sp. (E2)	Enhanced anatomical characters such as thickness of epidermis, ground tissue, mesophyll, cortex and phloem tissues, diameter of xylem vessels and dimensions of vascular bundles of the root system	El-Afry (2012)
7.	*Piper nigrum*	*Bacillus licheniformis* K11	Higher expression levels of stress proteins like *Cadhn*, *VA*, *sHSP* and *CaPR-10*	Lim and Kim (2013)
8.	*Triticum aestivum*	*Bacillus amyloliquefaciens* 5113 and *A. brasilense* NO40	Enhanced expression of stress-related genes *APX1*, *SAMS1* and *HSP17.8* as well as activity of enzymes involved in the plant ascorbate-glutathione redox cycle	Kasim et al. (2013)
9.	*Zea mays*	*Proteus penneri* (Pp1), *Pseudomonas aeruginosa* (Pa2), and *Alcaligenes faecalis* (AF3)	Increased relative water content, protein, and sugars	Naseem and Bano (2014)
10.	*Lavandula dentata*	*Bacillus thuringiensis*	Increased IAA-induced proline and K content along with physiological and metabolic activities	Armada et al. (2014)
11.	*Trifolium repens*	*Pseudomonas putida* and *Bacillus thuringiensis*	Decreased stomatal conductivity, electrolyte leakage and proline content	Ortiz et al. (2015)

(continued)

Table 26.2 (continued)

S. No	Plants	Microbes	Effect of microbes on plants under drought conditions	References
12.	*Oryza. sativa* L.	*P. jessenii* R62, *P. synxantha* R81 and *A. nitroguajacolicus* strainYB3 and strain YB5	Enhanced plant growth and induction of stress-related enzymes (SOD, CAT, POD and APX)	Gusain et al. (2015)
13.	*Triticum aestivum* L.	*Rhizobium*	Accumulation of osmoprotectant compounds like trehalose and glycine betaine	O'Callaghan (2016)
14.	*Triticum aestivum* L.	*Piriformospora indica*	Increased water absorption, root growth, biomass, chlorophyll and modulated activities of different antioxidants	Hosseini et al. (2017)
15.	*Bouteloua gracilis*	Microbial consortia	Inoculated plants exhibited enhanced growth and photosynthesis and dampened drought stress over short timescales, but also increased susceptibility to drought over long time scales	Ulrich et al. (2019)

affects seed germination, water and nutrient uptake, reduction in nitrogen fixation, decrease in K^+ and Ca^{2+} uptake, enzyme inactivation, early senescence in leaves, burn-like lesions and crop productivity (Munns 2002). Increased amount of salt within plant cell hampers the plant growth and microbial activities (Kumar and Verma 2018). Plant itself responds to salinity stress by activating signalling pathways which help plants as defence regime (Khan et al. 2015; Kumar and Verma 2018). Many studies discovered that inoculation of PGPM assuages the harmful effect of salt stress (Table 26.3). Plant growth-promoting endophytic bacteria colonizes in the healthy host plant tissues and help the plants to mitigate abiotic and biotic stresses (Mandyam and Jumpponen 2014). PGPM also regulate the metabolic processes and strengthen the plant defence system during salt stress conditions (Nadeem et al. 2016). ACC deaminase decreases the stress-induced ethylene in plants by degrading ACC into α-ketobutyrate and ammonia (Glick 2014). Exopolysaccharides secreted by microbes help in binding to cations making it unavailable for plant uptake and thus reduce the salinity stress (Upadhyay et al. 2011).

Table 26.3 A list of plant and microbe interaction to withstand salinity stress

S. No.	Plants	Microbes	Effect of microbes on plants during salinity stress	References
1.	*Glycine max* L	*Arthrobacter, Bacillus, Azospirillum* and *Pseudomonas*	Increased shoot and root biomass as well as proline content in plant tissues	Naz et al. (2009)
2.	*Triticum aestivum*	*Bacillus subtilis* and *Arthrobacter* sp.	Increased biomass and total soluble sugars and reduced sodium concentration in plant tissues	Upadhyay et al. (2012)
3.	*Hordeum vulgare* L.	*Curtobacterium flaccumfaciens*	Increased barley growth up to 300%	Cardinale et al. (2015)
4.	*Triticum aestivum*	*Bacillus licheniformis* HSW-16	Stimulated plant growth through production of IAA and mitigate stress-induced damage	Singh and Jha (2016)
5.	*Triticum aestivum*	*Enterobacter* sp. NIASMVII	Synthesis of IAA and enhanced seed germination rate	Sorty et al. (2016)
6.	*Zea mays*	*Pseudomonas* sp.	Enhanced biosynthesis of IAA and stimulated root and shoot biomass	Mishra et al. (2017a, b)
7.	*Cicer arietinum* L.	*B. subtilis* NUU4 and *Mesorhizobium ciceri* IC53	Increased root and shoot biomass and improved nodule formation	Egamberdieva et al. (2017)
8.	*Brassica napus* L.	*Enterobacter cloacae* HSNJ4	Enhanced plant hormone content and reduced ethylene and malondialdehyde content. Improved root, shoot and chlorophyll content	Li et al. (2017)
9.	*Rice*	*Enterobacter* sp.	Improved growth and reduced ethylene levels and antioxidant enzyme activities	Sarkar et al. (2018a)
10.	*Avena sativa*	*Klebsiella* sp.	Enhanced plant growth, water content, dry shoot and root weight	Sapre et al. (2018)
11.	*Citrus macrophylla*	*Pseudomonas putida KT2440* or *Novosphingobium* sp. *HR1*	Accumulation of leaf by indole-3-acetic acid (IAA) and a delayed in the decrease of quantum yield (*Φ*PSII). Inhibited root chloride and proline accumulation	Vives-Peris et al. (2018)
12.	*Oryza sativa*	*Burkholderia* sp.	Improvement in various morphological and biochemical characteristics, ROS scavenging antioxidant enzymatic activities and reduced amounts of ethylene	Sarkar et al. (2018b)

(continued)

Table 26.3 (continued)

S. No.	Plants	Microbes	Effect of microbes on plants during salinity stress	References
13.	*Sulla carnosa*	*Acinetobacter* sp. *(Br3)*, *Pseudomonas putida (Br18)* and *Curtobacterium* sp. *(Br20)*	Increased dry biomass, photosynthetic efficiency, chlorophyll leaf content, total soluble sugar content and antioxidant enzyme activities	Hmaeid et al. (2019)

26.5.3 Heavy Metal Stress

Accumulation of heavy metals in soil due to numerous anthropogenic activities together with mining, industrial practices and modern agricultural practices and extensive industrialization is adversely affecting soil health and crop productivity (Tiwari and Lata 2018). Heavy metals also have detrimental effects on growth and developmental processes of plants (Panuccio et al. 2009; Tiwari and Lata 2018; Hassan et al. 2017). Plants have different resistance strategies to avoid or resist heavy metal toxicity but beyond certain limits these mechanisms fail and survival of plant becomes tough (Clemens and Ma 2016). Use of rhizospheric microbes for removal of heavy metals is an emerging technology to reduce heavy metal stress in plants. Rhizospheric microbes protect the plant from heavy metal stress and have the ability to prevent the accumulation of heavy metals in soil (Mishra et al. 2017a, b). Microbes acquire countless resistance methods for their survival in the incidence of toxic heavy metals which include metal sorption, immobilization, transformation, bioaccumulation, precipitation and enzymatic oxidation or reduction to a non-toxic form and efflux of heavy metals from the cell (Hassan et al. 2017). They have the tendency to perk up plant growth and crop production by converting the complex waste into simple non-toxic compounds and can lower the detrimental effects of heavy metals (Mustapha and Halimoon 2015). Plant-associated microbes protect the plants from diseases and promote plant growth and development by fabrication of growth regulator such as IAA and ACC deaminase and reducing ethylene concentration (Glick 2010).

Numerous bacteria belonging to genera *Bacillus*, *Pseudomonas* and *Arthrobacter* are commonly present in heavy metal-contaminated sites predominantly composed of *Firmicutes*, *Proteobacteria* and *Actinobacteria* (Pires et al. 2017). Fungal cell walls have negative charge due to the presence of special functional groups, e.g. carboxylic, hydroxyl, amine or sulfhydryl, amide and phosphate, in different wall components which helps in binding of the metal to the cell (Tobin 2001; Ong et al. 2017). It is reported that filamentous AM fungi of genera *Trichoderma*, *Glomus*, *Penicillium*, *Aspergillus* and *Mucor* have the potential to alleviate heavy metal toxicity (Ezzouhri et al. 2009; Pires et al. 2017; Oladipo et al. 2018). According to Narendrula-Kotha and Nkongolo (2017) *Ascomycota* and *Basidiomycota* are the most common fungi present in heavy metal-contaminated soils. Khan (2005) reported that arbuscular mycorrhizal (AM) fungi are most outstanding soil microorganisms in heavy metal-contaminated soils. They act symbiotically with many plant roots and trigger nutrient absorption in plants (Saxena et al. 2017). Various reports of responses of plants inoculated with microbes during heavy metal tolerance are provided in the following table (Table 26.4).

26.5.4 Temperature Stress

Environmental and climatic variations adversely affect crop productivity and food security worldwide. Heat stress and cold conditions adversely impact functional, structural, biochemical and genetic modifications in plants that affect crop production. Heat stress may disrupt the cell membrane, membrane permeability, water content (transpiration), cell differentiation, membrane integrity, cell elongation, cell expansion and microtubular organization in plants (Kumar and Verma 2018). Moreover, heat stress also alters the carbon flux of the chloroplast stroma and thylakoid membrane and disturbs photosynthetic activities which results in declined crop yield (Bita and Gerats 2013). In addition, exposure to low temperature and high temperature leads to inactivation of various enzymatic functions, proteins, reactive oxygen species accumulation in wheat crop plants, ultimately leading to oxidative stress. *Bacillus* spp. produce heat-resistant endospores which makes them suitable candidates in terms of stability and efficient biological products (Yánez-Mendizábal et al. 2012). Meena et al. (2015) studied the effect of *Pseudomonas aeruginosa* on wheat under high-temperature condition. It was suggested that wheat seed treatment with *Pseudomonas aeruginosa* resulted in decline in the cell membrane injury and enhancement in plant height, root length, leaf area, total dry matter, total chlorophyll content and relative water content. It was further reported that *Pseudomonas putida* strain AKMP7 improved survival and growth of wheat plants under heat stress. It was found that inoculation reduced membrane injury and the activity of several antioxidant enzymes such as SOD, APX and CAT. The levels of cellular metabolites were also improved. A stimulation in the root and shoot length, dry biomass and grain formation of wheat was also reported during temperature stress conditions (Ali et al. 2010). Kang et al. (2015) studied the effect of *Serratia nematodiphila* on the biochemical and physio-hormonal attributes of pepper (*Capsicum annuum* L.) plants grown under low-temperature stress. Inoculation of *Serratia nematodiphila* alleviated the injurious effects of low temperature on pepper of 5 °C. It was revealed that ABA was enhanced endogenously in pepper plants, followed by stimulation of endogenous jasmonic acid and reduction in salicylic acid (Kang et al. 2015).

Table 26.4 Utilization of rhizospheric microbes in heavy metal stress tolerance in plants

Sl. No.	Plant	Microbe inoculated	Heavy metals	Effect of microbes on plants during heavy metal stress	References
1.	*Alnus firma*	*Bacillus thuringiensis*	As, Pb, Ni, Zn, cu	Enhanced plant biomass, chlorophyll content, nodule number and heavy metal accumulation	Babu et al. (2013)
2.	*Sedum plumbizincicola*	*Phyllobacterium myrsinacearum* RC6b	Cd, Zn, cu	Production of 1-aminocyclopropane-1-carboxylic acid deaminase, indole-3-acetic acid, siderophore and phosphate solubilization. Increased growth and accumulation of metals in plant organs	Ma et al. (2013)
3.	*Oryza sativa*	*Bacillus Licheniformis* NCCP-59	Ni	Improved seed germination rate and biochemical attributes of the plant	Jamil et al. (2014)
4.	*Miscanthus sinensis*	*Pseudomonas koreensis*	As, cd, cu, Pb and Zn	Increased biomass, chlorophyll and protein content. Higher SOD and CAT while lowered malondialdehyde content	Babu et al. (2015)
5.	*Vicia faba*	*Rhizobium* sp. *CCNWSX0481*, *Rhizobium leguminosarum* bv. *viciae*, *Enterobacter cloacae* and *Pseudomonas* sp.	Cu	Increased dry weight and decreased metal accumulation in plant organs. Altered activities of antioxidant enzymes	Fatnassi et al. (2015)
6.	*Eruca sativa*	*Pseudomonas putida*	Ni	Increased root and shoot length, fresh and dry weight along with Ni uptake	Kamran et al. (2016)
7.	*Solanum lycopersicum*	*Funneliformis mosseae* (syn. *Glomus mosseae*), *Rhizophagus intraradices* (syn. *Glomus intraradices*) and *Claroideoglomus etunicatum* (syn. *Glomus etunicatum*)	Cd	Enhanced activity of antioxidant enzymes and reduction in the MDA content	Hashem et al. (2016)
8.	*Spartina densiflora*	*P. agglomerans RSO6* and *RSO7* and *B. aryabhattai RSO25*	As, cu, Pb and Zn	Enhanced germination rate	Paredes-Páliz et al. (2016)

(continued)

Table 26.4 (continued)

Sl. No.	Plant	Microbe inoculated	Heavy metals	Effect of microbes on plants during heavy metal stress	References
9.	*Eruca sativa*	*Pseudomonas putida*	Ni	Increased root, shoot length fresh and dry weight and Ni uptake	Kamran et al. (2016)
10.	*Althea rosea*	*Bacillus thuringiensis* 002, *Bacillus fortis* 162, *Bacillus subtilis* 174	Ni	Improved root and shoot biomass of treated plants	Khan et al. (2017a)
11.	*Catharanthus roseus*	*Pseudomonas fluorescens* RB4 and *Bacillus subtilis* 189	Cu, Pb	Improved translocation and metal bioconcentration factors and increased fresh weight (FW)	Khan et al. (2017b)
12.	*Hibiscus cannabinus*	*Enterobacter* sp. strain EG16	Cd	Improved plant growth, probably as a result of increased plant uptake of Fe and immobilization of cd^{2+} that decreased accumulation of Cd in different plant tissues	Chen et al. (2017)
13.	*Cicer arietinum*	*Bacillus subtilis*, *Bacillus thuringiensis* and *Bacillus megaterium*	Ni, Pb	Enhanced accumulation of heavy metals in plant shoots	Khan et al. (2017a, b)
14.	*Capsicum annuum*	*Funneliformis mosseae* or *Rhizophagus intraradices*	Cu	Inoculation with mycorrhizal fungi increased metal tolerance and improved plant growth and stability of membranes along with photosynthetic activities	Ruscitti et al. (2017)
15.	*Cicer arietinum*	*Trichoderma*	As	Increased GPX, SOD and GR activities, chlorophyll pigments with higher accumulation of stress-responsive amino acids (proline, cysteine, glycine and methionine), enhanced seed germination, plant height, dry weight and pods	Tripathi et al. (2017)
16.	*Cicer arietinum*	*Bacillus subtilis*, *Bacillus thuringiensis* and *Bacillus megaterium*	Ni, cd, Pb	Increased accumulation of heavy metals in plant shoots	Khan et al. (2018)

(continued)

Table 26.4 (continued)

Sl. No.	Plant	Microbe inoculated	Heavy metals	Effect of microbes on plants during heavy metal stress	References
17.	*Lathyrus sativus*	*R. leguminosarum*, *B. simplex*, *Variovorax* sp., *Luteibacter* sp., *P. fluorescens*	Pb	Increased proline biosynthesis, carotenoid and chlorophyll pigments as well as total soluble sugar concentration, altered activities of SOD, GPOX, CAT and APX enzymes in leaves and roots	Abdelkrim et al. (2018)
18.	*Lens culinaris*	*Bacillus anthracis*, *Bacillus cereus*	Cr	Increased shoot and root length, fresh and dry weight, number of leaves, chlorophyll and carotenoid content	Hadia-e-Fatima (2018)
19.	*Lycopersicon esculentum*	*Pseudomonas aeruginosa* and *Burkholderia gladioli*	Cd	PGPRs induced cd tolerance through enhanced expression of the *SOD*, *POD* and *PPO* genes, reduced expression of *CAT*, *GR*, *GST*, *GPOX* and *APOX* genes	Khanna et al. (2019)
20.	*Medicago sativa*	*Paenibacillus mucilaginosus* and *Sinorhizobium meliloti*	Cu	Enhanced activities of antioxidant enzymes and improved cu uptake in plant tissues	Ju et al. (2019)

26.6 Plants under Biotic Stresses

Living organisms, particularly fungi, nematodes, insects, arachnids, viruses, bacteria and weeds cause biotic stress in plants. In agricultural practices, biotic stress is a foremost reason of pre- and postharvest losses (Singla and Krattinger 2016). Exposure to such stressful conditions by their surroundings adversely affects their growth, development and their metabolic processes throughout their life cycle (Jeandroz and Lamotte 2017). Infection caused by virus, fungi, bacteria, etc., leads to induce the defensive mechanism inside the plant cells to resist the further attack of microbes, the phenomenon called as induced systemic resistance (ISR). Synthesis of allopathic compounds like antibiotics, siderophores, etc., by plant growth-promoting mycorrhiza competes for nutrition and ecotype, which further declines the growth of pathogens (Jain et al. 2013). In *Panax ginseng*, systemic resistance was observed against *Phytophthora* where *B. amyloliquefaciens* strain HK34 has promoted the resistance against pathogen *P. cactorum* (Lee et al. 2015). Reports were also found with *Bacillus* and *Pseudomonas* strains, which provide resistance in many crops like *Oryza sativus* (Chithrashree et al. 2011) against *Xanthomonas oryzae*.

Against the primary infection, systemic acquired resistance (SAR) provides complete defensive strategy. In this phenomenon, a plant is able to identify the pathogen molecular pattern and contributes in the synthesis of metabolites and plant growth regulators by altering the gene expression, hence detoxifying the pathogens (Sunkar et al. 2012). In tomato plants, synthesis of indole acetic acid, biocontrol features and phosphate solubilization process, etc., growth-stimulating efficiency is activated due to the isolation of *Bacillus* and *Arthrobacter* species from the rhizosphere (Banerjee et al. 2010). Thus microbes play a pivotal role in promoting the microbial diversity and maintaining the functional equilibrium in the degraded land.

26.7 Commercial Application of Microbes for Stress Management during Sustainable Agriculture

Under different stress conditions, plant growth-promoting bacteria (PGPB) and mycorrhizal fungi help in regulating the plant growth and development. Even the application of proficient plant growth-promoting mycorrhizal fungi leads to the improved sustainable agriculture (Kumar and Verma 2018). Conversely some more novel strategies are also required to consider the interaction of plants and microbes for the control of growth and spreading of diseases under sustainable agriculture system (Finkel et al. 2017). Application of PGPM stimulates the synthesis of plant growth regulators, hence managing the nutritional and hormonal balance by inducing the resistance against plant pathogens (Spence and Bais 2015). They also synthesize the plant metabolites, which cause increase in the mortality rate of pathogens, as siderophore production in rhizosphere by the microbes leads to less availability of iron to them (Shahid et al. 2017). Under adverse conditions, some microbes combat the harmful effects by alteration in the gene expressions via sigma factor and also help in altering the activities of certain significant enzymes such as chitinase, glucanase, etc., thus regulating plant growth and development (Gupta et al. 2015a, b).

Arbuscular mycorrhiza (AM) most commonly exists in soil and plays a key role in uptake, transport and translocation of minerals and nutrients in plants, hence regulating the nutrient cycle. They can also act as an impending alternative for pesticides and inorganic fertilizers (Kumar and Verma 2018). Microbial applications can be used as biofertilizers or biopesticides for the improvements of various growth traits of plants. They are also helpful in the suppression of certain plant disease and degradation of fungal cell wall by changing the activities of crucial enzymes due to synthesis of antibodies and, hence, ameliorate the adverse effects of biotic stress (Ahmad et al. 2018). These strategies in agricultural practices can improve the production of organic food, vegetables and also financial income of the farmers.

26.8 Conclusions and Future Prospects

The present scenario depicts that different types of environmental stresses hinder plant growth and metabolism which ultimately affects the survival of the plant. They are known to be the major constraints for productivity, quality, security and yield of the crops. The most promising approach nowadays, is the utilization of beneficial microorganisms as a stress removal tools and exploration of plant-microbial and soil associations. The growth of plants and their yield is dependent upon nutrient availability at soil-root surface interface that is under the influence of biological factors such as roots and microbes of rhizospheric origin. The microbes enhance growth of plants by regulating hormonal balance, nutrition, siderophore production and modulation of antioxidative defence system of the plants. The use of microbes therefore solves the problems associated with sustainable agriculture including food safety, quality and productivity. On the basis of the favourable aspects of microorganisms, they can be recommended to be used as formulations in the commercial market after testing. Thus, the development of stable formulations is established as the other most effective approach towards sustainable agriculture through replacement in the use of chemical pesticides and fertilizers. Although, precautionary field trials with different rhizobacterial strains should be encouraged before the commercial exploitation of plant growth-promoting microorganisms.

References

Abdelkrim S, Jebara SH, Saadani O, Jebara M (2018) Potential of efficient and resistant plant growth-promoting rhizobacteria in lead uptake and plant defence stimulation in *Lathyrus sativus* under lead stress. Plant Biol 20(5):857–869

Ahemad M, Khan MS (2012) Effect of fungicides on plant growth promoting activities of phosphate solubilizing *Pseudomonas putida* isolated from mustard (*Brassica campestris*) rhizosphere. Chemosphere 86(9):945–950

Ahmad M, Zahir ZA, Asghar HN, Asghar M (2011) Inducing salt tolerance in mung bean through co-inoculation with rhizobia and plant-growth-promoting rhizobacteria containing 1-aminocyclopropane-1-carboxylate deaminase. Can J Microbiol 57(7):578–589

Ahmad M, Pataczek L, Hilger TH, Zahir ZA, Hussain A, Rasche F, Schafleitner R, Solberg SO (2018) Perspectives of microbial inoculation for sustainable development and environmental management. Front Microbiol 9:2992

Ali MA, Ali M, Sattar M, Ali L (2010) Sowing date effect on yield of different wheat varieties. J Agric Res 48(2):157–162

Armada E, Roldán A, Azcon R (2014) Differential activity of autochthonous bacteria in controlling drought stress in native *Lavandula* and *Salvia* plants species under drought conditions in natural arid soil. Microb Ecol 67(2):410–420

Babalola OO (2010) Beneficial bacteria of agricultural importance. Biotechnol Lett 32(11):1559–1570

Babu AG, Kim JD, Oh BT (2013) Enhancement of heavy metal phytoremediation by *Alnus firma* with endophytic *Bacillus thuringiensis* GDB-1. J Hazard Mater 250:477–483

Babu AG, Shea PJ, Sudhakar D, Jung IB, Oh BT (2015) Potential use of *Pseudomonas koreensis* AGB-1 in association with *Miscanthus sinensis* to remediate heavy metal (loid)-contaminated mining site soil. J Environ Manag 151:160–166

Badri DV, Chaparro JM, Zhang R, Shen Q, Vivanco JM (2013) Application of natural blends of phytochemicals derived from the root exudates of *Arabidopsis* to the soil reveal that phenolic-related compounds predominantly modulate the soil microbiome. J Biol Chem 288(7):4502–4512. https://doi.org/10.1074/jbc.M112.433300

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57(1):233–266. https://doi.org/10.1146/annurev.arplant.57.032905.105159

Banerjee S, Palit R, Sengupta C, Standing D (2010) Stress induced phosphate solubilization by ‘Arthrobacter’ sp. and ‘bacillus’ sp. isolated from tomato rhizosphere. Aust J Crop Sci 4(6):378

Barnard RL, Osborne CA, Firestone MK (2013) Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. ISME J 7(11):2229

Battisti DS, Naylor RL (2009) Historical warnings of future food insecurity with unprecedented seasonal heat. Science 323(5911):240–244

Berendsen RL, Pieterse CM, Bakker PA (2012) The rhizosphere microbiome and plant health. Trends Plant Sci 17(8):478–486

Bertin C, Yang X, Weston LA (2003) The role of root exudates and allelochemicals in the rhizosphere. Plant Soil 256:67–83

Bhattacharyya PN, Jha DK (2012) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. World J Microbiol Biotechnol 28(4):1327–1350

Bita C, Gerats T (2013) Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. Front Plant Sci 4:273

Borneman J, Becker JO (2007) Identifying microorganisms involved in specific pathogen suppression in soil. Annu Rev Phytopathol 45:153–172

Broeckling CD, Broz AK, Bergelson J, Manter DK, Vivanco JM (2008) Root exudates regulate soil fungal community composition and diversity. Appl Environ Microbiol 74(3):738–744. https://doi.org/10.1128/AEM.02188-07

Cardinale M, Ratering S, Suarez C, Montoya AMZ, Geissler-Plaum R, Schnell S (2015) Paradox of plant growth promotion potential of rhizobacteria and their actual promotion effect on growth of barley (*Hordeum vulgare* L.) under salt stress. Microbiol Res 181:22–32

Chaparro JM, Badri DV, Bakker MG, Sugiyama A, Manter DK, Vivanco JM (2013a) Root exudation of phytochemicals in *Arabidopsis* follows specific patterns that are developmentally programmed and correlate with soil microbial functions. PLoS One 8(2):e55731. https://doi.org/10.1371/journal.pone.0055731

Chaparro JM, Badri DV, Vivanco JM (2013b) Rhizosphere microbiome assemblage is affected by plant development. Int Soc Microb Ecol J 8(4):790–803. https://doi.org/10.1038/ismej.2013.196

Chen Y, Yang W, Chao Y, Wang S, Tang YT, Qiu RL (2017) Metal-tolerant *Enterobacter* sp. strain EG16 enhanced phytoremediation using *Hibiscus cannabinus* via siderophore-mediated plant growth promotion under metal contamination. Plant Soil 413(1–2):203–216

Cherif H, Marasco R, Rolli E, Ferjani R, Fusi M, Soussi A, Cherif A (2015) Oasis desert farming selects environment-specific date palm root endophytic communities and cultivable bacteria that promote resistance to drought. Environ Microbiol Rep 7(4):668–678

Chithrashree S, Udayshankar AC, Nayaka SC, Reddy MS (2011) Plant growth-promoting rhizobacteria mediate induced systemic resistance in rice against bacterial leaf blight caused by *Xanthomonas oryzae* pv. Oryzae. Biol Control 59:114–122

Chodak M, Gołębiewski M, Morawska-Płoskonka J, Kuduk K, Niklińska M (2015) Soil chemical properties affect the reaction of forest soil bacteria to drought and rewetting stress. Ann Microbiol 65(3):1627–1637

Clemens S, Ma JF (2016) Toxic heavy metal and metalloid accumulation in crop plants and foods. Annu Rev Plant Biol 67:489–512

Coats VC, Rumpho ME (2014) The rhizosphere microbiota of plant invaders: an overview of recent advances in the microbiomics of invasive plants. Front Microbiol 5:368

Damayanti TA, Pardede H, Mubarik NR (2007) Utilization of root-colonizing bacteria to protect hot-pepper against tobacco mosaic tobamovirus. HAYATI J Biosci 14(3):105–109

de Zelicourt A, Al-Yousif M, Hirt H (2013) Rhizosphere microbes as essential partners for plant stress tolerance. Mol Plant 6(2):242–245

Di Benedetto NA, Corbo MR, Campaniello D, Cataldi MP, Bevilacqua A, Sinigaglia M, Flagella Z (2017) The role of plant growth promoting bacteria in improving nitrogen use efficiency for sustainable crop production: a focus on wheat. Aims Microbiology 3(3):413–434

Doornbos R, Loon L, Bakker PHM (2012) Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere: a review. Agron Sustain Dev 32(1):227–243. https://doi.org/10.1007/s13593-011-0028-y

Egamberdieva D, Wirth SJ, Shurigin VV, Hashem A, Abd Allah EF (2017, 1887) Endophytic bacteria improve plant growth, symbiotic performance of chickpea (*Cicer arietinum* L.) and induce suppression of root rot caused by *Fusarium solani* under salt stress. Front Microbiol 8

El-Afry MM (2012) Anatomical studies on drought-stressed wheat plants (*Triticum aestivum* L.) treated with some bacterial strains. Acta Biologica Szegediensis 56(2):165–174

Evangelisti E, Rey T, Schornack S (2014) Cross-interference of plant development and plant–microbe interactions. Curr Opin Plant Biol 20:118–126

Ezzouhri L, Castro E, Moya M, Espinola F, Lairini K (2009) Heavy metal tolerance of filamentous fungi isolated from polluted sites in Tangier, Morocco. Afr J Microbiol Res 3(2):35–48

Fahad S, Hussain S, Bano A, Saud S, Hassan S, Shan D (2015) Potential role of phytohormones and plant growth-promoting rhizobacteria in abiotic stresses: consequences for changing environment. Environ Sci Pollut Res 22:4907–4921

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA (2009) Plant drought stress: effects, mechanisms and management. In: Sustainable agriculture. Springer, Dordrecht, pp 153–188

Fatnassi IC, Chiboub M, Saadani O, Jebara M, Jebara SH (2015) Phytostabilization of moderate copper contaminated soils using co-inoculation of *Vicia faba* with plant growth promoting bacteria. J Basic Microbiol 55(3):303–311

Finkel OM, Castrillo G, Paredes SH, González IS, Dangl JL (2017) Understanding and exploiting plant beneficial microbes. Curr Opin Plant Biol 38:155–163

Franken P (2012) The plant strengthening root endophyte Piriformospora indica: potential application and the biology behind. Appl Microbiol Biotechnol 96(6):1455–1464

Garcia-Contreras R, Maeda T, Wood TK (2016) Can resistance against quorum-sensing interference be selected? Int Soc Microb Ecol J 10(1):4–10

Gemperline E, Keller C, Li L (2016) Mass spectrometry in plant-omics. Anal Chem 88:3422–3434

Giuffrida F, Carla C, Angelo M, Cherubino L (2016) Effects of salt stress imposed during two growth phases on cauliflower production and quality. J Sci Food Agr 97:1552–1560

Glick BR (2010) Using soil bacteria to facilitate phytoremediation. Biotechnol Adv 28(3):367–374

Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 169(1):30–39

Glick BR (2015) Biocontrol mechanisms beneficial plant-bacterial interactions. Springer, Berlin, pp 123–157

Gonzalez JE, Marketon MM (2003) Quorum sensing in nitrogen fixing rhizobia. Microbiol Mol Biol Rev 67:574–592

Gopalakrishnan S, Sathya A, Vijayabharathi R, Srinivas V (2016) Formulations of plant growth-promoting microbes for field applications. In: Microbial inoculants in sustainable agricultural productivity. Springer, New Delhi, pp 239–251

Goswami S, Das S (2015) A study on cadmium phytoremediation potential of Indian mustard, *Brassica juncea*. Int J Phytoremediation 17(6):583–588

Govindasamy V, Senthilkumar M, Magheshwaran V, Kumar U, Bose P, Sharma V, Annapurna K (2010) *Bacillus* and *Paenibacillus* spp.: potential PGPR for sustainable agriculture. In: Plant growth and health promoting bacteria. Springer, Berlin, Heidelberg, pp 333–364

Gow NAR, Campbell TA, Morris BM, Osborne MC, Reid B, Shepherd SJ, van West P (1999) Signals and interactions between phytopathogenic zoospores and plant roots. In: England R, Hobbs G, Bainton N, Roberts DM (eds) Microbial Signaling and communication eds, Society for General Microbiology symposium, vol 57. Cambridge University Press, Cambridge, pp 285–305

Griggs D, Stafford-Smith M, Gaffney O, Rockstrom J, Ohman MC, Shyamsundar P, Steffen W, Glaser G, Kanie N, Noble I (2013) Policy: sustainable development goals for people and planet. Nature 495:305–307

Gunina A, Kuzyakov Y (2015) Sugars in soil and sweets for microorganisms: review of origin, content, composition and fate. Soil Biol Biochem 90:87–100

Guo B, Zhang Y, Li S, Lai T, Yang L, Chen J, Ding W (2016) Extract from maize (*Zea mays* L.): antibacterial activity of DIMBOA and its derivatives against *Ralstonia solanacearum*. Molecules 21(10):1397

Gupta G, Panwar J, Jha PN (2013) Natural occurrence of Pseudomonas aeruginosa, a dominant cultivable diazotrophic endophytic bacterium colonizing *Pennisetum glaucum* (L.) R. Br. Appl Soil Ecol 64:252–261

Gupta G, Parihar SS, Ahirwar NK, Snehi SK, Singh V (2015a) Plant growth promoting rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture. J Microb Biochem Technol 7(2):096–102

Gupta G, Parihar SS, Ahirwar NK, Snehi SK, Singh V (2015b) Plant growth promoting Rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture. J Microb Biochem Technol 7:096–102

Gusain YS, Singh US, Sharma AK (2015) Bacterial mediated amelioration of drought stress in drought tolerant and susceptible cultivars of rice (*Oryza sativa* L.). Afr J Biotechnol 14(9):764–773

Hadia-e-Fatima AA (2018) Micro-remediation of chromium contaminated soils. Peer J 6

Haichar FEZ, Santaella C, Heulin T, Achouak W (2014) Root exudates mediated interactions belowground. Soil Biol Biochem 77:69–80

Haldar S, Sengupta S (2015) Plant-microbe cross-talk in the Rhizosphere: insight and biotechnological potential. Open Microbiol J 9:1–7

Hashem A, Abd Allah EF, Alqarawi AA, Al Huqail AA, Egamberdieva D, Wirth S (2016) Alleviation of cadmium stress in *Solanum lycopersicum* L. by arbuscular mycorrhizal fungi via induction of acquired systemic tolerance. Saudi J Biol Sci 23(2):272–281

Hassan S, Mathesius U (2012) The role of flavonoids in rootrhizosphere signalling: opportunities and challenges for improving plant microbe interactions. J Exp Bot 63:3429–3444

Hassan R, Shaaban MI, Abdel Bar FM, El-Mahdy AM, Shokralla S (2016) Quorum sensing inhibiting activity of *Streptomyces coelicoflavus* isolated from soil. Front Microbiol 7:659

Hassan TU, Bano A, Naz I (2017) Alleviation of heavy metals toxicity by the application of plant growth promoting rhizobacteria and effects on wheat grown in saline sodic field. Int J Phytoremediation 19(6):522–529

Hassani MA, Duran P, Hacquard S (2018) Microbial interactions within the plant holobiont. Microbiome 6:58

Hayat R, Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60(4):579–598

Hayat S, Faraz A, Faizan M (2017) Root exudates: composition and impact on plant–microbe interaction. In: Ahmas I, Husai FM (eds) Biofilms in plant and soil health, pp 179–193

He S, McMahon KD (2011) Microbiology of "Candidatus Accumulibacter" in activated sludge. Microb Biotechnol 4:603–619

Heidari M, Golpayegani A (2012) Effects of water stress and inoculation with plant growth promoting rhizobacteria (PGPR) on antioxidant status and photosynthetic pigments in basil (*Ocimum basilicum* L.). J Saudi Soc Agric Sci 11(1):57–61

Helman Y, Chernin L (2015) Silencing the mob: disrupting quorum sensing as a means to fight plant disease. Mol Plant Pathol 16:316–329

Hmaeid N, Wali M, Mahmoud OMB, Pueyo JJ, Ghnaya T, Abdelly C (2019) Efficient rhizobacteria promote growth and alleviate NaCl-induced stress in the plant species *Sulla carnosa*. Appl Soil Ecol 133:104–113

Ho, Y.N., Mathew, D.C., & Huang, C.C. (2017). Plant-Microbe ecology: interactions of plants and symbiotic microbial communities. https://doi.org/10.5772/intechopen.69088

Hong KW, Koh CL, Sam CK, Yin WF, Chan KG (2012) Quorum quenching revisited-from signal decays to signalling confusion. Sensors 12:4661–4696. https://doi.org/10.3390/s120404661

Hosseini F, Mosaddeghi MR, Dexter AR (2017) Effect of the fungus *Piriformospora indica* on physiological characteristics and root morphology of wheat under combined drought and mechanical stresses. Plant Physiol Biochem 118:107–120

Jain S, Vaishnav A, Choudhary DK (2013) Bacteria-induced systemic resistance and growth promotion in *Glycine max* L. Merrill upon challenge inoculation with *Fusarium exosporium*. Proc Nat Acad Sci India B: Biol Sci 83:561–567

Jamil M, Zeb S, Anees M, Roohi A, Ahmed I, ur Rehman S, Rha ES (2014) Role of *Bacillus licheniformis* in phytoremediation of nickel contaminated soil cultivated with rice. Int J Phytoremediation 16(6):554–571

Jeandroz S, Lamotte O (2017) Plant responses to biotic and abiotic stresses: lessons from cell Signaling. Front Plant Sci 13:1772

Joshi P, Bhatt AB (2011) Diversity and function of plant growth promoting rhizobacteria associated with wheat rhizosphere in north Himalayan region. Int J Environ Sci 1(6):1135

Ju W, Liu L, Fang L, Cui Y, Duan C, Wu H (2019) Impact of co-inoculation with plant-growth-promoting rhizobacteria and rhizobium on the biochemical responses of alfalfa-soil system in copper contaminated soil. Ecotoxicol Environ Saf 167:218–226

Kai M, Haustein M, Molina F, Petri A, Scholz B, Piechulla B (2009) Bacterial volatiles and their action potential. Appl Microbiol Biotechnol 81:1001–1012

Kai M, Effmert U, Piechulla B (2016) Bacterial-plant-interactions: approaches to unravel the biological function of bacterial volatiles in the rhizosphere. Front Microbiol 7:108

Kamran MA, Eqani SAMAS, Bibi S, Xu RK, Monis MFH, Katsoyiannis A, Chaudhary HJ (2016) Bioaccumulation of nickel by *E. sativa* and role of plant growth promoting rhizobacteria (PGPRs) under nickel stress. Ecotoxicol Environ Saf 126:256–263

Kanchiswamy CN, Malnoy M, Maffei ME (2015) Chemical diversity of microbial volatiles and their potential for plant growth and productivity. Front Plant Sci 6:151

Kang SM, Radhakrishnan R, Khan AL, Kim MJ, Park JM, Kim BR, Shin DH, Lee IJ (2014) Gibberellin secreting rhizobacterium, *Pseudomonas putida* H-2-3 modulates the hormonal and stress physiology of soybean to improve the plant growth under saline and drought conditions. Plant Physiol Biochem 84:115–124

Kang SM, Khan AL, Waqas M, You YH, Hamayun M, Joo GJ, Shahzad R, Choig K-S, Lee IJ (2015) Gibberellin-producing *Serratia nematodiphila* PEJ1011 ameliorates low temperature stress in *Capsicum annuum* L. Eur J Soil Biol 68:85–93

Kasim WA, Osman ME, Omar MN, El-Daim IAA, Bejai S, Meijer J (2013) Control of drought stress in wheat using plant-growth-promoting bacteria. J Plant Growth Regul 32(1):122–130

Kaur G, Asthir B (2017) Molecular responses to drought stress in plants. Biol Plant 61(2):201–209

Kaushal M, Wani SP (2016) Plant-growth-promoting rhizobacteria: drought stress alleviators to ameliorate crop production in drylands. Ann Microbiol 66(1):35–42

Kaymak HC (2010) Potential of PGPR in agricultural innovations. In: Plant growth and health promoting bacteria. Springer, Berlin, Heidelberg, pp 45–79

Khan AG (2005) Role of soil microbes in the rhizospheres of plants growing on trace metal contaminated soils in phytoremediation. J Trace Elem Med Biol 18(4):355–364

Khan AL, Waqas M, Hussain J, Al-Harrasi A, Hamayun M, Lee IJ (2015) Phytohormones enabled endophytic fungal symbiosis improve aluminum phytoextraction in tolerant *Solanum lycopersicum*: an examples of *Penicillium janthinellum* LK5 and comparison with exogenous GA3. J Hazard Mater 295:70–78

Khan WU, Ahmad SR, Yasin NA, Ali A, Ahmad A (2017a) Effect of *Pseudomonas fluorescens* RB4 and *Bacillus subtilis* 189 on the phytoremediation potential of *Catharanthus roseus* (L.) in cu and Pb-contaminated soils. Int J Phytoremediation 19(6):514–521

Khan WU, Yasin NA, Ahmad SR, Ali A, Ahmed S, Ahmad A (2017b) Role of Ni-tolerant *Bacillus* spp. and Althea rosea L. in the phytoremediation of Ni-contaminated soils. Int J Phytoremediation 19(5):470–477

Khan N, Bano A, Zandi P (2018) Effects of exogenously applied plant growth regulators in combination with PGPR on the physiology and root growth of chickpea (*Cicer arietinum*) and their role in drought tolerance. J Plant Interact 13(1):239–247

Khanna K, Jamwal VL, Kohli SK, Gandhi SG, Ohri P, Bhardwaj R, Ahmad P (2019) Plant growth promoting rhizobacteria induced cd tolerance in *Lycopersicon esculentum* through altered antioxidative defense expression. Chemosphere 217:463–474

Krol A, Amarowwicz R, Weidner S (2015) The effects of cold stress on the phenolic compounds and antioxidant capacity of grapevine (*Vitis vinifera* L.) leaves. J Plant Physiol 189:97–104

Kumar A, Verma JP (2018) Does plant—microbe interaction confer stress tolerance in plants: a review? Microbiol Res 207:41–52

Kumar A, Chanderman A, Makolomakwa M, Perumal K, Singh S (2016) Microbial production of phytases for combating environmental phosphate pollution and other diverse applications. Crit Rev Environ Sci Technol 46:556–591

Kuzyakov Y, Blagodatskaya E (2015) Microbial hotspots and hot moments in soil: concept and review. Soil Biol Biochem 83:184–199

Lakshmanan V, Selvaraj G, Bais HP (2014) Functional soil microbiome: belowground solutions to an aboveground problem. J Plant Physiol 166(2):689–700

Lata C, Prasad M (2011) Role of DREBs in regulation of abiotic stress responses in plants. J Exp Bot 62(14):4731–4748

Lee BD, Dutta S, Ryu H, Yoo SJ, Suh DS, Park K (2015) Induction of systemic resistance in Panax ginseng against *Phytophthora cactorum* by native *Bacillus myloliquefaciens* HK34. J. Ginseng Research 39:213–220

Li X, Zhang T, Wang X, Hua K, Zhao L, Han Z (2013) The composition of root exudates from two different resistant peanut cultivars and their effects on the growth of soil-borne pathogen. Int J Biol Sci 9:164–173. https://doi.org/10.7150/ijbs.5579

Li H, Lei P, Pang X, Li S, Xu H, Xu Z, Feng X (2017) Enhanced tolerance to salt stress in canola (*Brassica napus* L.) seedlings inoculated with the halotolerant *Enterobacter cloacae* HSNJ4. Appl Soil Ecol 119:26–34

Li SL, Li ZG, Yang LT, Li YR, He ZL (2018) Differential effects of cold stress on chloroplasts structures and photosynthetic characteristics in cold-sensitive and cold-tolerant cultivars of sugarcane. Sugar Tech 20:11–20

Lim JH, Kim SD (2013) Induction of drought stress resistance by multi-functional PGPR *Bacillus licheniformis* K11 in pepper. Plant Pathol J 29(2):201

Ma Y, Rajkumar M, Luo Y, Freitas H (2013) Phytoextraction of heavy metal polluted soils using *Sedum plumbizincicola* inoculated with metal mobilizing *Phyllobacterium myrsinacearum* RC6b. Chemosphere 93(7):1386–1392

Machado RM, Bryla DR, Vargas O (2014) Effects of salinity induced by ammonium sulfate fertilizer on root and shoot growth of highbush blueberry. Acta Hortic 1017:407–414

Machado J, Campos A, Vasconcelos V, Freitas M (2017) Effects of microcystin-LR and cylindrospermopsin on plant-soil systems: a review of their relevance for agricultural plant quality and public health. Environ Res 153:191–204

Macho AP, Zipfel C (2014) Plant PRRs and the activation of innate immune signaling. Mol Cell 54(2):263–272

Malla MA, Dubey A, Yadav S, Kumar A, Hashem A, Abd Allah EF (2018) Understanding and designing the strategies for the microbe-mediated remediation of environmental contaminants using Omics approaches. Front Microbiol 9:1132

Mandyam K, Jumpponen A (2014) Unraveling the dark septate endophyte functions: insights from the *Arabidopsis* model. In: Advances in endophytic research. Springer, New Delhi, pp 115–141

Mani D, Kumar C (2014) Biotechnological advances in bioremediation of heavy metals contaminated ecosystems: an overview with special reference to phytoremediation. Int J Environ Sci Technol 11:843–872

Martínez-Viveros O, Jorquera MA, Crowley DE, Gajardo GMLM, Mora ML (2010) Mechanisms and practical considerations involved in plant growth promotion by rhizobacteria. J Soil Sci Plant Nutr 10(3):293–319

Mayak S, Tirosh T, Glick BR (2004) Plant growth-promoting bacteria confer resistance in tomato plants to salt stress. Plant Physiol Biochem 42(6):565–572

Meena RK, Singh RK, Singh NP, Meena SK, Meena VS (2015) Isolation of low temperature surviving plant growth–promoting rhizobacteria (PGPR) from pea (*Pisum sativum* L.) and documentation of their plant growth promoting traits. Biocatal Agric Biotechnol 4(4):806–811

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37(5):634–663

Mhlongo MI, Piater LA, Madala NE, Labuschagne N, Dubery IA (2018) The chemistry of plant–microbe interactions in the Rhizosphere and the potential for metabolomics to reveal Signaling related to Defense priming and induced systemic resistance. Front Plant Sci 9:112

Mishra M, Kumar U, Mishra PK, Prakash V (2010) Efficiency of plant growth promoting rhizobacteria for the enhancement of *Cicer arietinum* L. growth and germination under salinity. Adv Biol Res 4(2):92–96

Mishra J, Singh R, Arora NK (2017a) Alleviation of heavy metal stress in plants and remediation of soil by rhizosphere microorganisms. Front Microbiol 8:1706

Mishra SK, Khan MH, Misra S, Dixit VK, Khare P, Srivastava S, Chauhan PS (2017b) Characterisation of *Pseudomonas* spp. and *Ochrobactrum* sp. isolated from volcanic soil. Antonie Van Leeuwenhoek 110(2):253–270

Mommer L, Kirkegaard J, van Ruijven J (2016) Root–root interactions: towards a rhizosphere framework. Trends Plant Sci 21(3):209–217

Morris CE, Sands DC, Bardin M, Jaenicke R, Vogel B, Leyronas C, Ariya PA, Psenner R (2011) Microbiology and atmospheric processes: research challenges concerning the impact of airborne micro-organisms on the atmosphere and climate. Biogeosciences 8:17–25

Mosa KA, Saadoun I, Kumar K, Helmy M, Dhankher OP (2016) Potential biotechnological strategies for the Cleanup of heavy metals and metalloids. Front Plant Sci 7:303

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25(2):239–250

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Ann Rev Plant Biol 59:651–681

Mustapha MU, Halimoon N (2015) Microorganisms and biosorption of heavy metals in the environment: a review paper. J Microbiol Biochem Technol 7:253–256

Nadeem SM, Ahmad M, Zahir ZA, Javaid A, Ashraf M (2014) The role of mycorrhizae and plant growth promoting rhizobacteria (PGPR) in improving crop productivity under stressful environments. Biotechnol Adv 32(2):429–448

Nadeem SM, Ahmad M, Naveed M, Imran M, Zahir ZA, Crowley DE (2016) Relationship between in vitro characterization and comparative efficacy of plant growth-promoting rhizobacteria for improving cucumber salt tolerance. Arch Microbiol 198(4):379–387

Narendrula-Kotha R, Nkongolo KK (2017) Microbial response to soil liming of damaged ecosystems revealed by pyrosequencing and phospholipid fatty acid analyses. PLoS One 12(1):e0168497

Naseem H, Bano A (2014) Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. J Plant Interact 9(1):689–701

Naz I, Bano A, Ul-Hassan T (2009) Isolation of phytohormones producing plant growth promoting rhizobacteria from weeds growing in Khewra salt range, Pakistan and their implication in providing salt tolerance to *Glycine max* L. Afr J Biotechnol 8(21)

Newton AC, Fitt BDL, Atkins SD, Walters DR, Daniell TJ (2010) Pathogenesis, parasitism and mutualism in the trophic space of microbe– plant interactions. Trends Microbiol 18(8):365–373

Nizzetto LI (2010) Past, present, and future controls on levels of persistent organic pollutants in the global environment. Environ Sci Technol 44:6526–6531

O'Callaghan M (2016) Microbial inoculation of seed for improved crop performance: issues and opportunities. Appl Microbiol Biotechnol 100(13):5729–5746

Ojuederie OB, Babalola OO (2017) Microbial and plant-assisted bioremediation of heavy metal polluted environments: a review. Int J Environ Res Public Health 14:1504

Oladipo OG, Awotoye OO, Olayinka A, Bezuidenhout CC, Maboeta MS (2018) Heavy metal tolerance traits of filamentous fungi isolated from gold and gemstone mining sites. Braz J Microbiol 49(1):29–37

Olanrewaju OS, Glick BR, Babalola OO (2017) Mechanisms of action of plant growth promoting bacteria. World J Microbiol Biotechnol 33(11):197

Olanrewaju OS, Ayangbenro AS, Glick BR, Babalola OO (2019) Plant health: feedback effect of root exudates-rhizobiome interactions. Appl Microbiol Biotechnol 103:1155–1166

Ong GH, Ho XH, Shamkeeva S, Manasha Savithri Fernando AS, Wong LS (2017) Biosorption study of potential fungi for copper remediation from peninsular Malaysia. Remediat J 27(4):59–63

Ortiz N, Armada E, Duque E, Roldán A, Azcón R (2015) Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: effectiveness of autochthonous or allochthonous strains. J Plant Physiol 174:87–96

Ortíz-Castro R, Contreras-Cornejo HA, Macías-Rodríguez L, López-Bucio J (2009) The role of microbial signals in plant growth and development. Plant Signaling & Behaviour 4(8):701–712

Pandey PK, MCk S, Singh AK, Singh S, Pandey AK, Pathak M, Kumar M, Shakywar RC, Patidar RK, Devi MB (2016) Arsenal of endophytic actinobacterial microbes. Int J Curr Microbiol App Sci 5:62–66

Panuccio MR, Sorgonà A, Rizzo M, Cacco G (2009) Cadmium adsorption on vermiculite, zeolite and pumice: batch experimental studies. J Environ Manag 90(1):364–374

Paredes-Páliz KI, Pajuelo E, Doukkali B, Caviedes MÁ, Rodríguez-Llorente ID, Mateos-Naranjo E (2016) Bacterial inoculants for enhanced seed germination of *Spartina densiflora*: implications for restoration of metal polluted areas. Mar Pollut Bull 110(1):396–400

Pathma J, Kennedy RK, Sakthivel N (2011) Mechanisms of fluorescent pseudomonads that mediate biological control of phytopathogens and plant growth promotion of crop plants. In: Bacteria in agrobiology: plant growth responses. Springer, Berlin, Heidelberg, pp 77–105

Pii Y, Mimmo T, Tomasi N, Terzano R, Cesco S, Crecchio C (2015) Microbial interactions in the rhizosphere: beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process. A review. Biol Fertil Soils 51(4):403–415

Pires C, Franco AR, Pereira SI, Henriques I, Correia A, Magan N, Castro PM (2017) Metal (loid)-contaminated soils as a source of culturable heterotrophic aerobic bacteria for remediation applications. Geomicrobiol J 34(9):760–768

Poole P (2017) Shining a light on the dark world of plant root–microbe interactions. Proc Natl Acad Sci U S A 114(17):4281–4283

Pravisya P, Jayaram KM, Yusuf A (2019) Biotic priming with *Pseudomonas fluorescens* induce drought stress tolerance in *Abelmoschus esculentus* (L.) Moench (okra). Physiol Mol Biol Plants 25:101–112

Raghunandan K, McHunu S, Kumar A, Kumar KS, Govender A, Permaul K, Singh S (2014) Biodegradation of glycerol using bacterial isolates from soil under aerobic conditions. J Environ Sci Health A Toxic/Hazard Subst Environ Eng 49:85–92

Raghunandan, K., Kumar, A., Kumar, S., Permaul, K., & Singh, S. (2018). Production of gellan gum, an exopolysaccharide, from biodiesel-derived waste glycerol by *Sphingomonas* spp. *3Biotech*, *8*, 71

Ramos J, Marques L, van Dillewijn S, Espinosa-Urgel P, Segura M, Duque AE et al (2018) Laboratory research aimed at closing the gaps in microbial bioremediation. Trends Biotechnol 29:641–647

Rizwan M, Ali S, Zia M, Rehman U, Rinklebe J, Tsang DCW, Bashir A, Maqbool A, Tack FMG, Ok YS (2018) Cadmium phytoremediation potential of brassica crop species. Sci Total Environ 631–632:1175–1191

Rodríguez VM, Soengas P, Villaverde VA, Sotelo T, Cartea ME, Velasco P (2015) Effect of temperature stress on the early vegetative development of *Brassica oleracea* L. BMC Plant Biol 15:145

Rosier A, Bishnoi U, Lakshmanan V (2016) A perspective on interkingdom signaling in plant-beneficial microbe interactions. Plant Mol Biol 90:537–548

Rothballer M, Uhl J, Kunze J, Schmitt-Kopplin P, Hartmann A (2018) Detection of the bacterial quorum-sensing signaling molecules N-acylhomoserine lactones (HSL) and N-acyl-homoserine (HS) with an enzyme-linked immunosorbent assay (ELISA) and via ultrahigh-performance liquid chromatography coupled to mass spectrometry (UHPLC-MS). Methods Mol Biol 1673:61–72

Ruscitti M, Arango M, Beltrano J (2017) Improvement of copper stress tolerance in pepper plants (*Capsicum annuum* L.) by inoculation with arbuscular mycorrhizal fungi. Theor Exp Plant Physiol 29(1):37–49

Santoyoa G, Moreno-Hagelsiebb G, Orozco-Mosquedac M, del Glick BR (2016) Plant growth-promoting bacterial endophytes. Microbiol Res 183:92–99

Sapre S, Gontia-Mishra I, Tiwari S (2018) *Klebsiella* sp. confers enhanced tolerance to salinity and plant growth promotion in oat seedlings (*Avena sativa*). Microbiol Res 206:25–32

Sarkar A, Ghosh PK, Pramanik K, Mitra S, Soren T, Pandey S, Maiti TK (2018a) A halotolerant *Enterobacter* sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. Res Microbiol 169(1):20–32

Sarkar A, Pramanik K, Mitra S, Soren T, Maiti TK (2018b) Enhancement of growth and salt tolerance of rice seedlings by ACC deaminase-producing *Burkholderia* sp. MTCC 12259. J Plant Physiol 231:434–442

Sasse J, Martinoia E, Northen T (2017) Feed your friends: do plant exudates shape the root microbiome? Trends Plant Sci 23:25–41

Saxena B, Shukla K, Giri B (2017) Arbuscular mycorrhizal fungi and tolerance of salt stress in plants. In: Arbuscular Mycorrhizas and stress tolerance of plants. Springer, Singapore, pp 67–97

Schmidt R, Köberl M, Mostafa A, Ramadan EM, Monschein M, Jensen KB, Berg G (2014) Effects of bacterial inoculants on the indigenous microbiome and secondary metabolites of chamomile plants. Front Microbiol 5:64

Shahid I, Rizwan M, Baig DN, Saleem RS, Kauser AM, Mehnaz S (2017) Secondary metabolites production and plant growth promotion by *Pseudomonas chlororaphis* and *P. aurantiaca* strains isolated from cactus, cotton, and Para grass. J Microbiol Biotechnol 27(3):480–491

Shrivastava P, Kumar R (2015) Soil salinity: a serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. Saudi J Biol Sci 22(2):123–131

Shukla N, Awasthi RP, Rawat L, Kumar J (2012) Biochemical and physiological responses of rice (*Oryza sativa* L.) as influenced by *Trichoderma harzianum* under drought stress. Plant Physiol Biochem 54:78–88

Singh RP, Jha PN (2016) A halotolerant bacterium *Bacillus licheniformis* HSW-16 augments induced systemic tolerance to salt stress in wheat plant (*Triticum aestivum*). Front Plant Sci 7:1890

Singla, J., & Krattinger, S.G. (2016). Biotic stress resistance gene in wheat, In: Wrigley CW, Faubion J, Corke H, Seetharaman K (eds). Encyclopedia of food grains. Oxford: Elsevier, 388–392

Sorty AM, Meena KK, Choudhary K, Bitla UM, Minhas PS, Krishnani KK (2016) Effect of plant growth promoting bacteria associated with halophytic weed (*Psoralea corylifolia* L) on germination and seedling growth of wheat under saline conditions. Appl Biochem Biotechnol 180(5):872–882

Souza RD, Ambrosini A, Passaglia LM (2015) Plant growth-promoting bacteria as inoculants in agricultural soils. Genet Mol Biol 38(4):401–419

Spaepen S, Vanderleyden J, Remans R (2007) Indole-3-acetic acid in microbial and microorganism-plant signaling. FEMS Microbiol Rev 31(4):425–448

Spence C, Bais H (2015) Role of plant growth regulators as chemical signals in plant–microbe interactions: a double edged sword. Curr Opin Plant Biol 27:52–58

Sunkar R, Li YF, Jagadeeswaran G (2012) Functions of microRNAs in plant stress responses. Trends Plant Sci 17:196–203

Tauqeer HM, Ali S, Rizwan M, Ali Q, Saeed R, Tikhar UI, Ahmad R, Farid M, Abbasi GH (2016) Phytoremediation of heavy metals by *Alternanthera bettzickiana*: growth and physiological response. Ecotoxicol Environ Saf 126:138–146

Tiwari S, Lata C (2018) Heavy metal stress, signaling, and tolerance due to plant-associated microbes: an overview. Front Plant Sci 9:452

Tiwari S, Lata C, Chauhan PS, Nautiyal CS (2016) *Pseudomonas putida* attunes morphophysiological, biochemical and molecular responses in *Cicer arietinum* L. during drought stress and recovery. Plant Physiol Biochem 99:108–117

Tobin JM (2001) Fungal metal biosorption. In British mycological society symposium series. 23: 424–444)

Tripathi P, Singh PC, Mishra A, Srivastava S, Chauhan R, Awasthi S, Tripathi RD (2017) Arsenic tolerant *Trichoderma* sp. reduces arsenic induced stress in chickpea (*Cicer arietinum*). Environ Pollut 223:137–145

Trivedi P, Pandey A, Palni LMS (2005) Carrier-based preparations of plant growth-promoting bacterial inoculants suitable for use in cooler regions. World J Microbiol Biotechnol 21(6–7):941–945

Tyc O, Zweers H, de Boer W, Gardeva P (2015) Volatiles in inter-specific bacterial interactions. Front Microbiol 6:412

Ulrich DE, Sevanto S, Ryan M, Albright MB, Johansen RB, Dunbar JM (2019) Plant-microbe interactions before drought influence plant physiological responses to subsequent severe drought. Sci Rep 9(1):249

Upadhyay SK, Singh JS, Singh DP (2011) Exopolysaccharide producing PGPR under salinity condition. Pedosphere 21(2):214e22

Upadhyay SK, Singh JS, Saxena AK, Singh DP (2012) Impact of PGPR inoculation on growth and antioxidant status of wheat under saline conditions. Plant Biol 14(4):605–611

van der Meer JR, Belkin S (2010) Where microbiology meets microengineering: design and applications of reporter bacteria. Nat Rev Microbiol 8:511–522

Van Loon LC (2007) Plant responses to plant growth-promoting rhizobacteria. In: New perspectives and approaches in plant growth-promoting rhizobacteria research. Springer, Dordrecht, pp 243–254

Vardharajula S, Zulfikar Ali S, Grover M, Reddy G, Bandi V (2011) Drought-tolerant plant growth promoting bacillus spp.: effect on growth, osmolytes, and antioxidant status of maize under drought stress. J Plant Interact 6(1):1–14

Venkateshwaran M, Volkening JD, Sussman MR, Ané JM (2013) Symbiosis and the social network of higher plants. Curr Opin Plant Biol 16(1):118–127

Venturi V, Keel C (2016) Signaling in the rhizosphere. Trends Plant Sci 21:187–198

Verma C, Das AJ, Kumar R (2017) PGPR-assisted phytoremediation of cadmium: an advancement towards clean environment. Curr Sci 113:4

Vimal SR, Singh JS, Arora NK, Singh S (2017) Soil-plant-microbe interactions in stressed agriculture management: a review. Pedosphere 27(2):177–192

Vives-Peris V, Gómez-Cadenas A, Pérez-Clemente RM (2018) Salt stress alleviation in citrus plants by plant growth-promoting rhizobacteria *Pseudomonas putida* and *Novosphingobium* sp. Plant Cell Rep 37(11):1557–1569

Wei-wei LIU, Wei MU, Bing-Yu ZHU, You-Chen DU, Feng LIU (2008) Antagonistic activities of volatiles from four strains of *Bacillus* spp. and *Paenibacillus* spp. against soil-borne plant pathogens. Agric Sci China 7:1104–1114

Weston LA, Ryan PR, Watt M (2012) Mechanisms for cellular transport and release of allelochemicals from plant roots into the rhizosphere. J Exp Bot 63:3445–3454

Wille L, Monika M, Messmer MM, Studer B, Hohmann P (2019) Insights to plant–microbe interactions provide opportunities to improve resistance breeding against root diseases in grain legumes. Plant Cell Environ 42:20–40

Yánez-Mendizábal V, Viñas I, Usall J, Torres R, Solsona C, Abadias M, Teixidó N (2012) Formulation development of the biocontrol agent *Bacillus subtilis* strain CPA-8 by spray-drying. J Appl Microbiol 112(5):954–965

Youssef MMA, Eissa MFM (2014) Biofertilizers and their role in management of plant parasitic nematodes. A review. E3 J Biotechnol Pharm Res 5(1):1–6

Zahir ZA, Arshad M, Frankenberger WT (2004) Plant growth promoting rhizobacteria: applications and perspectives in agriculture. Adv Agron 81(1):98–169

Zahir ZA, Munir A, Asghar HN, Shaharoona B, Arshad M (2008) Effectiveness of rhizobacteria containing ACC deaminase for growth promotion of peas (*Pisum sativum*) under drought conditions. J Microbiol Biotechnol 18(5):958–963

Zandalinas SI, Mittler R, Balfagón D, Arbona V, Gómez-Cadenas A (2018) Plant adaptations to the combination of drought and high temperatures. Physiol Plant 162(1):2–12

Zhang H, Murzello C, Sun Y, Kim MS, Xie X, Jeter RM, Paré PW (2010) Choline and osmotic-stress tolerance induced in *Arabidopsis* by the soil microbe *Bacillussubtilis* (GB03). Mol Plant-Microbe Interact 23(8):1097–1104

Zhang N, Wang D, Liu Y (2014) Effects of different plant root exudates and their organic acid components on chemotaxis, biofilm formation and colonization by beneficial rhizosphere-associated bacterial strains. Plant Soil 374:689–700

Zhang Y, Ruyter-Spira C, Bouwmeester HJ (2015) Engineering the plant rhizosphere. Curr Opin Biotechnol 32:136–142

Zhou R, Hyldgaard B, Yu X, Rosenqvist E, Ugarte RM, Yu S, Wu Z, Ottosen CO, Zhao T (2018) Phenotyping of faba beans (*Vicia faba* L.) under cold and heat stresses using chlorophyll fluorescence. Euphytica 214:68

Złoch M, Thiem D, Gadzała-Kopciuch R, Hrynkiewicz K (2016) Synthesis of siderophores by plant-associated metallotolerant bacteria under exposure to Cd2+. Chemosphere 156:312–325

Zuniga A, Donoso RA, Ruiz D, Ruz GA, Gonzalez B (2017) Quorum sensing systems in the plant growth-promoting bacterium *Paraburkholderia phytofirmans* PsJN exhibit cross-regulation and are involved in biofilm formation. Mol Plant-Microbe Interact 30(7):557–565

Chapter 27
Breeding Plants for Future Climates

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Contents

Abstract At present, the erratic environmental conditions along with ever-increasing human population have created a problem for the agricultural researchers to fulfill the world food demand, with present rate of increase in crop production. Increase in world mean temperature along with shortage of freshwater has further worsened this situation. Due to increasing greenhouse effect in last few decades, it has increased the average world temperature more than 1.5 °C that increased the evapotranspiration and created a problem of aridity in some areas of the world. It is

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estimated that till 2050, there is a need to double the world food production with a rate of 2–5% per year but present rate of only 0.9%. It is only possible by increasing the crop production area or by crop production per capita. The former one is not possible in present environmental conditions due to limited sources of freshwater. However, it is possible to achieve the latter one through different ways, when there is a limited supply of water. It is possible through the selection from the available germplasm that can perform better with better production under the changing environmental conditions, and it seems the important and foremost way to deal with the problems of world food demand. Crop breeding for the selection of varieties with better production under changing and stressful environmental conditions is gaining interest. In this regard, the selection of crop varieties against different abiotic stresses for better production seems to be the most important one. Normally, the breeding for the selection of stress-tolerant crop varieties is based on different agronomic traits (traits of interest) such as plant biomass production, yield attributes, and different stress tolerance indices that are considered necessary ones. The stress tolerance mechanism in plants is a phenomenon of different cellular physio-biochemical attributes. However, it is a complex mechanism because the stress tolerance in crops is multigenic and complex mechanism and is purely under the control of genetics. In this regard, present interest and focus of researchers in the study of quantitative trait loci (QTLs) has played an important role for the selection and development of stress-tolerant crop varieties in a short time. Though the fruitful success regarding the QTL-based selection has been achieved, but due to the complexity in multigenic nature of stress tolerance, the behavior of the crop varieties changes under the changing environmental conditions. The present chapter is a comprehensive update regarding selection of stress-tolerant crop varieties for better production under the changing environmental conditions. So, in the future in view of changing environmental scenario, it is necessary to find out or develop the crop varieties that can perform better with better production under such conditions that will be fruitful to fulfill the world food demand for ever-increasing world population at present and in the near future.

Keywords Environmental stresses · Crop plants · Breeding · Physiological traits · Agronomic traits · QTLs

27.1 Introduction

Climate can be defined as the change in weather conditions in a given region for a long period of time that range from decades to millions of years. The climate change may be concise to a specific region or across the entire earth (Sahney et al. 2010). Farmers have developed ways to the changing climatic conditions but the changing weather conditions in a way are major problems for the proper crop growth and production (Adger et al. 2007). Changing environmental conditions are major threat to annual food production that causes the problem of malnutrition and food security. Furthermore, these changing environmental conditions could lead to different abiotic stresses like drought (Hendrix and Glaser 2007; Lobell et al. 2008). Among environmental issues the changes in rainfall patterns is major one, which could cause drought in one area and flooding in others with a significant decline in crop production and final yield (Hendrix and Glaser 2007) that causes the problem of food security for ever-increasing world population (Brown and Funk 2008).

Due to increased urbanization a huge amount of greenhouse gasses have been added in environments that have resulted in annual increase in temperature. It is estimated that the average increase in temperature is about 0.8 °C globally, while in Pakistan the average temperature increase is 0.5 °C that results in an increase in number of heat shocks per year (El-Sharkawy 2014). This increase in temperature has been resulted in decreased plant growth due to increased transpiration rate and low availability of irrigation water (El-Sharkawy 2014).

The gradual increase in earth's temperature can cause the melting of the ice caps, rise on the sea level, and many other environmental challenges. The main reason behind this is the accumulation of the greenhouse gases and in the future it could be more dangerous for the health, safety, and welfare of the ecosystem (Mahmood et al. 2010). High temperature can result in increased growth for the crops growing in cooler but in most of cases the negative results in crop yield are expected under high temperature. High temperature results in water shortage in crops growing in the areas with low rainfall. High temperature directly affects the different physiological and biochemical processes in the plants (Karl et al. 2009). There are four major compounds that are responsible for the greenhouse effect. These compounds include CO_2 that took play their 50–55% role in greenhouse effect. The other compounds include chlorofluorocarbons (CFCs), methane, and nitric oxide (NO_2) (Nepstad et al. 2009; Smith and Gregory 2013). Furthermore, increased deforestation along with high atmospheric CO_2 in the environment may result in more increase in mean atmospheric temperature and problems could be more severe. High temperature significantly affects the plant growth especially at early growth stages. Normally, the temperature ranging from 35 to 45 °C results in heat stress (Mahmood et al. 2010; Ulukan 2011). Heat stress directly affects the plant metabolism that leads to the damage to the cellular membranes due to overproduction of reactive oxygen species (Yousfi et al. 2010).

Human activities are affecting earth's natural environment since after the industrial revolution around 1750. This significantly affected the ratio between incoming solar radiations and outgoing infrared radiations that are the major part of earth energy balance. The increased concentration of all greenhouse gases in the atmosphere has further increased the atmospheric temperature. CO_2 is increased due to industrialization, urbanization, and increased consumption and burning of fossil fuels. Agriculture, landfills, and natural gas distributions have increased the concentration of methane in the environment. NO_2 have been increased due to increased use of fertilizers and fossil fuels. All these factors collectively increased the effect of global warming that result in annual increase in temperature of the atmosphere

(IPCC 2007). Global temperature has been significantly increased during the twentieth century (Alexander et al. 2006). Average global temperature has been risen 1.1°F just in past thirty years (Hansen et al. 2006). There is a direct correlation between annual increase in temperature and increased concentration of greenhouse gasses. It has been estimated by the IPCC that the human activities have increased the concentration of greenhouse gasses up to 70% from 1970 to 2004. The IPCC states that the rise of global temperatures is due to human activity and predicts the average global temperature can rise 2 to 11.5°F by 2100 (IPCC 2013).

At present due to rapid increase in population, it increased the demand for food with better nutritional quality. Along with the world population increase, the changing environmental condition has further created a problem to fulfill this demand. There is a need of 2.9% in crop production till 2050 to fulfill the food demand of ever-increasing population. Further food production, storage, and marketing are also directly linked to weather extremes and climatic changing conditions. Global food security can be defined as when all the people have access to safe and nutritious food to meet their dietary needs (FAO 1996). World food supply is dependent on few crops especially cereals, oil seeds, sugars, and soybeans. The demand for these crops is increasing with increasing population, but due to change in environmental condition and adverse effects of abiotic stress, the growth and production of these crops is affected adversely (Curtis and Halford 2014). Yields of these crops are directly depending on environmental conditions. Sudden change in the environment and harsh climatic conditions reduce the crop production.

Climatic changes have significant effects on water resources, human health, and food security especially in developing countries (Magadza 2006). Huge literature has been cited to study the effect of the environment on crop yield especially in cereals like wheat, maize, and rice. Environmental changes are one of the most significant factors that directly affect the crop growth and production (Magadza 2006). During past few decades climatic conditions have changed so rapidly that significantly affected the annual food production. Changes in rainfall patterns and annual increase in atmospheric temperature due to global warming have significantly decreased the crop production and the problem is getting more severe in the coming future (Reddy and Pachepsky 2000). Climatic changes are a global phenomenon but developing countries are affected more due to its dependence on agriculture. Food security and availability of water are highly susceptible to changing environmental conditions. Due to these changing environmental conditions and annual increase in temperature, it is estimated that the Himalayan glaciers will disappear by 2035. This rapid melting of glacier will result in floods in some areas and water shortage in others (Misra 2014). Many studies have revealed that the climatic change has direct effect on food production (Janjua et al. 2010; Kirby et al. 2016). It is estimated that the wheat production of South Asian countries will decrease up to 50% by 2050 (Mahmood et al. 2010). It is stated by Peterson Institute that global warming will decrease the agricultural productivity by 10–25 % in almost all developing countries and if it remains unchanged it will also reduce the agricultural capacity. Therefore climate changes have serious threat to food production if the problem is not resolved (Cline 2007). Due to global warming, the areas suitable for crop growth are becoming too hot and too dry and the problem is becoming more severe in the coming future (Hatfield et al. 2008; Karl et al. 2009; Gornall et al. 2010; Muller et al. 2011).

Any external factor that negatively or positively affects the plant growth, metabolism, reproductive mechanism, as well as yield and productivity is termed as "stress." Stresses can be categorized into two main classes such as abiotic (environmental) and biotic (biological) stresses. Abiotic stresses include nonliving factors such as water, temperature, salinity, light, and heavy metal stress that may be imposed by the environment on plants while biotic stresses are caused by living organisms such as insect, diseases, or any other plants that may be exposed to the plant during its lifetime (Rhodes and Nadolska-Orczyk 2001; Kranner et al. 2010) (Tables 27.1 and 27.2).

Abiotic stresses are result of nonbiological factors that alter the growth, reproduction, and life cycle of plants. Some sources of abiotic stresses are changes in water status, temperature, salinity, soil nutrient levels, etc. These stresses are classified into external environmental or nutritional stresses that can either positively (eustress) or negatively (distress) affect plant growth and metabolism. These stresses can affect the plants through disturbance in its life cycle by disturbing its cellular mechanism at physiological and molecular levels (Shao et al. 2009; Kranner et al. 2010).

Among different abiotic stresses, drought or water deficiency is one of the major hindering factors affecting all the growth and metabolic processes by dehydration that ultimately reduced the crop productivity (Zhu 2001; Sazzad 2007). The foremost effect of water stress is an imbalance in osmotic and metabolic activities resulting in closure of stomata and losses of turgidity. So, water stress restricts the uptake of CO_2 that represses the cell growth and, therefore, reduces the process of photosynthesis (Shinozaki and Yamaguchi-Shinozaki 2000). The prolonged exposure of plants to these water deficit conditions results in permanent wilting and ultimately the death of plants.

All plant species require optimal temperature for their normal growth and metabolism. Therefore, this optimal temperature is an important factor for distribution of plant species on the planet. The optimal of daytime temperature for plants ranges between −70 and 60 °C that is significantly affected by local topology (Sazzad 2007; Kranner et al. 2010). Another major factor that disturbs the life cycle of plants from germination (beginning) to reproduction is temperature stress. The changes in temperature can cause uncontrollable damages or even plant death. Temperature stress also causes the initiation of other stresses such as drought and salinity. Temperature stress is divided into two types, i.e., cold (low temperature) and heat (high temperature) stress. The former can cause unmanageable physical and mechanical damages to plants that result in severe cell disruption, while latter one reduces the growth and nutrient uptake. Freezing stress also results in freezing injuries. It is the result of cell desiccation that occurs when water moves from cells to intercellular spaces due to high water potential outside the cell. Cold stress leads to molecular precipitation, membrane damage, cell lysis, and production of reactive oxygen species, especially at molecular level. Another most important temperature

Table 27.1 Studies showing the selection of drought-tolerant crop genotypes when grown under different agroclimatic conditions

Crop type	Experimental conditions	Studied characteristics	No. of lines/ genotypes used	Selected tolerant lines	Studied area	References
Beta vulgaris	Greenhouse experiment	Growth and yield parameters, sugar, proline, and LRWC	Ten populations and two control varieties	SC C2×S7, SC C2×S10, and SC C2×S11	Iran	Taghizadegan et al. (2019)
Oryza sativa L.	Glass house	Relative water content, osmotic potential, membrane damage, chlorophyll content, phenolic acids, MDA, and total phenolic content	Two varieties	PR-115	India	Khan et al. (2017)
Zea mays L.	Pot experiment	Growth and yield, lipid peroxidation rate and lipoxygenase activity, antioxidant activity, osmolyte accumulation profile	Three hybrids	Dong-Dan 80	China	Anjum et al. (2017a, b)
Triticum aestivum L.	Greenhouse experiment	Number of days to heading (DTH), days to maturity (DTM), productive tiller number (TN), plant height (PH), spike length (SL), spikelet per spike (SPS), kernels per spike (KPS), thousand kernel weight (TKW), and grain yield (GY) and proline content (PC)	96 genotypes	LM29, LM22, LM04, LM77, LM71, LM23, LM100, LM27, LM85, LM96, LM03, LM31, LM35, LM44	South Africa	Mwadzingeni et al. (2016)
Beta vulgaris	Field experiment	Root yield, brix % age, brown sugar yield, chlorophyll content, and root yield	17 genotypes	Cauvery and Srenada	Bangladesh	Ganapati et al. (2016)
Triticum aestivum L.		TOL, STI, SSI, HM, GMP, MP, modified *STI* under optimum conditions (K1STI), and STI under stress condition (K2STI)	13 hybrids	Bio-9681 and HQPM-7	Rajasthan	Kumar et al. (2015)
Brassica napus L.	Field experiment	Stress sensitivity index (SSI), tolerance index (TOL), MP, GMP, and STI	28 cultivars	Nk fair and Oase	Iran	Majidi et al. (2015)
Solanum lycopersicum	Lab experiment	SSI, STI, TOL, GMP, MP, YI, and YSI	15 cultivars	C11, C15, and C10	Jeddah	Metwali et al. (2015)

Beta vulgaris	Greenhouse experiment	Seven drought indices including SSI, STI, TOL, MP, HARM, GMP, and yield loss ratio (S)	Four cultivars	Hayola 408 and Hayola 308	Iran	Naderi and Emam (2014)
Solanum lycopersicum	Pot experiment	SSI, relative drought index (RDI), MP, STI, SI, dry weight yield index, superiority index, GMP, harmonic mean (HM), drought resistance index (DI), modified stress tolerance index (MSTI), abiotic tolerance index (ATI), stress susceptibility percentage index (SSPI), sensitivity drought index (SDI), relative decrease (RD)	41 tomato population	G125, G105, and G104	Serbia	Brdar-Jokanović et al. (2014)
Brassica napus L.	Pot experiment	Plant height, SFW, SDW, RL, RFW, RDW, LA, leaf Na^+, leaf K^+, K^+/Na^+	11 canola cultivars	KS-75 and Rainbow highly tolerant, Shiralee, DGL, Westar, KH-65, and Legend as moderately tolerant	Pakistan	Haq et al. (2014a, b)
Helianthus annuus	Field experiment	Mean productivity (MP), STI, GMP, HARM, SNPI, YI, DI, modified stress tolerance index in optimum irrigation (MPSTI), and modified stress tolerance index in moderate and severe stress (MsSTI)	56 landraces	Anghane 4, Marand-Dizaj-Ghalami, Salmas-Sadaghian, Gharagoz1, Saribaglou 5	Iran	Gholinezhad et al. (2014)
Zea mays L.		Protein NIR, starch, oil, protein Kjeldahl, tryptophan, QI, and kernel type	13 landraces	L3, IP2, and IP8	Serbia	Ignjatovic-Micic et al. (2014)
Solanum lycopersicum	Laboratory experiment	Germination rate and percentage, shoot and root length and their ratio, shoot and root fresh and dry weight, shoot and root moisture content, shoot to root ratio, and relative water content	120 lines	19905, 19906, LA0716, and LA0722	Pakistan	Shamim et al. (2014)

(continued)

Table 27.1 (continued)

Crop type	Experimental conditions	Studied characteristics	No. of lines/ genotypes used	Selected tolerant lines	Studied area	References
Beta vulgaris	Field experiment	Mean productivity, STI, GMP, STI, yield stability index, and modified stress tolerance index	15 cultivars	Karun, NK Aviator, and NK Octans	Iran	Aliakbari et al. (2014)
Zea mays L.	Field experiment	Germination %, overall survival %	62 maize inbred lines and their hybrid test cross	2, 13, 18, 28, 31, 38, 39, 42, 47, 50, 54, 57, 58, 61	USA	Meeks et al. (2013)
Triticum aestivum L.	Field experiment	STI, SSI, TOL, HAM, GMP, MP, YI, YSI, x DI, ATI, stress non-stress product index (SNPI), MSTI, and SSPI were calculated based on grain yield under drought (Ys) and irrigated conditions (Yp)	15 genotypes	Saji and Rizhav	Iran	Dehbalaei et al. (2013)
Zea mays L.	Field experiment	WUE, GMP, SSI, YSI, Ypi, LR, and SEN	135 F_2 and F_3 progenies	KDV2/CML444-14 and KDV2/CML440-224	Kenya	Ngugi et al. (2013)
Helianthus annuus L.	Field experiment	1000-kernel weight, biological weight, grain yield, harvest index (HI), and oil percentage	Five cultivars	Favorit	Iran	Rafiei et al. (2013)
Beta vulgaris	Field experiment	MP, GMP, and STI	Two populations	111-HSF.42	Iran	Rajabi et al. (2013)
Triticum aestivum L.	Field experiment	Yield, biomass and HI	50 lines	hs65	India	Ramya et al. (2016)
Helianthus annuus L.	Field experiment	Yield stability index (YSI), stress susceptibility index (SSI), tolerance (TOL), mean productivity (MP), geometric mean productivity (GMP), stress tolerance index (STI), and harmonic mean (HAM)	8 cultivars	Azargol	Iran	Taherabadi et al. (2013)

Zea mays L.	Field experiment	Average daily precipitation, daily high temperature, relative water content, plant height, plant growth	Five inbred lines	Tx205, C2A554-4, and B76	USA	Chen et al. (2012)
Triticum aestivum L.	Field experiment	STI, GMP, MP, SSI, TOL, YI, YSI, drought response index (DRI), DI, MSTI, relative drought index (RDI), ATI, and SSPI	13 landraces	WC- 4953S (20), WC-47572 (19), and WC-47574 (4)	Iran	Farshadfar et al. (2012)
Zea mays L.	Field experiment	STI, SSI, TOI, MP, GMP, HM, and golden mean (GM)	8 hybrids	KSC704 hybrid and H4	Iran	Moradi et al. (2012)
Triticum aestivum L.	Field experiment	MP, GMP, tolerance, SSI, and STI	18 genotypes	G18, G14, G11, and G4	Iran	Mohammadi et al. (2012)
Helianthus annuus L.	Laboratory experiment	GSI (germination stress index), PHSI (plant height stress index), RLSI (root length stress index), DMSI (dry matter stress index), RWCSI (relative water content stress index)	7 genotypes	S473, S471, and S475 and hybrid Pacific 77	Thailand	Saensee et al. (2012)
Triticum aestivum L.	Field experiment	Photosynthetic pigments (chl. *a*, *b*, carotenoids), antioxidative defense mechanism (enzymatic and nonenzymatic), membrane stability, lipid per oxidation	5 varieties	KW, UP 2752, and PBW 343	India	Chakraborty and Pradhan (2012)
Helianthus annuus L.	Pot experiment	Growth parameters, MDA, H_2O_2, and proline contents, antioxidant activity	Two cultivars	Aydın	Turkey	Baloğlu et al. (2012)
Solanum lycopersicum	Greenhouse experiment	Growth and yield parameters as well as water use efficiency	Four genotypes	Pakmore, VF, and drought-tolerant breeding line (L 03306)	Saudi Arabia	Wahb-Allah et al. (2011)
Fragaria × *ananassa*	Pot experiment	Chlorophyll, carbohydrates, proline content, relative water content, membrane stability	Two cultivars	Kurdistan	Iran	Ghaderi and Siosemardeh (2011)

(continued)

Table 27.1 (continued)

Crop type	Experimental conditions	Studied characteristics	No. of lines/ genotypes used	Selected tolerant lines	Studied area	References
Brassica napus L.	Field experiment	Chlorophyll content, leaf relative water content, leaf area	Four cultivars	Elite	Isfahan	Sepehri and Golparvar (2011)
Beta vulgaris	Field experiment	Stress susceptibility index (SSI), tolerance index (TOL), stress mean productivity (MP), geometric mean productivity (GMP), stress tolerance index (STI), yield index (YI), and yield stability index (YSI)	23 genotypes	Modena, Geronimo, Elite, Syn-4, and SLM046	Iran	Rad and Abbasian (2011a, b)
Triticum aestivum L.	Field experiment	Relative water content, growth, and yield components	Two cultivars	Inqlab-91	Faisalabad	Akram (2011)
Triticum drum L.	Field experiment	Yield potential and stability under stressful conditions	14 wheat cultivars	Gidara-II, Sarıçanak-98, Balcalı-2000, Altıntoprak-98, Aydın-93, and Harran-95	Turkey	Kilic and Yagbasanlar (2010)
Triticum drum L.	Field experiment	SSI, STI, YC, YSI, MP, and GMP	24 cultivars	1, 6, 7, 19, 20, and 21	Iran	Talebi et al. (2009)
Triticum aestivum L.	Field experiment	Yield and yield components	25 varieties	Sarsabz and Kiran-95	Pakistan	Mirbahar et al. (2009)
Triticum aestivum L.	Laboratory experiment	Ys, Yp, SSI, STI, TOL, GMP, MP, and MSTI	42 genotypes	Sardar, Sabalan, and 4057	Iran	Shahryari et al. (2008)
Beta vulgaris	Glasshouse	Growth and yield components as well as photosynthetic attributes	Four cultivars	Hayola 401, Hayola 308	Iran	Naderikharaji et al. (2008)
Beta vulgaris	Field experiment	Growth attributes	Nine genotypes	MSTC2 and 7233.P3	Iran	Mohammadian et al. (2005)

Table 27.2 Studies showing the selection of salt-tolerant crop genotypes when grown under different agroclimatic conditions

Crop type	Experimental conditions	Studied characteristics	No. of lines/ genotypes used	Selected tolerant lines	Studied area	References
Avena sativa	Laboratory experiment	Seed germination, shoot and root length, dry weight of shoot and root, total dry weight of seedling	Seven cultivars	NDO-2 and UPO-212, salt tolerant and moderately salt tolerant, respectively	India	Chauhan et al. (2016)
Zea mays L.	Greenhouse experiment	Growth parameters, photosynthetic pigments, relative water contents, and Na^+ and K^+ concentrations	Two cultivars	S2000	Pakistan	Gul et al. (2016)
Triticum aestivum L.	Hydroponic experiment	Membrane stability (MS) and its injury (M1)	20 cultivars	Moderately tolerant cultivars (Dagdas-94, Eraybey, Altay-2000, Mesut, Somez-01, Bayraktar 2000, Gun-91, and Ekiz), highly tolerant cultivars (Karahan-99, Gerek-79, Konya-2002, and Kinaci-97)	Turkey	Kaya and Arısoy (2016)
Oryza sativa L.	Pot experiment	Physiological, parameters, and antioxidant enzyme	12 cultivars	Niewdam Gs.no.00621	Thailand	Chunthaburee et al. (2016)
Zea mays L.	Hydroponic	Root length, shoot and root dry mass, relative water content, leaf water loss, stability of membrane, tolerance index (TOL)	13 maize inbred lines	SC2 andAD3 lines	Argentina	Collado et al. (2016)
Brassica napus	Field experiment	Number of pods per plant, pod length, pod weight, kernel number per pod, 100 kernel weight, and kernel yield	14 cultivars	Modena and Opera	Iran	Ahmadzadeh et al. (2015)
Lactuca sativa	Hydroponic	Growth; stomatal conductance; Na^+, Ca^{2+}, and K^+ content in shoot; proline	Five cultivars	Parris Island lettuce cultivar	Romania	Bartha et al. (2015)

(continued)

Table 27.2 (continued)

Crop type	Experimental conditions	Studied characteristics	No. of lines/ genotypes used	Selected tolerant lines	Studied area	References
Piper nigrum	Greenhouse experiment	Growth parameters, chlorophyll content, leaf gas exchange, RLWC, and STI	26 cultivars	CV. paramo	Iran	Bavani et al. (2015)
Oryza sativa L.	Pot experiment	Shoot, root parameters, Na^+ /K^+	22 cultivars	Pachaperumal, Periavellai, At 303, Adakari, Bg 406, and CO 10	Sri Lanka	Pradheeban et al. (2015)
Brassica napus	Hydroponic system	Growth , Na^+, K^+, and their ratio	11 cultivars	Con-II, Con-III, Dunkeld, and Oscar	Pakistan	Haq et al. (2014a, b)
Triticum aestivum L. and *Hordeum vulgare*	Greenhouse experiment	Protein assay, peroxidase, Na^+, K^+, and the K^+/Na^+ ratio, proline	Four cultivars each	Barley cultivar "Kavir" and wheat cultivar "Bam"	Iran	Izadi et al. (2014)
Oryza sativa L.	Pot experiment	TOL, SSI, MP, GMP, STI, HM, YI, YSI	Eight cultivars	Dasht	Northern Iran	Kamyab-Talesh et al. (2014)
Helianthus annuus	Pot experiment	Germination	Three cultivars	Sandaomei	China	Luan et al. (2014)
Piper nigrum	Lab experiment	Germination and growth parameters	Three cultivars	Anaheim Chili	Tunisia	Hassen et al. (2014)
Triticum drum	Field and pot experiment	Germination and growth attributes	119 landraces	Malta2	Japan	Turki et al. (2014)
Solanum tuberosum	Hydroponic	Growth, proline content, K^+/Na^+ accumulation, H_2O_2, and relative water content	Six cultivars	Mozart and Desiree	Netherlands	Jaarsma et al. (2013)

Triticum drum	Greenhouse experiment	Height of plant, length of peduncle, area of flag leaf, area of penalty leaf, number of leaf, length of spike, no. of grains, and weight of grains	Ten cultivars	Boomer and PGS	Iran	Kahrizi et al. (2013)
Triticum aestivum L.	Pot experiment	Chlorophyll content (Chl.), leaf relative water content (LRWC), Na^+/K^+, activities of APX, GPX, SOD, CAT, GPX, H_2O_2, and membrane stability index	Ten cultivars	Sehar-06, Lu-26, NARC-09, BARC-09, and Pirsbak-09	Pakistan.	Rao et al. (2013)
Solanum tuberosum	Hydroponic	Na^+ accumulation	Six cultivars	Desiree and Russett Burbank	Netherlands	Jaarsma et al. (2013)
Brassica napus	Field experiment	Yield, component characters, and nutrient compositions	Eight genotypes	DSM12 and Hyola401	Iran	Valiollah (2013)
Triticum aestivum L.	Lab experiment	Germination, seedlings establishment, and respiration	20 lines/ cultivars	"Chamran," "Yavarous," "83-3," "Taro3," "Cross Boullani," "Cross Aadl," and "Dabira"	Iran	Shekoofa et al. (2013)
Hordeum vulgare	Lab experiment	Germination, growth, leaf chlorophyll, proline rate	Three cultivars	Nosrat	Iran	Somayeh et al. (2012)
Abelmoschus esculentus	Pot experiment	1000-grain weight, grain yield, biological yield, number of tillers, number of fertile tillers, spike length, salinity susceptibility index (SSI), and salt tolerance index (STI)	39 genotypes	Acc. No. 019232, Acc. No. 000010-10237, Chinese Red, Ikra III, and Acc. No. 015371	Pakistan	Haq et al. (2012)

(continued)

Table 27.2 (continued)

Crop type	Experimental conditions	Studied characteristics	No. of lines/ genotypes used	Selected tolerant lines	Studied area	References
Capsicum annuum	Greenhouse experiment	Growth parameters, chlorophyll, proline	Five cultivars	Awlad Haffouzz and Korba	Tunisia	Kaouther et al. (2012)
Brassica napus	Pot experiment	Proline metabolism	Two cultivars	Dunkled	Pakistan	Saadia et al. (2012)
Brassica napus	Hydroponic culture	Tolerance, mean productivity stress, susceptibility index, geometric mean, productivity stress, tolerance index	12 cultivars	Craker and Amica	Iran	Toorchi et al. (2012)
Brassica napus	Greenhouse experiment	Root and shoot fresh and dry weight, relative water content, Na^+/K^+, lipid per oxidation, CAT, SOD, POD, APX, GSG, GSSG	Five cultivars	SLM_{046}	Iran	Bybordi and Tabatabaei (2010)
Triticum aestivum L.	Lab experiment	Germination, growth, sugar, protein, chlorophyll, proline	Five varieties	HD2689	India	Datta et al. (2009)
Oryza sativa L.	Greenhouse experiment	Growth and physiological parameters	Seven varieties	Co39 and Moroberekan	Pakistan	Haq et al. (2009)
Brassica napus	Greenhouse experiment	Chlorophyll fluorescence, photosynthetic parameters	Ten cultivars/ accessions	Dunkeld and Hayola 401	Iran	Saeedipour (2009)

Triticum aestivum L.	Greenhouse	Shoot Na^+, K^+, K^+/Na^+ ratio, 1000-grain weight, grain yield, biological yield, number of tillers, number of fertile tillers, spike length, SSI, STI	15 cultivars	Kavir,Niknejad, Chamran, and Falat	Iran	Goudarzi and Pakniyat (2008)
Triticum aestivum L.	Laboratory experiment	No. of seeds, percent of callus formation, and regeneration	Four cultivars	LU-26	Islamabad	Akhtar (2006)
Helianthus annuus	Field experiment	Growth and yield, K+, Na+, Ca+, and Mg+ concentration	Ten genotypes	CRN-1435, HU-777, Super-25, and cultivar 6451	Pakistan	Ahmed et al. (2005)

stressor is extremely high temperature that can cause heat shocks. It can cause wilting by increasing the evaporation rate from leaves, and its prolonged exposure leads to permanent wilting or even death of plants (Thomashow 1998, 1999; Pearce 1999; Sazzad 2007) (Tables 27.3 and 27.4).

Like other abiotic stresses, salt stress also substantially decreases the growth as well as yield of crop plants and in many cases by 50% or more reduction all around the world. The foremost effect of salinity is that it disturbs the seed germination and viability. The presence of excess salt or ions around the roots decreases the water uptake potential of plants that ultimately reduces the growth through disturbed metabolism (Sazzad 2007; Kranner et al. 2010; Machado and Serralheiro 2017). Salinity is the cause of excessive quantity of water-soluble salts such as sodium carbonates, sodium sulfate, potassium sulfate, sodium nitrate, calcium sulfate, magnesium sulfate, sodium chloride, and magnesium chloride that not only negatively alters the different processes of plant metabolism and as a result both positively and negatively triggers its growth and metabolism (Sazzad 2007; Machado and Serralheiro 2017). Plants need all these salts in an optimal amount for regulating their normal metabolic activities. The presence of these salts above and below their optimal level may cause cell disruption. A number of these salts can help the plants in regulation of growth and metabolic activities while their excess amount may be toxic for plants (Sazzad 2007). For example, if sodium chloride is present in an optimal amount in the soil, it will improve the plant growth and metabolism up to some extent while at higher concentration it may inhibit the seed germination and seedling establishment as well as plant growth and development (Tester and Davenport 2003; Shabala et al. 2015). Plants can be divided into two classes on the basis of their salt tolerance mechanism, i.e., halophytes (salt tolerant) or glycophytes (salt sensitive). Halophytes can tolerate the negative effects of salinity by decreasing the uptake of salt from soil and by reducing the concentration of salt in cytoplasm as well as in cell wall through exclusion or vacuole storage. Glycophytes (salt sensitive) are less able to tolerate high salt level and can accumulate high salt concentration in cytosol that is toxic for plant metabolism (Munns et al. 2006; Sazzad 2007).

The elements with density greater than 5 g cm^{-3} are categorized as heavy metals. These mainly include Co, Cu, Cd, Pb, Fe, Ni, Mn, Zn, and Mo. These elements in some cases are essential for plants as they directly or indirectly affect the growth, metabolism, senescence, as well as many energy-generating processes in studied plant species. Many of these elements can stimulate various growth and metabolic activities in plants if they are present in low concentration in soil (Emamverdian et al. 2015). On the other hand, their concentration above threshold level in the soil is toxic to plants either causing the stress that is known as heavy metal stress. Heavy metal stress disturbs the plant growth by disturbing the activities of various enzymes through higher levels of free radicals or by replacing the uptake and mobility of many nutrients and essential elements. The toxic effects of these metals are directly depending on the nature of these metals and type of plant species as well (Jozefczak et al. 2012; Emamverdian et al. 2015).

Table 27.3 Studies showing the selection of temperature stress-tolerant crop genotypes when grown under different agroclimatic conditions

Crop type	Type of stress	Experimental conditions	Studied characteristics	No of lines/genotypes used	Selected tolerant lines	Studied area	References
Glycine max L.	Low and high temperature stress	Lab experiment	Growth and physiological parameters as well as cumulative stress response indices	64 cultivars	CZ 5225 LL and GS47R216 sensitive and tolerant to LT while cultivars 45A-46 and 5115LL tolerant and sensitive to HT, respectively	USA	Alsajri et al. (2019)
Oryza sativa L.	Cold stress	Greenhouse	Germination %age, germination index, seedling height, root length, no. of leaves or seedlings	40 rice accessions	CT6749-36-7-2-M-M, Milyang 80, PSRM1-17-4B-13, Ryong Sung 25	Egypt	Elgamal et al. (2018)
Vigna radiata	High temperature stress	Field experiment	Growth, morphology, and yield traits	41 elite mung bean lines	EC693357, EC693358, EC693369, Harsha, and ML1299	India	Sharma et al. (2016)
Oryza sativa L.	Heat stress	Field experiment	Days to 50% flowering, days to maturity, plant height, no. of spikelets/spike, fertility%, plant yield	1217	IR 87606-109-2-2 and IR 86991-146-2-1-1	Bangladesh	Masuduzzaman et al. (2016)
Zea mays L.	Cold stress	Growth chamber	Germination rate, index, root length, and seed vigor index values	22 inbred lines	CO439, CO438, CO450, CO435, and CO445	Korea	Farooqi and Lee (2016)

(continued)

Table 27.3 (continued)

Crop type	Type of stress	Experimental conditions	Studied characteristics	No of lines/ genotypes used	Selected tolerant lines	Studied area	References
Glycine max L.	Chilling stress	Growth room and pot experiment	Germination attributes, leaf electrolyte leakage, free proline content and catalase activity photosynthetic rate, leaf area	Six domestic soybean cultivars and Canadian-bred cultivars	Jutro and Nawiko	Lublin	Borowski and Michalek (2014)
Daucus carota subsp. sativus	High temperature stress	Field experiment	Quantitative, qualitative, and morphological traits	38 inbreds	IPC-4, IPC-8, IPC-11, IPC-13, IPC-124	New Delhi	Saha et al. (2016)
Triticum aestivum L.	Heat stress	Field experiment	Phenology	Five cultivars	Faisalabad-2008 and Iqlab-91	Pakistan	Sattar et al. (2015)
Zea mays L.	Cold stress		Growth parameters such as plant height, leaf length, leaf area, root development and root growth parameters, nutrient uptake	33 hybrids	DKC6697, DKC6804, and M2V707	MississippiState	Wijewardana et al. (2015)
Zea mays L.	High temperature stress	Tunnel and field conditions	Days to 50% tassel, days to 50% silk, plant height, cob height, no. of viable seeds	21 inbred lines	YH-1898 and YH-1921	Pakistan	Rahman et al. (2017)
Strawberry	Heat stress	Greenhouse experiment	LRWC, chlorophyll content, heat stress tolerance	15 cultivars	“Elsanta,” “R. Hope,” and “Camarosa”	Turkey	Kesici et al. (2013)

Triticum aestivum L.	Cold stress	Field experiment	Day to maturity (DM), grain number per head, plant height, 1000-kernel weight (1000-KW), and grain yield	15 cultivars	Sayson, Kavir, pishtaz	Iran	Habibi et al. (2012)
Oryza sativa L.	Cold stress	Field experiment	Germination and seedling stage	Six cultivars	Tarom, Domsiya, Hybrid, Nemat, Gerde, Unda	Iran	Soleymani and Shahrajabian (2012)
Brassica napus L.	High temperature stress	Field experiment	Yield and yield attributes	Two cultivars	Hyola401	Iran	Faraji et al. (2008)
Solanum lycopersicum	High temperature stress	Pot experiment	Photosynthetic pigments, gas exchange, fluorescence, and electrolyte leakage	Two genotypes	Nagcarlang	Cuba	Camejo et al. (2005)
Oryza sativa L.	Cold stress	Lab experiment	Germination parameters	24 genotypes	BR-IRGA 410 and IRGA 416	Brazil	Cruz and Milach (2004)
Oryza sativa L.	High temperature stress	Pot experiment	Percentage fertility, anther dehiscence, and size	Nine cultivars	Nipponbare and Akitakomachi	Japan	Matsui and Omasa (2002)
Brassica napus	Heat stress	Lab experiment	Fatty acid content, yield components	Three cultivars	Oscar	Australia	Aksouh et al. (2001)

(continued)

Table 27.3 (continued)

Crop type	Type of stress	Experimental conditions	Studied characteristics	No of lines/ genotypes used	Selected tolerant lines	Studied area	References
Solanum tuberosum	Heat stress	Greenhouse experiment	Gas exchange, leaf chlorophyll fluorescence net assimilation rate (NAR) and relative growth rate (RGR) parameters, and total dry weight (TDWT)	46 clones	LT-5, *S. acaule* (P1498066), and *S. circaefolium* (PI 498116)	Canada	Midmore and Prange (1991)

Table 27.4 Studies showing the selection of heavy metal-tolerant crop genotypes when grown under different agroclimatic conditions

Crop type	Experimental conditions	Studied characteristics	No. of lines/ genotypes used	Selected tolerant lines	Studied area	References
Zea mays L.	Pot experiment	Growth, leaf gas exchange, and photosynthetic pigments	Two cultivars	Dong-Dan 80	China	Anjum et al. (2017a, b)
Zea mays L.	Greenhouse experiment	Growth parameters, photosynthetic pigments, relative water contents, and Na^+ and K^+ concentrations	Two cultivars	S2000	Pakistan	Gul et al. (2016)
Zea mays L.	Hydroponic experiment	Growth and photosynthetic attributes	Seven hybrids	32-B-33 and 23-T-16	Pakistan	Akhtar et al. (2017)
Triticum aestivum L.	Field experiment	Growth and physiological attributes	Ten genotypes	Ulbinka, Zaulbinka, and Omskaya-18	Kazakhstan	Alybayeva et al. (2016)
Solanum lycopersicum	Glass house	Yield attributes and Cd accumulation in root, shoot, and leaf	100 genotypes	9086, Roma, Sitara TS-01, pak0010990, CLN-2123A, Picdeneato, 0.006231, and 7035	Pakistan	Hussain et al. (2015)
Vigna radiata	Pot experiment	Germination, growth and photosynthetic attributes	Three cultivars	M-6 and M-8	Pakistan	Hasnain et al. (2011)
Vigna radiata	Laboratory experiment	Growth parameters and stress tolerance indices	Eight cultivars	Tolerance response of genotypes: Dhauli > PDM-116 > LGG-407 > K-851 > TARM-22 > TARM-1 > TARM-21 > TARM-26.	India	Samantaray et al. (1998)

Plants have the ability to survive in the stressful environmental conditions that is plant species and growth stage specific. It also depends on the type and the duration of the stress. To cope with these adverse environmental conditions, plants have the ability to develop specific mechanisms that ultimately help the plants to complete their life cycles. These include some structural changes that lead from morphological to physiological adaptations (Jaleel et al. 2008; Hund et al. 2009; Gupta and Huang 2014). Morphological adaptations include the reduced leaf area, leaf rolling, early life cycle completion (escape), as well as the reduction in growth rate. Anatomical adaptations include the cuticle formation and pubescence that also play a significant role in plant stress tolerance by reducing the transpiration and evaporation rate. Similarly, plants also have developed some physiological mechanisms that help plants in ameliorating the adverse effects of different abiotic stresses by controlling the metabolic activities. These include the stomatal regulation, osmotic adjustment, oxidative defense mechanism (activity of enzymatic and nonenzymatic antioxidants), accumulation of various osmolytes (carbohydrates, betaines, proline, and other amino acids), as well as osmoprotectors through the production of chemical messengers in response to environmental stimuli that help in scavenging the ROS and regulate the osmotic potential of cell under stressful environmental conditions (Apel and Hirt 2004; Krishnan et al. 2008). Knowledge about responses of plants to these abiotic stresses and their stress tolerance mechanisms could be helpful in understanding the different adaptations of plants to extreme environmental conditions that are also relevant to the management and breeding programs (Mohammadi 2018).

Different strategies are being used to counteract these problems that include the manipulation of important agronomic characteristics, better use of irrigation water through different ways, use of chemicals/biochemical through different modes (such as amino acids, plant-based extract, plant growth regulators, biostimulants), fertilizers, pesticides, as well as the use of biophysical methods. Among these, the breeding for selection of stress-tolerant genotypes with better production under different environmental stresses is an important one and gaining interest. To fulfill the future world food demand for ever-increasing world population, the agriculturalists are mainly relying on crop breeding.

Breeding for stress tolerance and better crop production is in practice from ancient times that is based on different agronomic traits and yield attributes. In old times the breeding was mainly to obtain the better production and to develop high-yielding crop cultivars. At present due to environmental changes, and the lesser availability of freshwater for irrigation, there is a dire need to develop stress tolerance crop cultivars with better production under stressful environmental conditions to fulfill the demand of ever-increasing world population. Primarily for the development of higher yielding crop varieties, the major focus was on the agronomic traits, but with the development of modern tools and invents of molecular biology techniques, the breeding has become a multidisciplinary subject. Agronomic traits are the basic parameters for the selection of stress-tolerant crop cultivars. The parameters are also being employed for horticulture crops as well. The major focus for the selection of stress-tolerant genotypes from available germplasm through breeding is the selection against water stress tolerance (Mohammadi 2018).

27.2 Breeding Against Water Stress

The selection of crop genotypes for water stress tolerance is mainly based on stress susceptibility index (SSI), stress tolerance index (STI), relative drought index (RDI), stability index (SI), drought resistance index (DI), modified stress tolerance index (MDTI), stress susceptibility percentage index (SSPI), sensitivity drought index (SDI), abiotic tolerance index (ATI), drought response index (DRI), relative drought index (RDI), modified stress tolerance index in optimum irrigation (MPSTI), modified stress tolerance index in moderate and severe stress (MsSTI), modified STI under optimum conditions (K1STI) and STI under stress conditions (K2STI), and stress sensitivity index (SSI) which is based on plant growth and biomass production. Along with these indices, the mean productivity (MP), geometric mean productivity (GMP), yield index (YI), yield stability index (YSI), dry weight yield index (DWYI), harvest index (HI), superiority index, grain yield under drought (Ys), and irrigated conditions (Yp) are also necessary traits. For example, in wheat various drought-tolerant cultivars have been selected on the basis of different agronomic traits such as STI, SSI, TOL, DRI, DI MSTI, ATI, and SSPI that are further used for breeding (Shahryari et al. 2008; Talebi et al. 2009; Rad and Abbasian 2011a, b; Farshadfar et al. 2012; Mohammadi et al. 2012; Dehbalaei et al. 2013). In tomato selection, the agronomic traits that have been focused are SST, RDI, STI, SI, DWYI, STI, ATI, SSPI, SSI, and TOL, and different drought-tolerant cultivars were selected on the basis of these indices (Brdar-Jokanović et al. 2014; Metwali et al. 2015). In another experiment on corn that was performed under field conditions, the two corn hybrids such as KSC704 and H4 were selected out of eight hybrids as drought tolerant on the basis of various agronomic attributes such as STI, SSI, and ROL (Moradi et al. 2012). Majidi et al. (2015) reported that out of 28 canola cultivars that were grown under field water deficit conditions, only two cultivars were selected as drought-tolerant ones, cultivars that were based on different stress tolerance indices such as SSI, TOL, and STI. Furthermore, it was reported that out of eight sunflower cultivars, grown under field conditions for the selection of tolerant ones the genotype Azargol, selected on the basis of various stress tolerance indices such as TOL, SSI, and STI (Taherabadi et al. 2013). In a laboratory experiment, seven sunflower genotypes were grown in Petri dishes to find drought-tolerant potential of these genotypes on the basis of germination stress index (GSI), plant height stress index (PHSI), root length stress index (RLSI), dry matter stress index (DRSI), as well as relative water content stress index (RWCSI) as reported by Saensee et al. (2012). Four genotypes (S473, S471, and S475 and a hybrid Pacific 77) were reported as drought tolerant. In parallel with agronomic characteristics, yield attributes were also considered as important to select drought-tolerant varieties/genotypes such as MP, GMP, YI, YSI, DWY, superiority index, Ys, and Yp. For example, in wheat many drought-tolerant cultivars/varieties have been identified on the basis of different yield indices such as YI, YSI, GMP, MP, and HI (Talebi et al. 2009; Dehbalaei et al. 2013; Ramya et al. 2016; Aliakbari et al. 2014). Mirbahar et al. (2009) selected two wheat varieties (Sarsabz and kiran-95) out of the 25 genotypes that were grown under field water deficit conditions. These varieties were selected based on plant yield and yield components that showed more tolerance against water stress. The agronomic and yield attributes are the basis of different physiological alteration mechanisms. So, the selection based on the agronomic and physiological attributes, taken together, is found better than that of only considering the agronomic traits. Many studies have been reported about the selection of drought-tolerant varieties/genotypes on the basis of some physiological parameters such as germination attributes, biomass production, and plant photosynthetic activity, amino acid profile, and enzymatic and nonenzymatic antioxidative activities (Meena et al. 2016). For example, three maize hybrids were grown in pots to find out the drought tolerance potential of three maize hybrids on the basis of extent of reduction in growth, yield, extent of lipid peroxidation, and osmolyte accumulation (Anjum et al. 2017a, b). They reported that these biochemical and physiological attributes helped them to develop drought-tolerant hybrid Dong-Dan 80 that can survive in water deficiency with minimum yield reduction. In another study, conducted by Khan et al. (2017), they reported that out of two rice varieties one variety (PR-115) was selected as drought tolerant when grown in pots under water stress. The selection of drought-tolerant variety was also based on the different physiological parameters such as relative water content, osmotic potential, membrane damage, chlorophyll content, phenolic acids, MDA, and total phenolic content. For example, two cultivars were selected as tolerant ones out of the four cultivars when grown in glass house water deficit conditions (Naderikharaji et al. 2008). They made the selection based on growth and yield components as well as photosynthetic activities of these varieties. Chakraborty and Pradhan (2012) considered antioxidative defense mechanism, membrane stability, lipid peroxidation, as well as photosynthetic activities for the selection of stress-tolerant genotypes out of five wheat varieties that were grown in field under water deficiency. They selected three varieties (KW, UP 2752, and PBW 343) as tolerant ones depending on abovementioned physiological attributes. A greenhouse experiment was conducted to find out the drought tolerance potential of four tomato genotypes based on growth and seed yield as well as water use efficiency when grown under water shortage. Pakmore VF and the breeding line L 03306 showed good growth and yield performance and are selected to use for breeding programs as drought-tolerant genotypes (Wahb-Allah et al. 2011). Two strawberry cultivars (cv. Kurdistan and Selva) were grown in pots to find out their drought tolerance potential based on the various physiological attributes including chlorophyll, proline, and carbohydrate content, membrane stability index, as well as leaf relative water content. The cultivar Kurdistan was selected as tolerant one to use in breeding programs (Ghaderi and Siosemardeh 2011). Antioxidative and physiological responses of two sunflower cultivars (Musala and Aydın) were studied based on their efficiency to grow under PEG-induced water stress as reported by Baloğlu et al. (2012). The cultivar Aydin was nominated as drought-tolerant cultivar in terms of growth, MDA, H_2O_2, and proline contents as well as antioxidant activity.

27.3 Breeding Against Salt Stress

Salinity stress is a type of osmotic stress that includes the specific ion toxicity, especially of Na^+ in sodicity that not only disturbs the membrane potential but also cellular ion homeostasis. Along with ion toxicity, it also disturbs plant water relations especially the cause of physiological drought. Plants have developed specific mechanisms to avoid the toxicity of these toxic ions but this mechanism is species and cultivar specific (Munns 2005). This mechanism includes the ion exclusion at different organization levels (Munns 2005), accumulation in vacuole, and discrimination in the uptake of these toxic ions. The excessive toxic levels of these salts in the rooting medium compete with essential macro- and micronutrients such as Na^+ that competes with K^+, Ca^{2+}, Mg^{2+}, etc. So, breeding for toxic ion discrimination is an effective one to develop the salt-tolerant crop genotypes. Others include the excessive accumulation of osmotica to water relations through osmotic adjustment, better antioxidative defense mechanism, and better performance in different physio-biochemical attributes. Presence of one of the above mechanisms results in better crop production. Haq et al. (2012) reported that in okra the salt-tolerant genotypes were selected based on different yield attributes along with SSI and STI. They reported that among 39 genotypes, seven were selected as tolerant ones. A hydroponic experiment was conducted by Jaarsma et al. (2013) to identify the salt-tolerant genotypes in potatoes. They found that among seven different genotypes grown under salt stress cultivars "Mozart and Desiree" were selected as tolerant ones and the selection was based on different growth attributes, K^+/Na^+ ratio, proline content, H_2O_2, as well as relative water content. In durum wheat, different salt-tolerant cultivars were selected on the basis of different growth and yield attributes. Two salt-tolerant cultivars (Boomer and PGS) were selected, out of ten cultivars (Kahrizi et al. 2013). A hydroponic experiment was conducted by Kaya and Arısoy (2016) who reported that 20 wheat cultivars were grown under salt stress to select the salt-tolerant genotypes. They reported that eight genotypes were moderately tolerant and four were highly salt tolerant, selected against salt stress based on membrane stability (MS) and membrane injury (MI) indices. Antioxidant activity, photosynthetic attributes, and lipid peroxidation were recommended. Similarly, based on abovementioned attributes, among ten wheat genotypes, five were identified as tolerant ones that further for breeding program (Rao et al. 2013). A field study was conducted by Ahmadzadeh et al. (2015) to evaluate the effect of salinity stress on yield and yield components of fourteen rapeseed cultivars. Among all studied cultivars, they reported two high-yielding cultivars as tolerant ones on the basis of different growth, yield, and membrane stability indices. Growth and ionic relations (K^+, Na^+, Ca^+, and Mg^{2+}) of ten sunflower genotypes grown in field under saline environment were studied to select the salt-tolerant genotypes. Four genotypes were selected as tolerant ones based on abovementioned attributes (Ahmed et al. 2005). A laboratory experiment was conducted under saline conditions using various oat cultivars to find out the changes in germination and growth parameters. They found that among seven cultivars, NDO-2 and UPO-212 were selected as highly salt tolerant and moderately tolerant, respectively, based on their germination and growth behavior (Chauhan et al. 2016). Various physio-biochemical attributes were studied to evaluate salt-tolerant cultivars of rice grown in pots under saline conditions. Based on studied attributes cultivar Niewdam Gs.no.00621 was nominated as tolerant one as reported by Chunthaburee et al. (2016)). Various salt-tolerant wheat cultivars were also selected based on germination attributes, growth, and chlorophyll and proline contents in wheat (Datta et al. 2009), barely (Somayeh et al. 2012), and pepper (Hassen et al. 2014). Based on Na^+ accumulation various salt-tolerant potato cultivars were selected when grown in a hydroponic experiment as depicted by Jaarsma et al. (2013). Similarly, a pot study was conducted on rice to evaluate the salt-tolerant genotypes based on various stress tolerance and yield indices such as TOL, SSI, MP, GMO, STI, HM, YI, and YSI (Kamyab-Talesh et al. 2014). In another study, Toorchi et al. (2012) reported that various canola cultivars were identified as salt-tolerant ones based on TOL, MP and SI, GM through the agronomic and physiological mechanisms are considered important ones but these are purely controlled by genetics. In this regard selection based on QTLs is considered short term and easy way from the available germplasm (Table 27.5).

27.4 Breeding Against Temperature Stress

In present era due to erratic environmental conditions, especially the atmospheric temperature, it is necessary to develop crop genotypes that can better perform under such conditions. The main focus of breeders is on the development of genotypes that can perform under increasing temperature because the global temperature is rising rapidly every year. Along with the high temperature, the chilling stress is also disturbing the crop production in specific areas. In case of temperature stress, heat shock proteins (HSPs)/chilling stress protein is considered important one. In rice various stress-tolerant genotypes were selected against high temperature stress when grown under field conditions and these genotypes were selected on the basis of different growth and yield attributes such as days to 50% flowering, days to maturity, plant height, no. of spikelets/spikes, fertility, as well as plant yield (Masuduzzaman et al. 2016). In a pot experiment conducted by Matsui and Omasa (2002), it was reported that various rice cultivars were selected as tolerant ones under high temperature stress, based on percentage fertility, anther dehiscence, and size. Changes in gas exchange attributes, leaf chlorophyll florescence, relative growth rate (RGR), and total dry weight (TDW) of various tomato clones grown in a greenhouse under high temperature stress were reported by Midmore and Prange (1991). Based on these attributes, they selected three clones and reported that they were tolerant to high temperature stress. Alsajri et al. (2019) reported that different

Table 27.5 Studies showing the QTL-based selection of stress-tolerant crop genotypes when grown under different agroclimatic conditions

Crop type	Stress type	Studied QTLs	Studied attributes	References
Zea mays L.	Drought stress	69 studied; 21 were stable	Agronomic traits	Zhao et al. (2018)
Oryza sativa L.	Cold stress	35 QTLs were identified; two were stable	Spikelet fertility, panicle length, spikelet number per panicle, panicle number, panicle weight, culm length, heading date	Wainaina et al. (2018)
Triticum aestivum L.	Heat stress	Two marker-trait associations were detected on chromosome no 4A and 5A	Grain yield and its components	Tadesse et al. (2018)
Triticum aestivum L.	Salt stress	19 QTLs were detected; 11 were detected under normal condition and six under salt stress condition. The other two QTLs for ratio of TDW of wheat plants between salt stress and control (TDWR)	Maximum root length (MRL), root dry weight (RDW), shoot dry weight (SDW), total dry weight (TDW), and the ratio of TDW of wheat plants between salt stress and control (TDWR)	Ren et al. (2018)
Oryza sativa L.	Cold stress	17 QTLs were identified; three were tolerant (qCT3.12, qCT6.7, and qCT9.6)	Spikelet fertility	Liang et al. (2018)
Hordeum vulgare L.	Salinity stress	CM72 QTL on chromosome 3H	Germination, seedling emergence, and first leaf full expansion growth stages	Angessa et al. (2017)
Solanum lycopersicum L.	Heat stress	13 QTLs were identified	Pollen viability, pollen number, style length, anther length, style protrusion, female fertility, and flowering characteristics, i.e., inflorescence number and flowers per inflorescence	Xu et al. (2017)
Triticum aestivum L.	Heat stress	24 QTLs were identified	Grain yield (GY) and its components, physiological parameters	Bhusal et al. (2017)
Triticum aestivum L.	Salt stress	49 QTLs were identified and 2 were salt tolerant	Salt tolerance and micronutrient concentrations at seedling stage	Hussain et al. (2017)

(continued)

Table 27.5 (continued)

Crop type	Stress type	Studied QTLs	Studied attributes	References
Hordeum vulgare L.	Salt stress	11 tentative and 11 significant QTLs were identified and 1 for salinity tolerant	Gas exchange and stomatal regulation traits	Liu et al. (2017)
Oryza sativa L.	Salt stress	34 QTLs were identified and eight were stable under salt stress	Shoot length, root length, shoot fresh and root dry and fresh biomasses	Rahman et al. (2017)
Brassica napus L.	Salt stress	45 QTLs were identified, seven for aSTR, seven for SPAD, nine for EC, six for RDW, two for SOD, three for SP, three for SH, two for RL, three for LFW, and three for LDW	aSTR, salt tolerance rank; SPAD, chlorophyll; EC, electric conductivity; RL, root length; SH, seed height; SP, solution protein; SOD, superoxide dismutase; LDW, leaf dry weight; RDW, root dry weight; LFW, leaf fresh weight	Lang et al. (2017)
Triticum aestivum L.	Drought stress	98 QTLs were identified that were distributed on 20 different chromosomes, 66 QTL agronomic traits, and 32 QTLs, which affected drought sensitivity index	Different agronomic traits along with drought sensitivity index (DSI)	Gahlaut et al. (2017)
Indica rice	Fe, Zn, and Al	21, 30, and 21 QTLs were identified for Fe, Zn, and Al toxicity tolerance, respectively	Growth parameters, biomass production, and metal tolerance score (MTS)	Meng et al. (2017)
Triticum aestivum L.	Heat stress	Three stable QTLs were identified	Fv/Fm (maximum quantum efficiency of photosystem II)	Sharma et al. (2017)
Oryza sativa L.	Heat stress	Five QTLs were identified; two were stable	STI and SSI for % spikelet sterility, STI and SSI for yield per plant	Shanmugavadivel et al. (2017)
Oryza sativa L.	Salt stress	20 QTLs were detected, two (qSESI12.1 and qSESF12.1) on chromosome; 12 were salt tolerant	Growth and biomass production	Bizimana et al. (2017)
Lens culinaris Medik.	Drought stress	QTL(QSRLIV-61.63), QTL(QLRNIII-98.64)	Different root and shoot traits	Idrissi et al. (2016)

(continued)

Table 27.5 (continued)

Crop type	Stress type	Studied QTLs	Studied attributes	References
Solanum lycopersicum L.	Drought stress	19 QTLs were identified on chromosome no. 9	specific leaf area (SLA), SDW, yield, and maturity traits	Lounsbery et al. (2016)
Zea mays L.	As stress	14 QTLs were identified	Yield, production, and phytoremediation	Fu et al. (2016)
Zea mays L.	Salt stress	Eight QTLs were detected. Five were associated with salt tolerance	Shoot fresh weight, shoot dry weight, tissue water content, concentration of Na^+ and K^+, and their ratio in shoot	Cui et al. (2015)
Triticum durum	Salt stress	12 QTLs were identified	Growth attributes and biomass production and salt tolerance indices	Turki et al. (2015)
Pisum sativum L.	Drought stress	Ten QTLs were detected	Relative water content in soil (RWCS) and relative water content in leaves (LWCL)	Iglesias-García et al. (2015)
Oryza sativa L.	Drought stress	qDTY1.1, qDTY2.2, qDTY3.1, qDTY3.2, qDTY6.1, and qDTY12.1	Yield and yield components	Kumar et al. (2014)
Oryza sativa L.	Cold stress	Five QTLs were detected	Cold tolerance at germination (CTG) and early seedling (CTS) stages	Ranawake et al. (2014)
Solanum lycopersicum L.	Drought stress	18 QTLs were detected	Promptness index, radical root length, coleoptile length, and lateral root number at germinating stage and seedling survival rate	Qie et al. (2014)
Zea mays L.	Drought stress	45 QTLs were identified on all chromosomes except chromosome 9, five for grain yield per plant and 40 for eight yield components	Yield and yield components	Nikolic et al. (2013)
Oryza sativa L.	Heat tolerance	Two QTLs were identified on chromosome 1 and chromosome 4; 1 QTL was found tolerant one		Ye et al. (2012)

(continued)

Table 27.5 (continued)

Crop type	Stress type	Studied QTLs	Studied attributes	References
Oryza sativa L.	Salt stress	17 QTLs were identified, five QTLs might represent novel salt tolerance loci, and a major salt-tolerant QTL was also detected	RNC, root Na+ concentration; RKC, root K+ concentration; SNC, shoot Na+ concentration; SKC, shoot K+ concentration; STR, salt tolerance rating	Wang et al. (2012)
Triticum aestivum L.	Heat stress	Three QTLs were identified that were associated with heat tolerance	Heat susceptibility index (HSI) of thousand grain weight (HSITGW), (2) HSI of grain fill duration (HSIGFD), (3) HSI of grain yield (HSIYLD), and (4) canopy temperature depression (CTD)	Paliwal et al. (2012)
Hordeum vulgare L.	Salt stress	Five significant QTLs were identified for salinity tolerance	Concentration of Na^+ and K^+ in root and shoot	Zhou et al. (2012)
Oryza sativa L.	Salt stress	Three salt-tolerant QTLs were identified	Salt tolerance parameters	Islam et al. (2011)
Zea mays L.	As stress	Three QTLs were detected	As concentration in the four tissues	Ding et al. (2011)
Glycine soja Sieb. & Zucc.	Salt stress	A significant QTL was identified	Salt tolerance rating (STR) and leaf chlorophyll content (SPAD)	Tuyen et al. (2010)
Oryza sativa L.	Cd stress	Only a single QTL was detected	Grain Cd concentrations	Ishikawa et al. (2009)
Helianthus annuus L.	Water stress	Several QTLs were identified	Yield-related traits	Kiani et al. (2009)
Zea mays L.	Drought stress	Umc 11 on chromosome 1 and csu133 on chromosome 2	Morphophysiological traits and yield	Tuberosa et al. (2004)
Solanum lycopersicum L.	Salt stress	Five QTLs were identified	Salt tolerance parameters	Foolad et al. (2001)
Helianthus annuus L.	Water stress	19 QTLs were detected	Photosynthesis and water status traits	Hervé et al. (2001)

soybean cultivars were selected as high temperature tolerant on the basis of various growth and physiological parameters. Three cultivars of canola were grown in lab under heat stress to find out their tolerance. The cultivar “Oscar” was selected as tolerant one that was based on oil quality and different yield attributes (Aksouh et al. 2001). Changes in growth, morphology, and yield traits in different temperature stressed mung bean cultivars were observed to select the different tolerant cultivars and five cultivars were selected as the tolerant ones based on these changes (Sharma et al. 2016). In a greenhouse experiment conducted by Kesici et al. (2013), it was found that out of 15 cultivars that were subjected to heat stress to sort out various tolerant cultivars, two cultivars were selected as tolerant ones against heat stress. In another study conducted by Wijewardana et al. (2015), it was reported that various rice hybrids were subjected to cold stress to find out their chilling tolerance potential. Among 33 hybrids, three were selected as stress tolerant depending on different growth parameters and nutrient uptake. Cruz and Milach (2004) reported that out of 24 rice genotypes grown in field under cold stress, three hybrids were selected as stress-tolerant hybrids to check their stress tolerance potential based on different germination parameters.

27.5 Breeding Against Heavy Metal Stress

Due to industrialization, the agricultural lands are being contaminated with toxic effluents, a rich source of heavy metals, acids, and dyes that are severely affecting the crop production as well as health risk for the consumers depending on their soil concentration. High concentration of heavy metals in soil disturbs the nutrient uptake especially the essential ones. At cellular level after the uptake of heavy metals the disturbance in ion homeostasis takes place. So, in future due to rapid increase in heavy metal contaminated areas, it is necessary to select the genotypes that have heavy metal stress tolerance mechanism with the ability to reduce heavy metal stress including losses in production. Gul et al. (2016) conducted a greenhouse experiment to assess the interactive effects of heavy metal stress (Cd and Cu) on ecophysiological responses of two maize cultivars. They reported that cultivar S2000 was nominated as tolerant one while the cultivar Okmass was identified as sensitive one. In another study conducted on two maize cultivars grown in pots under Cd and As stress to develop tolerant cultivars, they found that the cultivar Dong Dan and Run Nong 35 were identified as tolerant and sensitive cultivars, respectively, and the selection was based on alteration in different growth, gas exchange, as well as photosynthetic attributes (Anjum et al. 2017a, b). Changes in growth and photosynthetic responses of different maize hybrids were observed to evaluate tolerant hybrids when grown in hydroponic culture under Cd stress. They reported that among seven hybrids, two were selected as tolerant ones. The differential responses of maize hybrids due to Cd stress will be useful in selection and breeding for Cd-tolerant genotypes (Akhtar et al. 2017). A field experiment was conducted on various wheat genotypes grown under Zn and Cd stress to find out the stress-tolerant genotypes based on different growth and physiological attributes as reported by Alybayeva et al. (2016). In a glass house experiment conducted by Hussain et al. (2015), it was found that out of 100 tomato genotypes, eight were selected as tolerant ones, when grown under Cd stress, and selection of these stress-tolerant genotypes was made on the basis of different yield parameters as well as accumulation of Cd in root, shoot, as well as leaf. In mung bean different stress-tolerant genotypes were selected to use in breeding program when grown under Ni stress, and these tolerant genotypes were selected on the basis of various growth parameters and different stress tolerance indices (Samantaray et al. 1998). Hussain et al. (2015) reported that three mung bean cultivars were grown in greenhouse under boron stress to find out their tolerance against stress based on germination, growth, and photosynthetic responses against boron stress. Based on the results, two cultivars, i.e., M-6 and M-8, were selected as tolerant ones.

27.6 Quantitative Trait Locus (QTL)-Based Selection of Crop Genotypes Under Different Environmental Stresses

In genetics, quantitative trait loci (QTLs) have gained great interest by the breeders for over a century as they play the most important role in natural variation in designing the phenotype in almost all eukaryotes, including crop plants. Number of traits that are important agriculturally, i.e., growth, stress tolerance, as well as plant yield, are controlled by a variety of genes in a given population and these genes are segregated according to Mendelian fashion. Mathar in 1949 defined these traits as “polygenes.” Afterward in 1975, Gelderman called these polygenes as QTLs. It can be defined as a specific region of DNA that is responsible for phenotypic expression of organisms and also associated with quantitative trait (Dhingani et al. 2015). Several techniques/methods have been employed for the detection of these genomic regions that are responsible for the phenotypes in quantitative term. These methods vary from a simple statistical test or models that include interaction between multiple markers (Martínez et al. 2016). A QTL may be single that shows major effect or present in the form of clusters of genes on genome that have significant minor effects on a specific trait. The number of QTLs present on a particular chromosome affects the changes in the phenotypic trait that explain the genetic makeup of that trait. For example, it explains how plant height can be controlled by a small number of genes having large effect or by a large group of genes having small effect collectively in a total expression. A variety of QTLs have been found involved with abiotic stress tolerance in crop plants that are associated with complex stress-related traits, such as growth, yield, and biomass production under drought, salinity, and heat stress. So, there is a need of developing QTLs that are responsible for improvement of agronomic as well as physiological traits in a number of crop plants such as maize, wheat, and rice subjected to different abiotic stresses (Yao et al. 2016; Gahlaut et al. 2017). As it is well known that developing stress-tolerant crop cultivars is the main focus of breeders especially for better production under changing environmental conditions that cause the large economic losses almost 70% of over the world. Abiotic stresses at any stage of plant growth disturbs the cellular biochemical reactions that as a result alter the morphology and physiology of plants (Sahoo et al. 2014) and this mechanism is purely genetically controlled that regulate up and down regulations and under adverse environmental conditions (Mizoi and Yamaguchi-Shinozaki 2013). However, the mechanism is stress type, plant species, and growth stage specific (Gall et al. 2015). In this regard, study of QTLs play significant role in learning plant genetic behavior and tells how to improve them under stressful conditions (Bo et al. 2015) and to understand the physiological and the genetic elements play significant role in source sink relationship when grown under stressful environment (Welcker et al. 2007). In evolutionary biology, QTL study plays a significant role in finding the location of genes of interest on a specific chromosome. Study of QTLs is an important tool for understanding the phenotypic and genotypic behavior of plants under stressful environment (Soda et al. 2015).

27.7 Development of Tolerant Crop Genotypes by Manipulating QTLs

Quantitative trait locus (QTL)-based selection for stress tolerance is gaining interest due to its role in solving the complex genetic mechanism controlling the stress-tolerant crop plants. QTL-based selection in crop plants is focusing especially on all of the morphological, physiological, and yield potential taken together. These mechanisms are considered important ones but these are purely genetically controlled. In this regard, QTL-based selection is considered a short term and easy way, from the available germplasm. For example, in rice 69 QTLs were identified for some agronomic traits such as plant height, for the induction of drought tolerance, ear weight, cob weight, 100-kernel weight, and ear length in two F2:3 populations both under stressed and non-stressed conditions. Out of these 69 QTLs, 52 were identified under water deficit conditions, while 21 were found stable and showed tolerance against water stress (Zhao et al. 2018). In a study conducted by Gahlaut et al. (2017) it was reported that in wheat 98 QTLs were identified on chromosome no. 20 and 66 QTLs for agronomic traits were selected and out of them 32 QTLs affected the drought sensitivity index. Lounsbery et al. (2016) reported that in *Solanum lycopersicum* L. plants 19 QTLs were identified on chromosome no. 9 that were associated with drought tolerance potential and the identification of tolerant QTLs was based on few traits such as SDW, yield, and maturity traits. Ten different QTLs were identified using composite interval mapping (CIM) and multiple interval mapping (MIP) to check the drought tolerance potential of pea plants focusing based on relative water content in soil (RWCS) and leaves (LWCL) as reported by Iglesias-García et al. (2015). Kumar et al. (2014) developed some high-yielding drought-tolerant rice varieties based on QTL analysis. Fourteen QTLs were detected using grain yield as selection criteria. Out of these fourteen QTLs, six were identified as high-yielding ones. In maize, 45 drought-tolerant QTLs (five for grain yield per plant and 40 for eight other yield components) were detected associated with yield and different yield components (Nikolic et al. 2013). A hydroponic experiment was conducted to identify some QTLs associated with salt-tolerant potential of some inbred wheat lines. A total of 19 QTLs were detected, 11 under normal condition and six under salt stress condition, and other two QTLs were identified for TDWR. The selection was based on MRL, RDW, SDW, TDW, and TDWR (Ren et al. 2018). In another study conducted by Angessa et al. (2017), they reported that two barely varieties were grown under salt stress to check their salt tolerance potential based on QTL analysis. Of all studied QTLs, 12 were detected on chromosomes 2H–6H based on seed germination, seedling emergence, and first leaf full expansion growth stages, but only one QTL showed stability both under controlled and stressful conditions, i.e., CM72 QTL, on chromosome 3H. Different recombinant inbred rice lines were genotyped using QTL analysis to check their stability when grown under salt stress. A total of 39 QTLs were detected, and eight were stable QTLs based on some growth parameters such as shoot length, root length, shoot fresh, and root dry and fresh biomasses (Rahman et al. 2017). Salt-tolerant potential of two rice varieties was checked based on QTL analysis. Five QTLs represented novel salt tolerance loci and a major salt-tolerant QTL was also detected based on RNC, RKC, SNC, SKC, and STR (Wang et al. 2012). Zhou et al. (2012) reported that five significant QTLs were identified for salinity tolerance in two rice varieties based on concentration of Na^+ and K^+ in root and shoot. Furthermore, Bizimana et al. (2017) identified 20 QTLs for salinity tolerance in two rice varieties. Among 20 QTLs, two were associated with salt tolerance based on growth and biomass production. In parallel with drought and salinity, QTL-based selection was also found helpful in developing new crop genotypes tolerant to other stresses such as temperature (heat and cold) and heavy metal stresses. For example, in wheat 24 QTLs were identified associated with heat tolerance based on grain yield (GY) and yield components and also on some physiological parameters as well (Bhusal et al. 2017). In another study conducted by Shanmugavadivel et al. (2017), they reported that two rice varieties (Aus cultivar and IR64) were crossed to check their heat tolerance potential based on QTL analysis. Five QTLs were identified associated with STI and SSI for % spikelet sterility, such as STI and SSI for yield per plant. Among these QTLs, two were tolerant ones. Liang et al. (2018) identified different QTLs in rice grown under cold stress. They reported that out of 17 QTLs, three were stable based on spikelet fertility. Wainaina et al. (2018) crossed two rice varieties for the identification and validation of QTLs for cold tolerance at the booting stage and other agronomic traits. They identified 35 QTLs for abovementioned traits. Among these, two were associated with cold tolerance potential. QTL analysis of rice was done to check their heavy metal tolerance potential at the seedling stage. A total of 21, 30, and 21 QTLs were identified for Fe, Zn, and Al toxicity tolerance, respectively (Meng et al. 2017). Ishikawa et al. (2009) reported that in rice only a single QTL was identified associated with Cd stress toxicity. In maize, 14 QTLs were identified that were found helpful in phytoremediation of As-contaminated soil and are also associated with yield and production of rice as reported by Fu et al. (2016).

References

Adger WN, Agrawala S, Mirza M, Conde C, Brien K, Pulhin J, Pulwarty R, Smit B, Takahashi, K (2007). Assessment of adaptation practices, options, constraints and capacity. In: Parry ML, Canziani OF, Palutikof JP, vander Linden PJ, Hanson CE (eds.) Climate change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 717–743

Ahmadzadeh N, Mostafavil K, Zabet M (2015) Effect of salinity stress on yield and yield components in rapeseed cultivars. Int Res J Appl Basic Sci 9:1592–1595

Ahmed I, Ali A, Mahmood IA, Salim M, Hussain N, Jamil M (2005) Growth and ionic relations of various sunflower cultivars under saline environment. *Helia* 28(42):147–158

Akhtar N (2006) Callogenesis and organogenesis response of wheat cultivars under sodium chloride salt stress. Pakistan J Biol Sci 9:2092–2096

Akhtar T, Zia-ur-Rehman M, Naeem A, Nawaz R, Ali S, Murtaza G, Maqsood MA, Azhar M, Khalid H, Rizwan M (2017) Photosynthesis and growth response of maize (*Zea mays* L.) hybrids exposed to cadmium stress. Environ Sci Pollut Res 24:5521–5529

Akram M (2011) Growth and yield components of wheat under water stress of different growth stages. Bangladesh J Agric Res 36(3):455–468

Aksouh NM, Jacobs BC, Stoddard FL, Mailer RJ (2001) Response of canola to different heat stresses. Australian J Agric Res 52:817–824

Alexander LV, Zhang X, Peterson TC, Caesar J, Gleason B, Klein Tank AMG, Haylock M, Collins D, Trewin B, Rahimzadeh F, Tagipour A, Rupa Kumar K, Revadekar J, Griffiths G, Vincent L, Stephenson DB, Burn J, Aguilar E, Brunet M, Taylor M, New M, Zhai P, Rusticucci M, Vazquez-Aguirre JL (2006) Global observed changes in daily climate extremes of temperature and precipitation. J Geophys Res 111(D5)

Aliakbari M, Razi H, Kazemeini SA (2014) Evaluation of drought tolerance in rapeseed (*Brassica napus* L.) cultivars using drought tolerance indices. Int J Adv Biol. Biomed Res 2:696–705

Alsajri F, Singh B, Wijewardana C, Irby J, Gao W, Reddy K (2019) Evaluating soybean cultivars for low-and high-temperature tolerance during the seedling growth stage. Agronomy 9:1–20

Alybayeva R, Kruzhaeva V, Alenova A, Salmenova I, Asylbekova A, Sadyrbaeva A (2016) The genetic potential of wheat resistance to heavy metals. Bioeng Biosci 4:34–41

Angessa TT, Zhang XQ, Zhou G, Broughton S, Zhang W, Li C (2017) Early growth stages salinity stress tolerance in CM72 x Gairdner doubled haploid barley population. PloS One 12:1–16

Anjum SA, Ashraf U, Tanveer M, Khan I, Hussain S, Shahzad B, Zohaib A, Abbas F, Saleem FM, Ali I, Wang LC (2017a) Drought induced changes in growth, osmolyte accumulation and antioxidant metabolism of three maize hybrids. Front Plant Sci 8:1–8

Anjum SA, Tanveer M, Hussain S, Ashraf U, Khan I, Wang L (2017b) Alteration in growth, leaf gas exchange, and photosynthetic pigments of maize plants under combined cadmium and arsenic stress. Water Air Soil Pollut 228:1–12

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Ann Rev Plant Biol 55:373–399

Baloğlu MC, Kavas M, Aydin G, Öktem HA, Yücel AM (2012) Antioxidative and physiological responses of two sunflower (*Helianthus annuus*) cultivars under PEG-mediated drought stress. Turk J Bot 36:707–714

Bartha C, Fodorpataki L, Martinez-Ballesta MC, Popescu O, Carvajal M (2015) Sodium accumulation contributes to salt stress tolerance in lettuce cultivars. J Appl Bot Food Qual 88:42–48

Bavani MRZ, Petvast G, Ghasemnezhad M, Forghani A (2015) Assessment of genotypic variation in salt tolerance of pepper (*Capsicum annuum* L.) Cultivar using gas exchange characteristic, growth parameters and chlorophyll content. South Western J Hort. Biol Environ 6:71–90

Bhusal N, Sarial AK, Sharma P, Sareen S (2017) Mapping QTLs for grain yield components in wheat under heat stress. PloS One 12:1–14

Bizimana JB, Luzi-Kihupi A, Murori RW, Singh RK (2017) Identification of quantitative trait loci for salinity tolerance in rice (*Oryza sativa* L.) using IR29/Hasawi mapping population. J Genetics 96:571–582

Bo K, Ma Z, Chen J, Weng Y (2015) Molecular mapping reveals structural rearrangements and quantitative trait loci underlying traits with local adaptation in semi-wild Xishuangbanna cucumber (*Cucumis sativus* L. var. xishuangbannanesis Qi et Yuan). Theor Appl Genet 128:25–39

Borowski E, Michalek S (2014) The effect of chilling temperature on germination and early growth of domestic and Canadian soybean (*Glycine max* (L.) Merr.) cultivars. Acta Scientiarum Polonorum Hortorum Cultus 13:31–43

Brdar-Jokanović M, Girek Z, Pavlović S, Ugrinović M, Zdravković J (2014) Shoot and root dry weight in drought exposed tomato populations. Genetika 46:495–504

Brown ME, Funk CC (2008) Food security under climate change. Science 319:580–581

Bybordi A, Tabatabaei SJ, Ahmadev A (2010) The influence of salinity stress on antioxidant activity in canola cultivars (*Brassica napus* L.). J Food Agric Environ 8:122–127

Camejo D, Rodríguez P, Morales MA, Dell'Amico JM, Torrecillas A, Alarcón JJ (2005) High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. J Plant Physiol 162:281–289

Chakraborty U, Pradhan B (2012) Oxidative stress in five wheat varieties (*Triticum aestivum* L.) exposed to water stress and study of their antioxidant enzyme defense system, water stress responsive metabolites and H_2O_2 accumulation. Brazilian J Plant Physiol 24:117–130

Chauhan A, Rajput N, Kumar D, Kumar A, Chaudhry AK (2016) Effect of different salt concentration on seed germination and seedling growth of different varieties of oat (*Avena sativa* L.). Int J Inf. Res Rev 3:2627–2632

Chen J, Xu W, Velten J, Xin Z, Stout J (2012) Characterization of maize inbred lines for drought and heat tolerance. J Soil Water Conserv 67:354–364

Chunthaburee S, Dongsansuk A, Sanitchon J, Pattanagul W, Theerakulpisut P (2016) Physiological and biochemical parameters for evaluation and clustering of rice cultivars differing in salt tolerance at seedling stage. Saudi J Biol Sci 23(4):467–477

Cline WR (2007) Global Warming and Agriculture: Impact Estimates by Country. Washington, DC, USA, Peterson Institute

Collado MB, Aulicino MB, Arturi MJ, Molina MDC (2016) Selection of maize genotypes with tolerance to osmotic stress associated with salinity. Agri Sci 7(02):82–92

Cruz RPD, Milach SCK (2004) Cold tolerance at the germination stage of rice: methods of evaluation and characterization of genotypes. Sci Agri 61(1):1–8

Cui D, Wu D, Somarathna Y, Xu C, Li S, Li P, Zhang H, Chen H, Zhao L (2015) QTL mapping for salt tolerance based on snp markers at the seedling stage in maize (*Zea mays* L.). Euphytica 203(2):273–283

Curtis, T., & Halford, N. G. (2014). Food security: the challenge of increasing wheat yield and the importance of not compromising food safety. Ann Appl Biol 164(3):354-372. cs/subtropics. Photosynthetica, 52(2), 161-178.

Datta JK, Nag S, Banerjee A, Mondai NK (2009) Impact of salt stress on five varieties of wheat (*Triticum aestivum* L.) cultivars under laboratory condition. J Appl Sci Environ Mgmt 13(3):93–97

Dehbalaei S, Farshadfar E, Farshadfar M (2013) Assessment of drought tolerance in bread wheat genotypes based on resistance/tolerance indices. Int J Agri Crop Sci 5(20):2352

Dhingani RM, Umrania VV, Tomar RS, Parakhia MV, Golakiya BA (2015) Introduction to QTL mapping in plants. Ann Plant Sci 4(04):1072–1079

Ding D, Li W, Song G, Qi H, Liu J, Tang J (2011) Identification of QTLs for arsenic accumulation in maize (*Zea mays* L.) using a RIL population. PLoS One 6(10):1–7

Elgamal WH, El Sayed MAA, El Shamey EAZ, Anis GB (2018) Genetic diversity for cold tolerance at seedling stage in rice (*Oryza sativa* L.) under Egyptian conditions. J Agric Sci 44:101–113

El-Sharkawy MA (2014) Global warming: causes and impacts on agroecosystems productivity and food security with emphasis on cassava comparative advantage in the tropics/subtropics. Photosynthetica 52(2):161–178

Emamverdian A, Ding Y, Mokhberdoran F, Xie Y (2015) Heavy metal stress and some mechanisms of plant defense response. Scientific World J 2015:1–18

FAO. (1996). Food, agriculture and food security: developments since the World Food Conference and prospects for the future. World Food Summit technical background document No. 1. Rome.

Faraji A, Latifi N, Soltani A, Rad AHS (2008) Effect of high temperature stress and supplemental irrigation on flower and pod formation in two canola (*Brassica napus* L.) cultivars at Mediterranean climate. Asian J Plant Sci 7(4):343–351

Farooqi MQU, Lee JK (2016) Cold stress evaluation among maize (*Zea mays* L.) inbred lines in different temperature conditions. Biotechnol Plant Breeding 4:352–361

Farshadfar E, Saeidi M, Honarmand SJ (2012) Evaluation of drought tolerance screening techniques among some landraces of bread wheat genotypes. Eur J Exp Biol 2(5):1585–1592

Foolad MR, Zhang LP, Lin GY (2001) Identification and validation of QTLs for salt tolerance during vegetative growth in tomato by selective genotyping. Genome 44(3):444–454

Fu Z, Li W, Xing X, Xu M, Liu X, Li H, Xue Y, Liu Z, Tang J (2016) Genetic analysis of arsenic accumulation in maize using QTL mapping. Sci Rep 6:1–8

Gahlaut V, Jaiswal V, Tyagi BS, Singh G, Sareen S, Balyan HS, Gupta PK (2017) QTL mapping for nine drought-responsive agronomic traits in bread wheat under irrigated and rain-fed environments. PLoS One 12(8):1–27

Gall H, Philippe F, Domon JM, Gillet F, Pelloux J, Rayon C (2015) Cell wall metabolism in response to abiotic stress. Plants 4:112–166

Ganapati RK, Rehman MM, Kabiraj RC, Sen R, Islam MS (2016) Screening of water stress tolerant sugar beet (*Beta vulgaris* l.) genotypes. Int J Sustain Crop Prod 11(3):29–35

Ghaderi N, Siosemardeh A (2011) Response to drought stress of two strawberry cultivars (cv. Kurdistan and Selva). Horti Environ Biotechnol 52(1):6–12

Gholinezhad E, Darvishzadeh R, Bernousi I (2014) Evaluation of Drought Tolerance Indices for Selection of Confectionery Sunflower (*Helianthus anuus* L.) Landraces under Various Environmental Conditions. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 42(1):187–201

Gornall J, Betts R, Burke E, Clark R, Camp J, Willett K, Wiltshire A (2010) Implications of climate change for agricultural productivity in the early twenty first century. Philos Trans Royal Soc B Biol Sci 365:2973–2989

Goudarzi M, Pakniyat H (2008) Evaluation of wheat cultivars under salinity stress based on some agronomic and physiological traits. J Agric Soc Sci 4(3):35–38

Gul S, Nawaz MF, Azeem M (2016) Interactive effects of salinity and heavy metal stress on ecophysiological responses of two maize (*Zea mays* L.) cultivars. *FUUAST*. J Biol 6(1):81–87

Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. Int J Genom 2014

Habibi F, Normohamady G, Sharif abad HH, Eivazi A, Heravan EM (2012) Effect of sowing date on cold tolerance and some agronomic traits in bread wheat genotypes grown at west Azerbaijan conditions. World Appl Sci J 16(2):232–239

Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. Proc Natl Acad Sci 103:14288–14293

Haq TU, Akhtar J, Nawaz S, Ahmad R (2009) Morpho-physiological response of rice (*Oryza sativa* L.) varieties to salinity stress. Pakistan J Bot 41(6):2943–2956

Haq UI, Khan AA, Khan IA, Azmat MA (2012) Comprehensive screening and selection of okra (*Abelmoschus esculentus)* germplasm for salinity tolerance at the seedling stage and during plant ontogeny. J Zhejiang Univ Sci B 13(7):533–544

Haq TU, Akhtar J, Ali A, Maqbool MM, Ibrahim M (2014a) Evaluating the response of some canola (*Brassica napus* L.) cultivars to salinity stress at seedling stage. Pakistan J Agric Sci 51(3):571–579

Haq T, Ali A, Nadeem SM, Maqbool MM, Ibrahim M (2014b) Performance of canola cultivars under drought stress induced by withholding irrigation at different growth stages. Soil Environ 33:43–50

Hasnain A, Mahmood S, Akhtar S, Malik SA, Bashir N (2011) Tolerance and toxicity levels of boron in mung bean (*Vigna radiata* (L.) Wilczek) cultivars at early growth stages. Pakistan J Bot 43(2):1119–1125

Hassen A, Maher S, Cherif H (2014) Effect of salt stress (NaCl) on germination and early seedling parameters of three pepper cultivars (*Capsicum annuum* L.). J Stress Physiol Biochem 10(1):14–25

Hatfield J, Boote K, Fay P (2008) Agriculture. In The effects of climate change on agriculture, land resources, water resources, and agronomy for enhanced wheat competitiveness with weeds. Aust J Agri Res 52:527–548

Hendrix CS, Glaser SM (2007) Trends and triggers: Climate, climate change and civil conflict in Sub-Saharan Africa. Polit Geogr 26:695–715

Hervé D, Fabre F, Berrios EF, Leroux N, Chaarani GA, Planchon C, Sarrafi A, Gentzbittel L (2001) QTL analysis of photosynthesis and water status traits in sunflower (*Helianthus annuus* L.) under greenhouse conditions. J Exp Bot 52(362):1857–1864

Hund A, Ruta N, Liedgens M (2009) Rooting depth and water use efficiency of tropical maize inbred lines, differing in drought tolerance. Plant and Soil 318(1-2):311–325

Hussain MM, Saeed A, Khan AA, Javid S, Fatima B (2015) Differential responses of one hundred tomato genotypes grown under cadmium stress. Genet Mol Res 14(4):13162–13171

Hussain B, Lucas SJ, Ozturk L, Budak H (2017) Mapping QTLs conferring salt tolerance and micronutrient concentrations at seedling stagein wheat. Sci Rep 7(1):1–14

Idrissi O, Udupa SM, De Keyser E, McGee RJ, Coyne CJ, Saha GC, Muehlbauer FJ, Damme PV, De Riek J (2016) Identification of quantitative trait loci controlling root and shoot traits associated with drought tolerance in a lentil (*Lens culinaris* Medik.) recombinant inbred line population. Front Plant Sci 7:1–11

Iglesias-García R, Prats E, Fondevilla S, Satovic Z, Rubiales D (2015) Quantitative trait loci associated to drought adaptation in pea (*Pisum sativum* L.). Plant Mol Biol Rep 33(6):1768–1778

Ignjatovic-Micic D, Kostadinovic M, Bozinovic S, Andjelkovic V, Vancetovic J (2014) High grain quality accessions within a maize drought tolerant core collection. Scientia Agricola 71(5):402–409

IPCC. (2007). Climate Change. 2007: Synthesis Report. Contributionnof working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change. core writing team. In: Pachauri RK, & Reisinger A (eds) Geneva: Intergovernmental Panel on Climate Change.

IPCC. (2013). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker, T. F., Qin, D., Plattner, G. K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., & Midgley, P. M, eds. Cambridge, UK/New York: Cambridge University Press. http://www.ipcc.ch/publications_and_data/publications_and_data_reports.shtml. Accessed 2 Jan 2015.

Ishikawa S, Abe T, Kuramata M, Yamaguchi M, Ando T, Yamamoto T, Yano M (2009) A major quantitative trait locus for increasing cadmium-specific concentration in rice grain is located on the short arm of chromosome 7. J Exp Bot 61(3):923–934

Islam MR, Hassan L, Salam MA, Collard BCY, Singh RK, Gregorio GB (2011) QTL mapping for salinity tolerance at seedling stage in rice. Emirat J Food Agric 23(2):137–146

Izadi MH, Rabbani J, Emam Y, Pessarakli M, Tahmasebi A (2014) Effects of salinity stress on physiological performance of various wheat and barley cultivars. J Plant Nutr 37(4):520–531

Jaarsma R, de Vries RS, de Boer AH (2013) Effect of salt stress on growth, Na^+ accumulation and proline metabolism in potato (*Solanum tuberosum*) cultivars. PLoS One 8(3):1–10

Jaleel CA, Manivannan P, Lakshmanan GMA, Gomathinayagam M, Panneerselvam R (2008) Alterations in morphological parameters and photosynthetic pigment responses of Catharanthus roseus under soil water deficits. Colloid Surf B Biointerf 61(2):298–303

Janjua PZ, Samad G, Khan NU, Nasir M (2010) Impact of climate change on wheat production: a case study of Pakistan. Pakistan Dev Rev 49:799–822

Jozefczak M, Remans T, Vangronsveld J, Cuypers A (2012) Glutathione is a key player in metal-induced oxidative stress defenses. Int J Mol Sci 13(3):3145–3175

Kahrizi S, Sedghi M, Sofalian O (2013) Evaluation of the effect of salt stress on some of agronomic and morphological characters in ten durum wheat cultivars. Ann West Univ Timisoara. Ser Biol 16(1):19–24

Kamyab-Talesh F, Mousavi SF, Asadi R, Rezaei M, Khaledian MR (2014) Evaluation of some rice cultivars' response to salinity stress using resistance indices. Archiv Agron Soil Sci 60(9):1303–1314

Kaouther Z, Mariem BF, Fardaous M, Cherif H (2012) Impact of salt stress (NaCl) on growth, chlorophyll content and fluorescence of Tunisian cultivars of chili pepper (*Capsicum frutescens* L.). J Stress Physiol Biochem 8(4):236–252

Karl TR, Melillo JM, Peterson TC (2009) Global climate change impacts in the United States. Cambridge University Press, Cambridge

Kaya YV, Arısoy RZ (2016) Salinity tolerance in bread wheat cultivars from Turkey. Roman Biotechnol Lett 21(2):11321–11327

Kesici M, Gulen H, Ergin S, Turhan E, Ahmet IPEK, Koksal N (2013) Heat-stress tolerance of some strawberry (Fragaria× ananassa) cultivars. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 41(1):238–243

Khan F, Upreti P, Singh R, Shukla PK, Shirke PA (2017) Physiological performance of two contrasting rice varieties under water stress. Physiol Mol Biol Plants 23(1):85–97

Kiani PS, Maury P, Nouri L, Ykhlef N, Grieu P, Sarrafi A (2009) QTL analysis of yield-related traits in sunflower under different water treatments. Plant Breeding 128(4):363–373

Kilic H, Yagbasanlar T (2010) The effect of drought stress on grain yield, yield components and some quality traits of durum wheat (*Triticum turgidum* ssp. durum) cultivars. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 38(1):164–170

Kirby JM, Mainuddin M, Mpelasoka F, Ahmad MD, Palash W, Quadir ME, Shah-Newaz SM, Hossain MM (2016) The impact of climate change on regional water balances in Bangladesh. Clim Change 135:481–491

Kranner I, Minibayeva FV, Beckett RP, Seal CE (2010) What is stress? Concepts, definitions and applications in seed science. New Phytol 188:655–673

Krishnan N, Dickman MB, Becker DF (2008) Proline modulates the intracellular redox environment and protects mammalian cells against oxidative stress. Free Radic Biol Med 44(4):671–681

Kumar A, Dixit S, Ram T, Yadaw RB, Mishra KK, Mandal NP (2014) Breeding high-yielding drought-tolerant rice: genetic variations and conventional and molecular approaches. J Exp Bot 65(21):6265–6278

Kumar R, Kaul J, Dubey RB, Singode A, GK C, Manivannan A, Debnath MK (2015) Assessment of drought tolerance in maize (*Zea mays* L.) based on different indices. SABRAO J Breed Genet 47(3):291–298

Lang L, Xu A, Ding J, Zhang Y, Zhao N, Tian Z, Liu Y, Wang Y, Liu X, Liang F, Zhang B, Qin M, Dalelhan J, Huang Z (2017) Quantitative trait locus mapping of salt tolerance and identification of salt-tolerant genes in *Brassica napus* L. Front Plant Sci 8:1–13

Liang Y, Meng L, Lin X, Cui Y, Pang Y, Xu J, Li Z (2018) QTL and QTL networks for cold tolerance at the reproductive stage detected using selective introgression in rice. PloS One 13(9):1–16

Liu X, Fan Y, Mak M, Babla M, Holford P, Wang F, Chen G, Scott G, Wang G, Shabala S, Zhou M, Chen ZH (2017) QTLs for stomatal and photosynthetic traits related to salinity tolerance in barley. BMC Genom 18(1):1–13

Lobell D, Burke M, Tebaldi C, Mastrandera M, Falcon W, Naylor R (2008) Prioritizing climate change adaptation needs for food security in 2030. Science 319:607–610

Lounsbery JK, Arms EM, Bloom AJ, St Clair DA (2016) Quantitative Trait Loci for water-stress tolerance traits localize on Chromosome 9 of Wild Tomato. Crop Sci 56(4):1514–1525

Luan Z, Xiao M, Zhou D, Zhang H, Tian Y, Wu Y, Guan B, Song Y (2014) Effects of salinity, temperature, and polyethylene glycol on the seed germination of sunflower (*Helianthus annuus* L.). Scientific World J 2014:1–9

Machado R, Serralheiro R (2017) Soil salinity: effect on vegetable crop growth. Management practices to prevent and mitigate soil salinization. Horticulturae 3(2):1–13

Magadza CHD (2006) Climate change impacts and human settlements in Africa: prospects for adaptation. Environ Moni Assess 61:193–205

Mahmood S, Wahid A, Javed F, Basra SMA (2010) Heat stress effects on forage quality characteristics of maize (*Zea mays*) cultivars. Int J Agric Biol 12:701–706

Majidi MM, Jafarzadeh M, Rashidi F, Mirlohi A (2015) Identification of canola cultivars with drought tolerance indices. Iran J Agric Sci 45(4):565–573

Martínez P, Robledo D, Rodríguez-Ramilo ST, Hermida M, Taboada X, Pereiro P, Rubiolo JA, Ribas L, Gómez-Tato A, Dios J, Piferrer F, Novoa B, Figueras A, Pardo BG, Fernández J, Viñas A, Bouza C (2016) Turbot (*Scophthalmus maximus*) genomic resources: application for boosting aquaculture production. In: Genomics in aquaculture. Academic, pp 131–163

Masuduzzaman, A., Ahmad, H., Haque, M., & Ahmed, M. M. E. (2016). Evaluation of rice lines tolerant to heat during flowering stage. Rice Res Open Access 4(6), 1-5.

Matsui T, Omasa K (2002) Rice (*Oryza sativa* L.) cultivars tolerant to high temperature at flowering: anther characteristics. Ann Bot 89(6):683–687

Meeks M, Murray S, Hague S, Hays D (2013) Measuring maize seedling drought response in search of tolerant germplasm. Agronomy 3(1):135–147

Meena HP, Bainsla NK, Yadav DK (2016) Breeding for Abiotic Stress Tolerance in Crop Plants. Daya Publishing House, New Delhi

Meng L, Wang B, Zhao X, Ponce K, Qian Q, Ye G (2017) Association mapping of ferrous, zinc, and aluminum tolerance at the seedling stage in indica rice using MAGIC populations. Front Plant Sci 8:1–15

Metwali EMR, Soliman HIA, Fuller MP, Almaghrabi OA (2015) Improving fruit quality in tomato (Lycopersicum esculentum Mill) under heat stress by silencing the vis 1 gene using small interfering RNA technology. Plant Cell, Tissue Organ Cult 121(1):153–166

Midmore DJ, Prange RK (1991) Sources of heat tolerance amongst potato cultivars, breeding lines, and Solanum species. Euphytica 55(3):235–245

Mirbahar AA, Markhand GS, Mahar AR, Abro SA, Kanhar NA (2009) Effect of water stress on yield and yield components of wheat (*Triticum aestivum* L.) varieties. Pakistan J Bot 41(3):1303–1310

Misra AK (2014) Climate change and challenges of water and food security. Int J Sustain Built Environ 3(1):153–165

Mizoi J, Yamaguchi-Shinozaki K (2013) Molecular approaches to improve rice abiotic stress tolerance. Methods Mol Biol 956:269–283

Mohammadi R (2018) Breeding for increased drought tolerance in wheat: a review. Crop Pasture Sci 69(3):223–241

Mohammadi P, Mohammadi M, Karizmizadeh R (2012) Selection for drought tolerance in durum wheat genotypes. Ann Biol Res 3(8):3898–3904

Mohammadian R, Moghaddam M, Rahimian H, Sadeghian SY (2005) Effect of early season drought stress on growth characteristics of sugar beet genotypes. Turkish J Agric Forest 29(5):357–368

Moradi H, Akbari GA, Khorasani SK, Ramshini HA (2012) Evaluation of drought tolerance in corn (*Zea mays* L.) new hybrids with using stress tolerance indices. Eur J Sustain Dev 1(3):543–560

Muller C, Cramera W, Harea WL, Lotze-Campen H (2011) Climate change risks for African agriculture. Proc Nat Acad Sci U S A 108:4313–4315

Munns R (2005) Genes and salt tolerance: bringing them together. New Phytologist 167(3):645–663

Munns R, James RA, Läuchli A (2006) Approaches to increasing the salt tolerance of wheat and other cereals. J Exp Bot 57(5):1025–1043

Mwadzingeni L, Shimelis H, Tesfay S, Tsilo TJ (2016) Screening of bread wheat genotypes for drought tolerance using phenotypic and proline analyses. Front Plant Sci 7:1–12

Naderi R, Emam Y (2014) Evaluation of rapeseed (*Brassica napus* L.) cultivars performance under drought stress. Aust J Crop Sci 8(9):1319–1323

Naderikharaji R, Pakniyat H, Biabani AR (2008) Effect of drought stress on photosynthetic rate of four rapeseed (*Brassica napus*) cultivars. J Appl Sci 8:4460–4463

Nepstad D, Soares-Filho BS, Merry F (2009) The end of deforestation in the Brazilian Amazon. Science 326:1350–1351

Ngugi K, Collins JO, Muchira S (2013) Combining, earliness, short anthesis to silking interval and yield based selection indices under intermittent water stress to select for drought tolerant maize. Aust J Crop Sci 7(13):2014–2020

Nikolic A, Andelkovic V, Dodig D, Drinic MS, Kravic N, Micic DI (2013) Identification of QTL-s for drought tolerance in maize, II: yield and yield components. Genetika 45(2):341–350

Paliwal R, Röder MS, Kumar U, Srivastava JP, Joshi AK (2012) QTL mapping of terminal heat tolerance in hexaploid wheat (*Triticum aestivum* L.). Theor Appl Genet 125(3):561–575

Pearce RS (1999) Molecular analysis of acclimation to cold. Plant Growth Regulation 29:47–76

Pradheeban L, Nissanka SP, Suriyagoda LDB (2015) Screening commonly cultivated rice cultivars in Sri Lanka with special reference to Jaffna for salt tolerance at seedling stage under hydroponics. Int J Agron Agric Res 7:1–13

Qie L, Jia G, Zhang W, Schnable J, Shang Z, Li W, Liu B, Li M, Chai Y, Zhi H, Diao X (2014) Mapping of quantitative trait locus (QTLs) that contribute to germination and early seedling drought tolerance in the interspecific cross Setaria italica× Setaria viridis. PloS One 9(7):1–8

Rad AHS, Abbasian A (2011a) Evaluation of drought tolerance in rapeseed genotypes under non stress and drought stress conditions. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 39(2):164–171

Rad AHS, Abbasian A (2011b) Evaluation of drought tolerance in winter rapeseed cultivars based on tolerance and sensitivity indices. Žemdirbystė-Agriculture 98(1):41–48

Rafiei F, Darbaghshahi MRN, Rezai A, Nasiri BM (2013) Survey of yield and yield components of sunflower cultivars under drought stress. Int J Adv Biol Biomed Res 1(12):1628–1638

Rahman MA, Bimpong IK, Bizimana JB, Pascual ED, Arceta M, Swamy BM, Diaw F, Rahman MS, Singh RK (2017) Mapping QTLs using a novel source of salinity tolerance from Hasawi and their interaction with environments in rice. Rice 10(1):1–7

Rajabi A, Vahidi H, Hadi MRHS, Taleghani DF (2013) Study on drought tolerance and interrelationships among some agronomic and morpho-physiological traits in sugar beet lines. Int J Agric Crop Sci 5(7):761–768

Ramya P, Singh GP, Jain N, Singh PK, Pandey MK, Sharma K, Kumar A, Prabhu KV (2016) Effect of recurrent selection on drought tolerance and related morpho-physiological traits in bread wheat. PloS One 11(6):1–17

Ranawake AL, Manangkil OE, Yoshida S, Ishii T, Mori N, Nakamura C (2014) Mapping QTLs for cold tolerance at germination and the early seedling stage in rice (*Oryza sativa* L.). Biotech Biotechnol Equip 28(6):989–998

Rao A, Ahmad SD, Sabir SM, Awan SI, Shah AH, Abbas SR, Shafique S, Khan F, Chaudhary A (2013) Potential antioxidant activities improve salt tolerance in ten varieties of wheat (*Triticum aestivum* L.). Am J Plant Sci 4(6A):69–76

Reddy VR, Pachepsky YA (2000) Predicting crop yields under climate change conditions from monthly GCM weather projections. Environ Modell Software 15:79–86

Ren Y, Xu Y, Teng W, Li B, Lin T (2018) QTLs for seedling traits under salinity stress in hexaploid wheat. Ciência Rural 48(3):1–9

Rhodes, D., & Nadolska-Orczyk, A. (2001). Plant stress physiology, in Encyclopaedia of Life Sciences (Nature Publishing Group). http://www.els.net.

Saadia M, Jamil A, Akram NA, Ashraf M (2012) A study of proline metabolism in canola (*Brassica napus* L.) seedlings under salt stress. Molecules 17(5):5803–5815

Saeedipour S (2009) Appraisal of Some Physiological Selection Criteria for Evaluation of Salt Tolerance in Canola. Int J Appl 4(2):179–192

Saensee K, Machikowa T, Muangsan N (2012) Comparative performance of sunflower synthetic varieties under drought stress. Int J Agric Biol 14(6):929–934

Saha S, Kalia P, Sureja AK, Sarkar S (2016) Breeding tropical carrots (*Daucus carota*) for enhanced nutrition and high temperature stress. Ind J Agric Sci 86(7):940–945

Sahney S, Benton MJ, Falcon-Lang HJ (2010) Rainforest collapse triggered Pennsylvanian tetrapod diversification in Euramerica. Geology 38:1079–1082

Sahoo RK, Ansari MW, Tuteja R, Tuteja N (2014) OsSUV3 transgenic rice maintains higher endogenous levels of plant hormones that mitigates adverse effects of salinity and sustains crop productivity. Rice 7(1):1–3

Samantaray S, Rout GR, Das P (1998) Differential nickel tolerance of mung bean (*Vigna radiata* L.) genotypes in nutrient culture. Agronomie 18(8-9):537–544

Sattar A, Iqbal MM, Areeb A, Ahmed Z, Irfan M, Shabbir RN, Aishia G, Hussain S (2015) Genotypic variations in wheat for phenology and accumulative heat unit under different sowing times. J Agric Environ Sci 2(8):1–8

Sazzad K (2007) Exploring plant tolerance to biotic and abiotic stresses. Swedish University of Agricultural Sciences, Uppsala

Sepehri A, Golparvar AR (2011) The effect of drought stress on water relations, chlorophyll content and leaf area in canola cultivars (*Brassica napus* L.). *Electronic*. J Biol 7:49–53

Shabala S, Wu H, Bose J (2015) Salt stress sensing and early signalling events in plant roots: current knowledge and hypothesis. Plant Sci 241:109–119

Shahryari R, Gurbanov E, Gadimov A, Hassanpanah D (2008) Tolerance of 42 bread wheat genotypes to drought stress after anthesis. Pakistan J Biol Sci 11(10):1330–1335

Shamim F, Saqlan SM, Athar HR, Waheed A (2014) Screening and Selection of Tomato Genotypes/Cultivars for Drought Tolerance Using Multivariate Analysis. Pakistan J Bot 46(4):1165–1178

Shanmugavadivel, P. S., Sv, A. M., Prakash, C., Ramkumar, M. K., Tiwari, R., Mohapatra, T., & Singh, N. K. (2017). High resolution mapping of QTLs for heat tolerance in rice using a 5K SNP array. Rice 10(1):28 1-11.

Shao HB, Chu LY, Jaleel CA (2009) Understanding water deficit stress-induced changes in the basic metabolism of higher plants—biotechnologically and sustainably improving agriculture and the ecoenvironment in arid regions of the globe. Crit Rev Biotechnol 29:131–115

Sharma L, Priya M, Bindumadhava H, Nair RM, Nayyar H (2016) Influence of high temperature stress on growth, phenology and yield performance of mungbean [*Vigna radiata* (L.) Wilczek] under managed growth conditions. Scientia Horticulturae 213:379–391

Sharma DK, Torp AM, Rosenqvist E, Ottosen CO, Andersen SB (2017) QTLs and potential candidate genes for heat stress tolerance identified from the mapping populations specifically segregating for Fv/Fm in wheat. Front Plant Sci 8:1–14

Shekoofa A, Bijanzadeh E, Emam Y, Pessarakli M (2013) Effect of salt stress on respiration of various wheat lines/cultivars at early growth stages. J Plant Nutr 36(2):243–250

Shinozaki K, Yamaguchi-Shinozaki K (2000) Molecular responses to dehydration and low temperature: differences and cross-talk between two stress signaling pathways. Curr Opin Plant Biol 3:217–223

Smith P, Gregory PJ (2013) Climate change and sustainable food production. Proc Nutr Soc 72:21–28

Soda N, Wallace S, Karan R (2015) Omics study for abiotic stress responses in plants. Adv Plants Agric Res 2:1–7

Soleymani A, Shahrajabian MH (2012) Study of cold stress on the germination and seedling stage and determination of recovery in rice varieties. Int J Biol 4(4):23–30

Somayeh M, Roghie RJ, Shadi K (2012) Effect of salinity stress on chlorophyll content, proline, water soluble carbohydrate, germination, growth and dry weight of three seedling barley (*Hordeum vulgare* L.) cultivars. J Stress Physiol Biochem 8(4):157–168

Tadesse W, Suleiman S, Tahir I, Sanchez-Garcia M, Jighly A, Hagras A, Baum MS (2018) Heat-tolerant QTLs associated with grain yield and its components in spring bread wheat under heat-stressed environments of Sudan and Egypt. Crop Sci 59:199–211

Taghizadegan M, Toorchi M, Vahed MM, Khayamim S (2019) Evaluation of sugar beet breeding populations based morpho-physiological characters under salinity stress. Pakistan J Bot 51(1):11–17

Taherabadi S, Ghobadi M, Ghobadi ME, Mohammadi G, Honarmand SJ (2013) Using stress resistance indices in sunflower cultivars under mild and severe drought stress conditions. Am-Euras J Agric Environ Sci 13(5):647–653

Talebi R, Fayaz F, Naji AM (2009) Effective selection criteria for assessing drought stress tolerance in durum wheat (*Triticum durum* Desf.). *General and Applied*. Plant Physiol 35(1/2):64–74

Tester M, Davenport R (2003) Na^+ tolerance and Na^+ Transport in higher plants. Ann Bot 91:503–527

Thomashow MF (1998) Role of cold-responsive genes in plant freezing tolerance. Plant Physiol 118:1–8

Thomashow MF (1999) Plant cold acclimation: Freezing tolerance genes and regulatory mechanisms. Annu Rev Plant Physiol Plant Mol Biol 50(1):571–599

Toorchi M, Naderi R, Kanbar A, Shakiba MR (2012) Response of spring canola cultivars to sodium chloride stress. Ann Biol Res 2(5):312–322

Tuberosa R, Salvi S, Sanguineti MC, Landi P, Maccaferri M, Conti S (2004) Maping QTLs regulating Morpho-physiological traits and yield: case studies, shortcomings and perspective in drought stressed maize. Ann Bot 89:941–963

Turki N, Shehzad T, Harrabi M, Tarchi M, Okuno K (2014) Variation in response to salt stress at seedling and maturity stages among durum wheat varieties. J Arid Land Stud 24:261–264

Turki N, Shehzad T, Harrabi M, Okuno K (2015) Detection of QTLs associated with salinity tolerance in durum wheat based on association analysis. Euphytica 201(1):29–41

Tuyen DD, Lal SK, Xu DH (2010) Identification of a major QTL allele from wild soybean (Glycine soja Sieb. & Zucc.) for increasing alkaline salt tolerance in soybean. Theor Appl Genet 121(2):229–236

Ulukan H (2011) Responses of cultivated plants and some preventive measures against climate change. Int J Agric Biol 13:292–296

Valiollah R (2013) Effect of salinity stress on yield, component characters and nutrient compositions in rapeseed (*Brassica napus* L.) genotypes. Agric Trop Subtrop 46(2):58–63

Wahb-Allah MA, Alsadon AA, Ibrahim AA (2011) Drought tolerance of several tomato genotypes under greenhouse conditions. World Appl Sci J 15(7):933–940

Wainaina CM, Makihara D, Nakamura M, Ikeda A, Suzuki T, Mizukami Y, Nonoyama T, Doi K, Kikuta M, Samejima H, Menge DM, Yamauchi A, Kitano H, Kimani JM, Inukai Y (2018) Identification and validation of QTLs for cold tolerance at the booting stage and other agronomic traits in a rice cross of a Japanese tolerant variety, Hananomai, and a NERICA parent, WAB56-104. Plant Prod Sci 21(2):132–143

Wang Z, Chen Z, Cheng J, Lai Y, Wang J, Bao Y, Huang J, Zhang H (2012) QTL analysis of Na^+ and K^+ concentrations in roots and shoots under different levels of NaCl stress in rice (*Oryza sativa* L.). PLoS One 7(12):1–9

Welcker C, Boussuge B, Bencivenni C, Ribaut JM, Tardieu F (2007) Are source and sink strengths genetically linked in maize plants subjected to water deficit? A QTL study of the responses of leaf growth and of Anthesis-Silking Interval to water deficit. J Exp Bot 58:339–349

Wijewardana C, Hock M, Henry RKR (2015) Screening corn hybrids for cold tolerance using morphological traits for early-season seeding. Crop Sci 55:851–867

Xu J, Driedonks N, Rutten MJ, Vriezen WH, de Boer GJ, Rieu I (2017) Mapping quantitative trait loci for heat tolerance of reproductive traits in tomato (*Solanum lycopersicum*). Mol Breed 37(58):1–9

Yao N, Lee CR, Semagn K, Sow M, Nwilene F, Kolade O, Boco R, Oyetunji O, Mitchell-Olds T, Ndjiondjop MN (2016) QTL mapping in three rice populations uncovers major genomic regions associated with African rice gall midge resistance. PloS One 11:1–17

Ye C, Argayoso MA, Redoña ED, Sierra SN, Laza MA, Dilla CJ, Mo Y, Thomson MJ, Chin J, Delaviña CB, Diaz GQ, Hernandez JE (2012) Mapping QTL for heat tolerance at flowering stage in rice using SNP markers. Plant Breed 131:33–41

Yousfi N, Slama I, Ghnaya T, Savoure A, Abdelly C (2010) Effects of water deficit stress on growth, water relations and osmolyte accumulation in *Medicago truncatula* and *M. laciniata* populations. CR Biol 333:205–213

Zhao X, Peng Y, Zhang J, Fang P, Wu B (2018) Identification of QTLs and meta-QTLs for seven agronomic traits in multiple maize populations under well-watered and water-stressed conditions. Crop Sci 58:507–520

Zhou G, Johnson P, Ryan PR, Delhaize E, Zhou M (2012) Quantitative trait loci for salinity tolerance in barley (*Hordeum vulgare* L.). Mol Breed 29:427–436

Zhu JK (2001) Cell signaling under salt, water and cold stresses. Curr Opin Plant Biol 4:401–406

Chapter 28
Adaptive Physiological Responses of Plants under Abiotic Stresses: Role of Phytohormones

Yawar Sadiq, Abbu Zaid, and M. Masroor A. Khan

Contents

Abstract Abiotic stress factors such as drought, flooding, cold, heat waves, ultra violet radiations, oxidizing agents and salinity in the current era of climate change is jeopardizing the plant growth and development leading to crop failure worldwide. Engineered plants with improved tolerance to abiotic stresses would provide opportunities to adapt crops to future climates coupled with enhanced food productivity and sustainable agricultural development. Growth and development of plants involve a wide range of sophisticated genetic, hormonal, metabolic and environmental

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events which are tightly regulated by internal and external cues, such as phytohormones (including various biostimulants and different organic and inorganic elicitors), temperature, light irradiation, etc. Out of these, phytohormones such as jasmonates, gibberellins, abscisic acid, brassinosteroids, nitric oxide, salicylic acid, etc. have evolved to control vital functions in regulating various plant physiological and developmental processes, ranging from seed germination, photosynthesis, leaf senescence, pollen growth, to plant defense responses, and ameliorating various abiotic stresses. The role of such phytohormones in conferring plant adaptation under dynamic climate changes is still in infancy stage. Few reports are available on the current topic. In this chapter, we attempt to summarize recent studies that have provided insights of the plant environmental adaptability and the multidimensional role of different phytohormones viz. salicylic acid (SA), nitric oxide (NO) and hydrogen sulphite (H_2S) in regulating various developmental processes and stress tolerance, taken together with the molecular mechanisms of phytohormone signalling.

Keywords Abiotic stress · Climate change · Metabolic engineering · Phytohormones · Abiotic stress tolerance

28.1 Introduction

According to an estimate of Food and Agricultural Organization [FAO] (2009), the aim of world agriculture for increasing the 70% food production by the year 2050 for approximately 2.3 billion newborn populations is facing a great hurdle in the light of hunger, poverty coupled with the dynamic environmental factors and overexploitation of natural endowments. A global emerging problem in current times is climate change and global warming which can be considered as ‘global warning’ to plant stress physiologists as well. A variation in global climate is further supposed to accelerate as global climatic projections indicate a significant increase of 2–4 °C in mean temperature over the next half of the present century (IPCC Intergovernmental Panel on Climate Change 2007). A global level, agriculture is widely considered as one of the prime prone sectors affected by a change in climatic conditions (Abbas 2013). Climate change and agriculture are correlated, as a change in climate of a particular region is the main reason of biotic and abiotic stresses, which pose severe impact on the agriculture. Changing environmental pattern and variability in climate accelerate the impacts of abiotic stresses in crop plants (Thornton et al. 2014; Raza et al. 2019). The crop productivity improvement under abiotic stress is one of the biggest and prime challenges faced by the agricultural scientific community worldwide. Despite extensive research being done in the field, the research for yielding abiotic stress-resistant crops remains very scanty. This can be attributed to the complex nature of environment × genotype interactions and particularly, the capacity to quantify the dynamic physiological response profile of crop plants to a dynamic environment (Moshelion and Altman 2015; Dalal et al. 2019).

Abiotic stress factors such as salinity, drought, heavy metals, UV-B radiation, air pollution and heat stress will further intensity these effects (Khan et al. 2015; Pereira 2016; Wani et al. 2018; Ali et al. 2019) and may strongly impact yield of crop plants and quality of agricultural products (Knutti et al. 2016; Pereira 2016; Feller et al. 2017). Efforts have been made to know potential tolerance mechanisms and plant response under such stressed conditions. As plants are sessile organisms, they continuously encounter different environmental pressures at morphological, physiological, biochemical and molecular levels. Plants have to adapt to these abiotic stresses induced adverse impacts at cellular and subcellular levels to optimally perform the growth and development. Under the danger of climate change, the adaptive underlying mechanisms of plants should perform optimally to counter these challenges. Nevertheless, these adaptive mechanisms can be engineered by exogenous application of phytohormones. In the present chapter, an attempt is made to exploit the tendency of external application of some phytohormones in different crop plants to boost their tolerance against environmental pressures. In the following section, we are discussing the potentiality of hydrogen sulphide, nitric oxide, and salicylic acid mediated mechanisms in countering salinity, drought, heat and metal stress in different species of plants.

28.2 Hydrogen Sulphide (H_2S)

Hydrogen sulphide (also known as dihydrogen sulphide or sulfane), is a chemical compound with the chemical formula H_2S. It is a colourless gas, with a characteristic foul odour of rotten eggs. Production of H_2S involves microbial (usually by sulphate reducing microorganisms) breakdown of organic matter in an anaerobic condition, such as sewers and sewages. H_2S is a new gaseous signalling molecule that have different sources and subcellular compartments generally associated with cysteine metabolism in a plant body (Gotor et al. 2013; Scuffi et al. 2014; Birke et al. 2015; Corpas et al. 2019a) that tends to regulate physiological process in plants (Li et al. 2016a; Mostofa et al. 2015; Banerjee et al. 2018; Corpas et al. 2019b) and have tendency to show adaptation to various environmental stresses which includes heavy metal exposure, temperature, drought and salt stresses (Lisjak et al. 2013; Li et al. 2016b; He et al. 2018). H_2S can likely exert anti-inflammatory, antioxidant, cyto-protective, antiapoptotic and organ protective effects, further improving environmental stress tolerance of cells (Yuan et al. 2017). It was believed to be a toxic gas and tend to have hazardous effects on environment but by recent several researches it has emerged as an important molecule that helps in signalling with numerous effects on various physiological processes both related to plants as well as animal systems. After nitric oxide (NO) and carbon monoxide (CO), H_2S has been recognized as the third endogenous gaso-transmitter in plants. Hydrogen sulphide plays a vital role in cell signalling pathways by being an important component. In plants, H_2S generation can be related to cysteine (cys) metabolism (Papenbrock et al. 2007). D-Cys desulfhydrase (D-CDES) and L-Cys desulfhydrase (LSD) derogate cysteine to hydrogen sulphide, ammonia and pyruvate and hence are responsible for the release of H_2S into cell (Kopriva 2006). Moreover, participation of H_2S in ethylene-induced stomatal closure has also been proven. Increase in glutathione level, alterations of enzyme activities and influences on both NO and H_2O_2 metabolisms are some of the intracellular effects of H_2S. Recent studies have also showed that in regulation of proharvest senescence of horticulture H_2S plays an important role. In the accompanying section, the role of H_2S under various abiotic stresses is discussed briefly.

28.2.1 Role of H_2S in Salt Stress

Salt stress is included in abiotic kind of stress that usually limits the agricultural productivity mostly seen in arid and semiarid regions of the world. It tends to be one of the major environmental stresses which results in ionic toxicity and induces an osmotic stress in plants to a major extent that leads to different nutritional disorders. H_2S is known to enhance the salt tolerance, as is seen in barley seedling roots where it acts as a messenger molecule resulting in the modulation of different physiological processes in plant by decreasing the net K^+ efflux (Chen et al. 2015). Moreover, the effect of H_2S was seen in poplar species as well. When poplar was subjected to salt stress, both long term as well as short term, it results in increased Na^+ efflux as well as an increased H^+ influx for its roots caused by NaHS. Depolarization-activated K^+ channels resulted in K^+ loss induced by NaCl. Other researches revealed about the role of H_2S in salt stress in rice plants. Results have shown a decreased growth with NaHS. Salt stressed rice plants have a decreased content of chlorophyll, carotenoid and soluble proteins. Under salt stress, a vital role of H_2S was witnessed in ion homeostasis, where the ability to decrease the uptake of Na^+ and Na^+/K^+ ratio and to balance mineral contents. Furthermore, it was revealed how implication of this gaso-transmitter, H_2S, can manage the salt stress that makes the rice plants to adapt the adversities of environment (Mostofa et al. 2015). In a study performed on the roots of *Arabidopsis thaliana*, Li et al. (2014) exposed the plants to 100 mM NaCl stress which caused electrolyte leakage and disturbed the Na^+/K^+ ratio. However, the follow-up treatment with NaHS enhanced the salt tolerance by maintaining the homeostasis of ions via regulating the plasma membrane Na^+/H^+ antiporter system. It has also been documented that salt stress also initiate biosynthesis of endogenous H_2S. In a study carried out in seedlings of *Medicago sativa*, Lai et al. (2014) found that there was subsequent increase in the biosynthesis of H_2S from 30 to 70 nmol g^{-1} FW when the concentration of NaCl increased from 50 to 300 mM. Integrity of photosynthetic apparatus can be deteriorated by salt stress which eventually has an immense effect on photosynthetic efficiency of plant. In *Nicotiana tabacum*, Da Silva et al. (2017b) observed that salinity stress induced the accumulation of endogenous H_2S was responsible for redox defense systems to prevent the inhibitory effects of salinity stress. Thus, it is clear that H_2S is an important molecule in plants implicated to confer salt stress tolerance.

28.2.2 Role of H_2S in Heat Stress

Heat stress can be defined as excessive increase in soil and air temperatures above a threshold level for ample time that cause usually an irreversible damage to plant physiological functions as well as its development which includes the rate of reproductive development or the photosynthetic rate which can be seen in decreased seed or fruit production. As the plants are sessile, they have to tolerate the temperatures provided by their environment which can never be always optimal (Bita and Gerats 2013). Heat stress can affect the plant in different manners either by high day or high night temperatures or by either high air or high soil temperatures. Several research groups have suggested the implication of H_2S to tolerate both high and low temperatures. Heat stress can be attributed as a direct effect of global warming (Banerjee and Roychoudhury 2018). A synchronized antioxidant network is activated by H_2S to achieve heat shock protection. It was seen that electrolyte leakage and the production of MDA due to membrane lipid peroxidation was significantly reduced by H_2S released from NaHS (Li et al. 2012). H_2S interacts with various physiological regulators like Ca^{2+} and proline. It has been seen that maize seedling when treated with NaHS have elevated the activity of pro-biosynthetic enzyme that facilitated viability of seedling under heat stress due to high endogenous accumulation of proline (Li et al. 2013). Under the heat stress the rate of germination of maize seeds can be increased by NaHS, a derivative of H_2S and also enhance the tissue viability and the accumulation of malondialdehyde (MDA) caused by heat treatment has also been lowered (Li et al. 2013). In maize the heat tolerance induced by salicylic acid (SA) is enhanced by NaHS that acts as H_2S donor (Li et al. 2015b). Recently, an increase in heat tolerance was achieved by the application of NaHS on wheat seedling through foliage. High temperature in plants also triggers the biosynthesis of the H_2S (Fu et al. 2013). In *Nicotiana tabacum*, when seedlings are under 35 °C, it was found that the expression of LCD was increased which was responsible for the biosynthesis of H_2S (Chen et al. 2016). H_2S donor also induces the thermotolerance in strawberry plants which were exposed to 42 °C (Christou et al. 2014). They observed that H_2S root pretreatment activates systemic thermotolerance via the coordinated network of transcriptional regulation of heat shock proteins and aquaporin.

28.2.3 Role of H_2S in Drought Stress

The availability of water content in soil is reduced and various environmental factors that cause a continuous loss of water either by transpiration (loss of water from aerial parts of plant in the form of moisture or water vapour) or by evaporation (process of vaporization) lead to a condition known as drought stress (also known as water stress). It is one of the most important abiotic environmental stresses and can be regarded as a multidimensional stress because it can cause alteration in various physiological as well as morphological functions of a plant. Drought stress connects plant development and yield. Primarily it can affect the crop productivity and hence can weaken the global food security and can increase other related adverse consequences like desiccation, osmotic imbalance, drooping and much more. Different plant species have different tolerance to drought stress. Drought stress tolerance and protection can be regulated by H_2S (Jin et al. 2011, 2013, 2017). Mitigation of drought susceptibility can be achieved by H_2S (Zhang et al. 2010b). Reduced activity of lipoxygenase (LOX) and malondialdehyde (MDA) content along with increased activities of ascorbate peroxidase (APX) and catalase (CAT) was reported when wheat seedlings were treated with NaHS, a derivative of H_2S (Zhang et al. 2010a). In seedlings of *Arabidopsis thaliana*, Shen et al. (2013) conducted an experiment and found that wild type seeds treated with polyethylene glycol (PEG-8000) mimicked drought stress, which trigger the biosynthesis of H_2S. They concluded their study by observing that H_2S improved drought resistance through regulating the expression of drought associated miRNAs in *Arabidopsis*. When wheat seeds were exposed to PEG 6000 induced drought stress for 2 days, a rapid increase from 1.5 to 3.5 mmol g^{-1} dry weight of H_2S production was measured (Zhang et al. 2010a). They further observed that H_2S treatment slowed down the activity of lipogenase. Some researchers showed that prolonged exposure to H_2S results in increased stomatal aperture whereas short-term exposure to H_2S can result in closure of stomata (García-Mata and Lamattina 2010; Lisjak et al. 2010, 2011). In case of wheat (*Triticum aestivum* L.), drought responsive genes regulated by H_2S were also studied.

28.2.4 Role of H_2S in Metal Stress

Increased anthropogenic and industrial activities lead to the contamination of water and soil by heavy metals growing as one of the most concerned global environmental problems (Fang et al. 2016; Ye et al. 2017; Wani et al. 2018). Metal stress is responsible for the retarded plant growth as well as development. Moreover, they have a deleterious effect on plant's physiological processes. The major heavy metal toxicants may include lead (Pb), cadmium (Cd), chromium (Cr), copper (Cu), nickel (Ni) and zinc (Zn) (Macomber and Hausinger 2011; Wang et al. 2013; Ye et al. 2017; Qin et al. 2018; Zhou et al. 2018; Wani et al. 2018). Various effects like chromosomal aberration, membrane damage, colonization inhibition, oxidative stress, antioxidant enzyme upregulation and even cell death can be caused by the presence of the heavy metals even if these are present in trace amounts (Gong et al. 2009; Ali et al. 2014, 2018; Huang et al. 2015). Blockage of the casparian strips or due to tapering by cell wall of roots can result in accumulation of heavy metals in root cells. The efficiency of toxicants removal and alleviation of heavy metals can be done by the application of H_2S. Lead, a heavy metal effects the germination, growth (root elongation and cell division) and various biochemical and physiological attributes (photosynthesis, nutrients uptake, respiration and hormonal equilibrium) in cauliflower, which are however mitigated by the application of NaHS, a donor of H_2S. Accumulation of higher amounts of zinc in soil can result from excessive use of zinc enriched fertilizers and the industrial activities. This accumulation can affect the quality of both vegetables and fruit crop. Both the shoot as well as root dry weight of pepper (*Capsicum annuum* L.) plant was reduced due to zinc stress, whereas, proline content and leaf electrolyte leakage (EL) were enhanced. Pertinence of NaHS increased both the shoot and root growth in zinc stressed plant, but also reduced the leaf EL and proline content in pepper plant. NaHS promoted the plant growth and photosynthesis in chromium stressed plant (Ali et al. 2013). While in wheat plants NaHS can help in relieving the reduction in germination of seeds caused by copper stress (Zhang et al. 2008). Moreover, oilseed rape (*Brassica napus* L.) stressed by heavy metal lead, alleviated by NaHS, results in growth, photosynthesis and cell structure improvement (Ali et al. 2014). Chen et al. (2018) studied the effect of exogenous H_2S on *Brassica oleracea* L. seed germination and seedling growth under Pb (0.25 and 0.5 mM) stress. They found that Pb markedly inhibited seed germination and seedling growth, root length, shoot length and fresh weight. In addition, they observed that NaHS elevated endogenous contents and reduced the Pb induced malonyldialdehyde, superoxide anion and hydrogen peroxide production. Zanganeh et al. (2018) studied the impacts of seed priming with H_2S along with salicylic acid on possible metabolic pathway of amino acids in maize plant under Pb stress. They observed that H_2S along with salicylic acid play a significant role in regulating the metabolism of methionine and arginine in maize under Pb stress condition. Mostofa et al. (2015) studied the alleviative role of H_2S in rice plants under Cd stress. Their results revealed Cd-induced growth inhibition and biomass reduction. Cd-mediated oxidative stress in rice plants was evidenced by observing increased levels of superoxide, hydrogen peroxide, methylglyoxal and malondialdehyde. H_2S reduced the extent of Cd-induced oxidative stress via enhancing redox status and the activities of enzymes related to reactive oxygen species metabolism and methylglyoxal detoxification system. They confirmed the beneficial effect of H_2S under Cd stress by using H_2S-scavenger hypotaurine that abolished the beneficial effect of H_2S in rice plants.

28.3 Nitric Oxide (NO)

Nitric oxide with the formula NO is a colourless gas and is considered as one of the principal oxides of nitrogen. Nitric oxide is a free radical, i.e. it is having an unpaired electron. It is a highly diffusible gas having the ability to diffuse through biological membranes readily. NO has an immense role in various physiological and biochemical (hence is a bioactive molecule) processes of plants. It shows dual character at different concentrations. At low concentrations, it acts as a signalling molecule whereas at higher concentrations, it can damage the cell resulting in nitro-oxidative stress. Hence it has been proven to be useful as well as harmful for plant. Beside this, NO is associated with signal transduction. NO, like H_2O_2 is considered as an important signalling molecule which makes plants to have adaptive responses to various biotic as well as abiotic environmental stresses (Qiao et al. 2014; Hossain et al. 2015; Santisree et al. 2015; Simontacchi et al. 2015; Sahay and Gupta 2017; Asgher et al. 2017; Sami et al. 2018; Nabi et al. 2019; Sharma et al. 2019). It has been seen that application of NO to seeds or seedlings of different plants resulted in making the plants tolerant to various stresses which includes heat, drought, and salt stresses mainly through two different ways; either by decreasing oxidative toxicity or by increasing antioxidative potential in numerous plants like citrus plants (Tanou et al. 2009), wheat (Wahid et al. 2007), *Capsicum annuum* (Kaya et al. 2019b), soybean (Ishibashi et al. 2011), maize (De Azevedo Neto et al. 2005), rice (Uchida et al. 2002; Yang et al. 2016), orange seedlings (Fan and Liu 2012), tomato (Siddiqui et al. 2017), strawberry (Kaya et al. 2019a) and other crop species (Hossain et al. 2015; Santisree et al. 2015; Simontacchi et al. 2015). During plant pathogen interactions, NO has an important additional defensive role to play (Durner et al. 1998; Gaupels et al. 2011; Mur et al. 2013). Various researches have revealed the association of NO with plant growth, seed germination, photosynthesis, leaf senescence, pollen growth, and orientation and it is rightly given a name of "plant growth regulator" (Beligni and Lamattina 2001). Moreover, NO has a significant interaction with other plant hormones such as auxins, gibberellins, abscisic acid, cytokinins, ethylene, salicylic acid, jasmonic acid, etc. under diverse stresses. The production of NO is suggested to take place through different pathways which are classified as oxidative or reductive steps.

28.3.1 Role of NO in Drought Stress

In drought stress, i.e. unavailability of water, there is an interaction between NO and abscisic acid (ABA) (Hancock et al. 2012; Sahay et al. 2019). An exogenous application of NO increased the drought tolerance in cut leaves and seedlings of *Triticum aestivum* by enhancing ABA synthesis with the help of a NO donor (Zhao et al. 2001). Many researchers through their researches in diverse crop plants have experimentally shown that there is an enhancement of plant tolerance to drought stress with the external application of NO (Lei et al. 2007, Hao et al. 2008, Shao et al. 2010, Tian and Lei 2006, Xing et al. 2004; Cechin et al. 2015; reviewed by Santisree et al. 2015; Montilla-Bascón et al. 2017). Moreover, researches have showed that NO is produced as a signal molecule in response to abscisic acid (Mioto and Mercier 2013). In case of *Zea mays*, it was seen that by the application of NO, it interact with CK's and results in regulation of photosynthesis and also an increase in adaptation towards drought stress (Shao et al. 2010). Similar results were also reported in case of *Arabidopsis thaliana* for the induction of senescence by interaction between CK's and NO (Mishina et al. 2007). Nevertheless, in *Arabidopsis thaliana,* it was found that over-expression of two ABA receptors (*AtPYL4* and *AtPYL5*) enhanced drought resistance, antioxidant enzyme activity and osmolyte levels. These observations also bring out the role of NO in drought stress response in Arabidopsis (Shi et al. 2014).

28.3.2 Role of NO in Salt Stress

A worldwide increase in salinity threatens the plant growth, development and production of agriculture (Zhu 2003; Ahmad et al. 2018a; Romero-Munar et al. 2019). According to an estimate there is more than 20% (~45 million ha) of arable land worldwide and approximately 50% of irrigated land is occupied by high salt concentration (Ahmad et al. 2015; Fatma et al. 2016). The high salt conditions are injurious to plant health, as it causes ionic, osmotic and oxidative stress, thereby inhibiting various biochemical and physiological processes responsible for optimal growth and development (Munns and Tester 2008; Khan et al. 2010; Ahanger et al. 2018; Khanam and Mohammad 2018; Jorge et al. 2019). Due to salinity-induced intracellular ion imbalance, the soil nutrient uptake is altered which leads to nutrition deficiencies in plants. While, salinity provokes disintegration of membranes, loss of metabolic functions, leakage of ions, DNA defragmentation, and consequently programmed cell death (Hasegawa et al. 2000; Ahanger and Agarwal 2017; Tang et al. 2019). Salt stress has a relevant effect on a plant as that of the drought stress do. Many experiments have shown the increase in resistance to salt stress (also known as salinity) on the application of NO to the affected plants (Khan et al. 2003; Fatma et al. 2016; Sehar et al. 2019). There are ample evidences suggesting the involvement of NO in alleviation of ill effects of salt stress on various plants. Under salt stress, *DELLA* proteins play an important role where it restrict the growth and regulate development. Root meristems inhibition under salt stress was achieved by NO generation by auxin concentration reduction (Liu et al. 2015). Furthermore, experiments showed a synergetic interaction between NO and SA resulting in the alleviation of salt stress (Liu et al. 2014). By the application of NO, there was an increase in antioxidant enzyme activity, witnessed in mitochondria of wheat seeds under salt stress, enhancing the germination rate and weight of radicals and coleoptiles. Further experiments were done with wheat plant in which it was seen that the starch content can be reduced and soluble sugar content can be increased on the pretreatment of wheat seeds with NO for 3 days (Almansouri et al. 2001). Association of NO with increased ATP content in wheat seeds was also observed. Enhancement of Na^+/K^+ ratio was provided by NO application in the callus of *Phragmites communis* (reed) and *Populus euphratica* (populus) providing tolerance to salt stress (Zhao et al. 2004). In a recent study, Sehar et al. (2019) studied the involvement of nitric oxide donor (sodium nitroprusside) in the reversal of glucose-inhibited photosynthetic responses in the presence or absence of salt stress (100 mM NaCl) in wheat plants. They found that NO improves photosynthesis of wheat plants in the absence of salt stress, and also reduces glucose-mediated repression of photosynthesis under salt stress. NO accomplished this effect through increase in antioxidant system and concomitant decrease in glucose and ethylene sensitivity under salt stress. In yet another recent experiment, Campos et al. (2019) studied the potential of NO and phytohormone crosstalk in *Lactuca sativa* plants to salinity stress conditions. Plant exposure to salt stress triggered ionic, osmotic and oxidative stress, which causes imbalance in hormone content, cell death and consequently decreased growth of plants. These changes were correlated with salt ions in tissues. However, NO caused a decrease in Na^+ accumulation and stabilized the mineral nutrient status. This resulted in maintenance of photosynthesis rate and growth re-establishment. The NO-signalling also balances the phytohormones content and caused an increase in antioxidant potential and osmotic regulation, with culminates tolerance to the salt stress. Hence it was proved that NO has an immense importance in physiological response alteration which enhances the growth of plant (Liu et al. 2007).

28.3.3 Role of NO in Heavy Metal Stress

There are alterations in root structures due to change in hormonal imbalance under heavy metal stress. One of the common aspects of stress caused by various heavy metals is ROS production (He et al. 2012; Wani et al. 2018). Various researches have showed that NO tends to have an important role in the protection against heavy metal stress like the toxic effects exerted by As (Singh et al. 2009), Cd (Hsu and Kao 2004), Al (Wang and Yang 2005), Cu (Yu et al. 2005) and B (Farag et al. 2017). Application of NO to the plants having toxicities of such heavy metals alleviates the effects under different conditions. NO content sometimes increases and sometimes decreases in response to heavy metal stress making a controversy. Researchers have shown that in case of few plants like pea (*Pisum sativum*) and *Arabidopsis thaliana*, Cd tend to reduce the NO production hence resulting in stress (Barroso et al. 2006; Rodríguez-Serrano et al. 2009; Zhu et al. 2012a, b; Xu et al. 2011). In *Arabidopsis thaliana,* NO accumulation induced by auxin increased the cadmium tolerance (Xu et al. 2011). Application of NO successfully shows an improvement in the antioxidative capacity of *Medicago truncatula* and reduction of auxin degradation in roots were also seen in the plant under Cd stress (Xu et al. 2010).

28.3.4 Role of NO in Temperature Stress

The adverse effects that results from heat stress can be enlisted as membrane damage, lipid peroxidation, enzyme inactivation, oxidative stress and ultimately disruption of DNA strands (Suzuki and Mittler 2006; Ali et al. 2019). Protein denaturation, oxidative and osmotic stresses and membrane rigidity that can cause ion leakage are some other effects of low temperature (Ruelland et al. 2009; Khan et al. 2017). To deal with such adversities, application of NO turned to be useful to the plants. It was seen that NO also helps in inducing various activities in cold stress like nitric oxide synthase (NOS) and S-nitrosoglutathione reductase (GSNOR) activities. Some residues of other compounds like S-nitrosothiols and nitrates were also observed in case of pea plant (Corpas et al. 2008). Nitrate reductase dependent-NO generation was detected in *Arabidopsis thaliana* plant when the plant was subjected to 4 °C (Zhao et al. 2009). At low temperatures, there is the production of ABA which leads to the closure of stomata or osmolyte production having deleterious effects on the physiology of plants (Ruelland et al. 2009; Kosová et al. 2012).

28.4 Salicylic Acid (SA)

Salicylic acid (ortho-hydroxy benzoic acid; SA), a ubiquitously distributed signalling molecule, phenolic in nature, plays a pivotal role in tolerance of various kinds of stresses in diverse crop plants; both biotic and abiotic. Additionally, it plays a role in plants growth and development along with defense responses. Furthermore, various physiological as well as molecular processes like uptake of nutrients, fruit ripening, stomatal movements, photosynthesis, biosynthesis of chlorophyll, pathogenesis-associated protein expression, etc. are regulated by the SA mainly in concentration dependent manner (Khan et al. 2015; Nazar et al. 2017; Zaid et al. 2019). Also, biosynthesis of various secondary metabolites like sinapyl alcohol dehydrogenase, cinnamyl alcohol dehydrogenase and cytochrome P450 are encoded by the SA genes along with the production of different chaperones, heat shock proteins and antioxidants (Jumali et al. 2011). SA is synthesized mainly via two different pathways: isochorismate synthase (ICS) and the phenylalanine ammonia lyase (PAL) in plastids. However, ICS pathway is the major route of biosynthesis of SA in most of the plants where, ICS is biosynthesized from chorismic acid, an end product of shikimic acid pathway (Uppalapati et al. 2007; Catinot et al. 2008; Jayakannan et al. 2015). Various researchers have reported a potential role of SA in amelioration of different abiotic stresses like drought (Miura et al. 2013; Nazar et al. 2015; Lee et al. 2019), salinity (Fahad and Bano 2012; Khodary 2004; Amirinejad et al. 2017; Tahjib-ul-Arif et al. 2018; Alsahli et al. 2019), chilling (Yang et al. 2012; Chen et al. 2016; Wang et al. 2018), metal (Zhao et al. 1995; Zaid et al. 2019) and heat (Fayez and Bazaid 2014; Munir and Shabbir 2018). Other effects of SA includes: ethylene biosynthesis is retarded by the exogenous supplementation of

SA, enhancement in the production of photosynthetic pigments and photosynthetic machinery and alleviation of deleterious effects in plants, resulting from exposure to heavy metal (Zhao et al. 1995; Zhang and Chen 2011). PR1 and PR2 (pathogenesis-related genes) are reported to be the SA-inducible genes mainly involved in the modulation of some abiotic stresses in plants (Miura et al. 2013). Also, there are reports suggesting the SA receptors to belong to the family of receptor-like protein kinases (RLKs) as SA is capable of modulating the expression of various RLKs in plants (Ohtake et al. 2000). Despite considerable investigations, the role of SA in stress tolerance at molecular level remains largely unknown.

28.4.1 Role of SA in Heat Stress

Over the past years, different researchers have identified a putative role of SA in regulation of heat stress in plants through the modulation of various physiological and metabolic processes. Heat stress tolerance in different plants under the influence of SA is mainly explained by the amendment of the antioxidant defence mechanism in plants. Activity of various antioxidant enzymes is modulated mainly through the endogenous H_2O_2 levels under the influence of SA in plants resulting in improvement of plant growth and development. Various researchers have reported the amelioration in growth, biochemical and physiological attributes of different plants viz. corn and soybean (Khan et al. 2003), wheat (Shakirova 2007), *Brassica juncea* (Fariduddin et al. 2003), wheat seedlings (Hayat et al. 2005), barley seedlings (Pancheva et al. 1996), maize (Khodary 2004), cucumber, grape and many other important plants (Shi et al. 2006; Wang et al. 2010) under heat stress, by the exogenous application of SA to the plant. Furthermore, survival percentage of maize seedlings has been reported to increase by the pretreatment of seeds under heat stress with SA. Also, an enhanced accumulation of osmolytes leading to an improvement of antioxidant system of the plants under heat stress has been reported (Li et al. 2015a, 2015b; Li 2015). After a pretreatment with SA and heat stress, *Agrostis stolonifera* showed an improvement in growth (increase in green leaf index), membrane stability, lipid peroxidation and photosynthesis. Similarly, the activities of different antioxidant enzymes like superoxide dismutase (SOD) and catalase (CAT) and contents of proline, phenolics and flavonoids in *Digitalis trojana* were enhanced by the pretreatment of SA in callus cultures under heat stress (Cingoz and Gurel 2016). A reduction in the oxidative damage by heat stress was recorded in *Arabidopsis* plants after the foliar-application of SA treatment (Larkindale and Knight 2002). Moreover, the leaf-applied SA induced long-term heat tolerance in the grape plant, which might be due to the Ca^{2+} homeostasis and antioxidant systems (Wang and Li 2006). Many other derivatives of SA (sulphosalicylic acid, methyl salicylate) have been reported to influence the heat tolerance in plants like cucumber and holm oak, respectively (Shi et al. 2006; Llusia et al. 2005). An increase in the contents of protein as well as proline was observed by both SA treatment and heat acclimation leading to the induction of POD and APX activities and a reduction in CAT activity (Chakraborty and Tongden 2005). Kaur et al. (2009) have observed that SA pretreatment leads to heat tolerance at seedling stage in *Brassica* species by increasing total soluble sugar and growth of plants as well as by enhancing the activities of some enzymes (invertase, CAT and POD). Moreover, the expression of some noteworthy proteins (heat shock proteins; HSPs) along with some new proteins was stimulated after pretreatment with SA. In yet another study, it has been reported that the expression of *HSP21* was modulated by the application of SA to the leaves of the plant (grapevine) under study. The levels of *HSP21* remained high throughout the experiment in the SA-treated plants as compared to the control, helping the plant to recover thus conferring heat tolerance to the plant (Wang et al. 2011). There are other reports related to heat tolerance by foliar application of SA, involving HSPs in tomato, mung bean and hyacinth bean. The genes involved in the ascorbate-glutathione cycle and activities of several reactive oxygen species (ROS) scavenging antioxidant enzymes are regulated by the SA treatment in these plants (Rai et al. 2018a, 2018b). In a study carried out by Liu et al. (2006), an interrelationship has been reported between SA and ABA. It was observed that the levels of SA and ABA was modulated during heat stress and the presence of SA (conjugated as well as free form) is much imported to the plant as compared to ABA in conferring heat tolerance to the plants. Clarke et al. (2004) correlated the level of SA and basal heat tolerance in *Arabidopsis* genotypes with modified SA signalling. Thus, from the above discussion, it is clear that SA modulated different mechanisms to confer heat stress tolerance in various crop plants.

28.4.2 Role of SA in Metal Stress

Heavy metals present in the agricultural lands due to various anthropogenic activities lead to perturbation of various physiological, biochemical and metabolic processes in different plants leading to a disturbed growth and reduced productivity (Weast 1984; Boussama et al. 1999; Aftab et al. 2011; Ahmad et al. 2018b; Wani et al. 2018). Various researchers have reported an important role of SA in alleviating the stress caused by the heavy metals present in the environment. Lead- and mercury-induced stress in rice has been studied by Mishra and Choudhuri (1999) where pretreatment with SA protected rice from the heavy metals induced membrane disruption. Also, Cd-induced toxicity in barley (Metwally et al. 2003), maize (Pál et al. 2002; Krantev et al. 2008), mustard (Zaid et al. 2019), peppermint (Ahmad et al. 2018b), soybean (Drazic and Mihailovi 2005), alfalfa (Drazic et al. 2006) and rice (Panda and Patra 2007; Chao et al. 2010) was positively alleviated by SA application (foliar applied or pretreatment) to these plants. Yang et al. (2003) studied the effect of Al on *Cassia tora* where it was found that SA application conferred tolerance to the plant to withstand the deleterious effects of the heavy metal stress. It was reported that the *Cassia tora* under Al stress accumulated citrate in their roots as result of SA application. Ill effects caused by lead and mercury in rice were also mitigated by the exogenous application of salicylic acid. It was reported that the enhancement in the activity of lipoxygenase was regulated by the application of SA (exogenous) (Mishra and Choudhuri 1999). Gill et al. (2016) studied the protective effects of exogenously applied SA on Cr toxicity in the black and yellow-seeded *Brassica napus* L. The findings of these authors demonstrated the enhanced activity of enzymatic antioxidants and gene expression, secondary metabolism and the transcript level of specific stress associated proteins in root and leaf of these plants under Cr toxicity. Cd tolerance due to the application of SA in different plants is attributed to the improvement of antioxidant system of the plant as SA enhances the activity of SOD, peroxidase, dehydroascorbate reductase, GR which help in scavenging the ROS produced in these plants (Ahmad et al. 2018b; Khanam and Mohammad 2016; Kazemi et al. 2011; Zhang et al. 2011; Bai et al. 2014). Furthermore, in a report by Krantev et al. (2008) similar results were recorded where the growth of the plant, activities of RUBP carboxylase and PEP, carboxylase and antioxidant enzymes (APX, SOD) were improved whereas, activity of CAT, rate of lipid peroxidation and leakage of electrolytes was reduced in maize leaves, thus conferring Cd tolerance to the plant. Along with the above mentioned physiological and biochemical processes, SA also modulates the expression of certain genes and proteins that lead to lower H_2O_2 content in the plants resulting in membrane stability under heavy metal stress (Chao et al. 2010). Kumari and Pandey-Rai (2018) studied the effect of SA on *Artemisia annua* under arsenic (As) stress. It was reported that SA helps in sequestration of As into the vacuoles and the regulation of artemisinin biosynthesis by the synthesis of oxylipins, which modulate the expression of MAPKs. Moreover, different transcription factors (MYC, WRKY) are upregulated by these MAPKs resulting into a positive effect on the biosynthesis of secondary metabolites (artemisinin) along with the mitigation of heavy metal stress.

28.4.3 Role of SA in Drought Stress

Drought stress (water deficit) that affects plants, is a multidimensional stress which leads to various dysfunctions (physiological and biochemical) at different organizational levels of the plant like turgor reduction, growth, photosynthetic rate, stomatal conductance and damages of cellular components, decrease in water potential, production of radical scavenging compounds, regulation and alteration of gene expression, etc. (Janda et al. 2007; Yordanov et al. 2000; Farooq et al. 2009; Aimar et al. 2011; Kunert et al. 2016; Joshi et al. 2016). In a study by Da Silva et al. (2017a), SA application enhanced the growth of sesame plant under drought stress resulting in mitigating the ill effects of the stress. Also, there are reports where SA application delimits the synthesis of ROS in plants under water stress. Furthermore, application of SA increases the expression of mitochondrial alternative oxidase (AOX; an important enzyme for stress tolerance) in stressed plants (Tang et al. 2017; Zhang and Chen 2011). Responses of tomato plant under drought stress showing negative growth, reduction in photosynthetic and biochemical parameters (membrane stability index, leaf water potential, NR and CA activity, contents of chlorophyll and relative water) and an upregulation of proline content and antioxidant enzymes (CAT, POX and SOD) were enhanced by the application of exogenous SA at lower concentration (Hayat et al. 2008). From the survey of scientific literature, various reports indicate a stress-tolerance role of SA in different plants like tomato and bean (Senaratna et al. 2000), *Salvia officinalis* (Abreu and Munné-Bosch 2008), wheat (Hamada 1998; Hamada and Al-Hakimi 2001; Singh and Usha 2003), barley (Bandurska and Stroinski 2005), sunflower (Hussain et al. 2008), etc. Soaking of seeds (wheat) in SA (an aqueous degraded product of acetyl SA), confer drought resistance to the seedlings, improving the shoot and root dry weights, transpiration rate by protecting the photosynthetic apparatus of the plant from oxidation (Hamada 1998; Hamada and Al-Hakimi 2001). Singh and Usha (2003) also confirmed these results, where the plants showed a marked enrichment in growth (moisture content, dry mass), physiology (activity of Rubisco and superoxide dismutase (SOD) and content of total chlorophyll) and yield of the plants irrespective of the concentration of SA or levels of drought stress applied when compared to the control plants. Similar reports where seeds of tomato and bean have been soaked in SA/acetyl SA to study the response of the plants to drought stress. It was recorded that the seedling survival rate increased by the applied concentration (0.1 Mm and 0.5 mM) of SA/acetyl SA (Senaratna et al. 2003). Bandurska and Stroinski (2005) interestingly reported that the application of SA to the barley plants improved ABA content, suggesting a concomitant role of ABA for the development of drought tolerance by the application of SA. However, some of the reports suggest that by the application of SA (to maize) did not improve drought tolerance, however rendering plants more susceptible to drought (Németh et al. 2002). Horváth et al. (2007) also reported negative results for the application of SA to Chinese spring wheat however, application of SA to winter wheat Cheyenne gave no effect to the plant. Contrary to the previous two plants application of an SA analogue (4-hydroxybenzoic acid) increased the drought tolerance in Cheyenne plants. Thus, suggesting the role of SA in imparting drought tolerance depends upon the type and concentration of SA applied and the genotype of the plant and severity of the stress (Yuan and Lin 2008).

28.4.4 Role of SA in Salinity Stress

Salinity is one of the important abiotic stresses, affecting the growth and physiology of plants. Salt stress may result into responses like, osmotic conductance, toxicity and imbalance of specific ion, and oxidative stress, leading to the production of reactive oxygen species (Tester and Davenport 2003) and inversely resulting in a decrease of plant weight and thus reduction in plant productivity (Ashraf and Harris 2004). SA is a phytohormone that modulates plant physiological responses conferring stress tolerance to the plant (Ahmad et al. 2011; Janda et al. 2012; Khan et al. 2014). In a report by Azooz et al. (2011), treatment with SA to *Vicia faba* under salt stress (sea water treatment) ameliorated the ill effects of salinity leading to an increase of osmolyte and free amino acids (proline) accumulation. Also an increase in biomass accumulation, growth and antioxidant system has been registered in the plant under study. Khan et al. (2014) have also confirmed the beneficial effects of SA application to salt-stressed *Vigna radiata* L. leading to a decrease in the levels of ethylene and better partitioning of salt ions. Also, some reports confirm an increase in the levels of endogenous ABA and proline along with an improvement of growth and yield of wheat plant under salt stress in response to SA application (Shakirova et al. 2003). Improvement of growth, accumulation of biomass, cell division, and activity improvement of photosynthetic apparatus as well as different antioxidant enzymes have been reported after the application of SA (Da Silva et al. 2017a). Janda et al. (2012) reported that salt stress have deleterious effects on the photosynthesis and membrane stability of barley plant; which were improved by the exogenous application of SA. Similar results were reported in maize, where the application of SA to salt-stressed plant leads to reduction in accumulation of Na and improvement of growth and development of the plant under salt stress (Gunes et al. 2007). Furthermore, various researchers have reported the amelioration of salt stress induced changes in different plants viz. barley (El-Tayeb 2005), wheat (Hamada and Al-Hakimi 2001; Sakhabutdinova et al. 2004), tomato (Tari 2002; Tari et al. 2004, 2010; Szepesi 2005; Szepesi et al. 2008a, b; Gémes et al. 2008), *Salvia officinalis* L. (Sahar et al. 2011), *Arabidopsis* (Poór et al. 2012) *Iris hexagona* (Wang et al. 2001). Moreover, application of SA to salt-stressed barley plants by improving the contents of photosynthetic pigment and maintenance of membrane integrity resulted in salt tolerance (El-Tayeb 2005). Application of SA to salt-stressed plants also result in a decrease in lipid peroxidation due to a decrease in Na content and a significant increase in the contents of K and Mg. The activities of various antioxidant enzymes (SOD, CAT, GPX) was also increased by the application of SA with a decrease in contents of dehydroascorbate reductase and in the ascorbate and glutathione contents (He and Zhu 2009). The activity of these antioxidant enzymes was also modulated by the application of SA in tomato plants along with an increase in the accumulation of various osmolytes (sugars, sugar alcohol, proline) in the plant (Tari 2002; Tari et al. 2004, 2010; Szepesi 2005; Szepesi et al. 2008a, b; Gémes et al. 2008). Sahar et al. (2011) also reported similar results in *Salvia officinalis* L. plant. In contrast to the earlier reports, Hao et al. (2012) studied a line of mutant *Arabidopsis* (snc1, NahG, npr1–1, snc1/NahG and wild type plant) where high SA accumulation lead to an increase in salt-induced damage and reduced SA proved to be favourable for the plant. Similarly, reports for soybean under salt stress show a decrease in the levels of endogenous free SA content (Hamayun et al. 2010). Thus, from the above literature it is clear that SA is a potent phytohormone which confers salt stress resistance in different crop plants.

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References

Abbas F (2013) Analysis of a historical (1981–2010) temperature record of the Punjab province of Pakistan. Earth Interact 17:1–23

Abreu ME, Munné-Bosch S (2008) Salicylic acid may be involved in the regulation of drought-induced leaf senescence in perennials: a case study in field-grown *Salvia officinalis* L. plants. Environ Exp Bot 64:105–112

Aftab T, Khan MMA, da Silva JAT, Idrees M, Naeem M (2011) Role of salicylic acid in promoting salt stress tolerance and enhanced artemisinin production in *Artemisia annua* L. J Plant Growth Regul 30:425–435

Ahanger MA, Agarwal RM (2017) Salinity stress induced alterations in antioxidant metabolism and nitrogen assimilation in wheat (*Triticum aestivum* L) as influenced by potassium supplementation. Plant Physiol Biochem 115:449–460

Ahanger MA, Alyemeni MN, Wijaya L, Alamri SA, Alam P, Ashraf M, Ahmad P (2018) Potential of exogenously sourced kinetin in protecting *Solanum lycopersicum* from NaCl-induced oxidative stress through up-regulation of the antioxidant system, ascorbate-glutathione cycle and glyoxalase system. PLoS One 13:e0202175

Ahmad P, Nabi G, Ashraf M (2011) Cadmium-induced oxidative damage in mustard *Brassica juncea* (L.) Czern. & Coss. Plants can be alleviated by salicylic acid. S Afr J Bot 77:36–44

Ahmad P, Hashem A, Abd-Allah EF, Alqarawi AA, John R, Egamberdieva D, Gucel S (2015) Role of Trichoderma harzianum in mitigating NaCl stress in Indian mustard (*Brassica juncea* L) through antioxidative defense system. Front Plant Sci 6:868

Ahmad P, Abd_Allah EF, Alyemeni MN, Wijaya L, Alam P, Bhardwaj R, Siddique KH (2018a) Exogenous application of calcium to 24-epibrassinosteroid pre-treated tomato seedlings mitigates NaCl toxicity by modifying ascorbate–glutathione cycle and secondary metabolites. Sci Rep 8:13515

Ahmad B, Jaleel H, Sadiq Y, Khan MMA, Shabbir A (2018b) Response of exogenous salicylic acid on cadmium induced photosynthetic damage, antioxidant metabolism and essential oil production in peppermint. Plant Growth Regul 86:273–286

Aimar D, Calafat M, Andrade AM, Carassay L, Abdala GI, Molas ML (2011) Drought tolerance and stress hormones: from model organisms to forage crops. In: Vasanthaiah H, Kambiranda D (eds) Plants and environment. InTech, Rijeka, Croatia, pp 137–164

Ali S, Farooq MA, Hussain S, Yasmeen T, Abbasi GH, Zhang G (2013) Alleviation of chromium toxicity by hydrogen sulfide in barley. Environ Toxicol Chem 32:2234–2239

Ali B, Song WJ, Hu WZ, Luo XN, Gill RA, Wang J, Zhou WJ (2014) Hydrogen sulfide alleviates lead-induced photosynthetic and ultrastructural changes in oilseed rape. Ecotoxicol Environ Saf 102:25–33

Ali S, Rizwan M, Zaid A, Arif MS, Yasmeen T, Hussain A, Abbasi GH (2018) 5-Aminolevulinic acid-induced heavy metal stress tolerance and underlying mechanisms in plants. J Plant Growth Regul 37:1423–1436

Ali S, Rizwan M, Arif MS, Ahmad R, Hasanuzzaman M, Ali B, Hussain A (2019) Approaches in enhancing thermotolerance in plants: an updated review. J Plant Growth Regul 12:1–25. https://doi.org/10.1007/s00344-019-09994-x

Almansouri M, Kinet JM, Lutts S (2001) Effect of salt and osmotic stresses on germination in durum wheat (*Triticum durum* Desf.). Plant Soil 231:243–254

Alsahli A, Mohamed AK, Alaraidh I, Al-Ghamdi A, Al-Watban A, El-Zaidy M, Alzahrani SM (2019) Salicylic acid alleviates salinity stress through the modulation of biochemical attributes and some key antioxidants in wheat seedlings. Pak J Bot 51:1551–1559

Amirinejad AA, Sayyari M, Ghanbari F, Kordi S (2017) Salicylic acid improves salinity-alkalinity tolerance in pepper (*Capsicum annuum* L.). Adv Hort Sci 31:157–163

Asgher M, Per TS, Masood A, Fatma M, Freschi L, Corpas FJ, Khan NA (2017) Nitric oxide signaling and its crosstalk with other plant growth regulators in plant responses to abiotic stress. Environ Sci Pollut Res 24:2273–2285

Ashraf M, Harris PJC (2004) Potential biochemical indicators of salinity tolerance in plants. Plant Sci 166:3–16

Azooz MM, Youssef AM, Ahmad P (2011) Evaluation of salicylic acid (SA) application on growth, osmotic solutes and antioxidant enzyme activities on broad bean seedlings grown under diluted seawater. Int J Plant Physiol Biochem 3:253–264

Bai X, Dong Y, Kong J, Xu L, Liu S (2014) Effects of application of salicylic acid alleviates cadmium toxicity in perennial ryegrass. Plant Growth Regul 75:695–706

Bandurska H, Stroinski A (2005) The effect of salicylic acid on barley response to water deficit. Acta Physiol Plant 27:379–386

Banerjee A, Roychoudhury A (2018) Small heat shock proteins: structural assembly and functional responses against heat stress in plants. In: Ahmad P, Ahanger MA, Singh VP, Tripathi DK, Alam P, Alyemeni MN (eds) Plant metabolites and regulation under abiotic stress. Academic Press, Elsevier, London, pp 367–374

Banerjee A, Tripathi DK, Roychoudhury A (2018) Hydrogen sulphide trapeze: Environmental stress amelioration and phytohormone crosstalk. Plant Physiol Biochem. https://doi.org/10.1016/j.plaphy.2018.08.028

Barroso JB, Corpas FJ, Carreras A, Rodríguez-Serrano M, Esteban FJ, Fernández-Ocana A, Del Río LA (2006) Localization of S-nitrosoglutathione and expression of S-nitrosoglutathione reductase in pea plants under cadmium stress. J Exp Bot 57:1785–1793

Beligni MV, Lamattina L (2001) Nitric oxide in plants: the history is just beginning. Plant Cell Environ 24:267–278

Birke H, De Kok LJ, Wirtz M, Hell R (2015) The role of compartment-specific cysteine synthesis for sulfur homeostasis during H_2S exposure in *Arabidopsis*. Plant Cell Physiol 56:358–367

Bita CE, Gerats T (2013) Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. Front Plant Sci 4:273

Boussama N, Quariti O, Ghorbal MH (1999) Changes in growth and nitrogen assimilation in barley seedlings under cadmium stress. J Plant Nutr 22:731–752

Campos FV, Oliveira JA, Pereira MG, Farnese FS (2019) Nitric oxide and phytohormone interactions in the response of *Lactuca sativa* to salinity stress. Planta:1–15

Catinot J, Buchala A, Abou-Mansour E, Métraux JP (2008) Salicylic acid production in response to biotic and abiotic stress depends on isochorismate in Nicotiana benthamiana. FEBS Lett 582:473–478

Cechin I, Cardoso GS, Fumis TDF, Corniani N (2015) Nitric oxide reduces oxidative damage induced by water stress in sunflower plants. Bragantia 74:200–206

Chakraborty U, Tongden C (2005) Evaluation of heat acclimation and salicylic acid treatments as potent inducers of thermotolerance in *Cicer arietinum* L. Curr Sci 89:384–389

Chao YY, Chen CY, Huang WD, Kao CH (2010) Salicylic acid mediated hydrogen peroxide accumulation and protection against cd toxicity in rice leaves. Plant Soil 329:327–337

Chen Z, Zhang L, Zhu C (2015) Exogenous nitric oxide mediates alleviation of mercury toxicity by promoting auxin transport in roots or preventing oxidative stress in leaves of rice seedlings. Acta Physiol Plant 37:194

Chen X, Chen Q, Zhang X, Li R, Jia Y, Jia A, Hu X (2016) Hydrogen sulfide mediates nicotine biosynthesis in tobacco (*Nicotiana tabacum*) under high temperature conditions. Plant Physiol Biochem 104:174–179

Chen Z, Yang B, Hao Z, Zhu J, Zhang Y, Xu T (2018) Exogenous hydrogen sulfide ameliorates seed germination and seedling growth of cauliflower under lead stress and its antioxidant role. J Plant Growth Regul 37:5–15

Christou A, Filippou P, Manganaris GA, Fotopoulos V (2014) Sodium hydrosulfide induces systemic thermotolerance to strawberry plants through transcriptional regulation of heat shock proteins and aquaporin. BMC Plant Biol 14:42

Cingoz GS, Gurel E (2016) Effects of salicylic acid on thermotolerance and cardenolide accumulation under high temperature stress in Digitalis trojana Ivanina. Plant Physiol Biochem 105:145–149

Clarke SM, Mur LAJ, Wood JE, Scott IM (2004) Salicylic acid dependent signaling promotes basal thermo tolerance but is not essential for acquired thermo tolerance in *Arabidopsis thaliana*. The Plant J 38:432–447

Corpas FJ, Chaki M, Fernandez-Ocana A, Valderrama R, Palma JM, Carreras A, Barroso JB (2008) Metabolism of reactive nitrogen species in pea plants under abiotic stress conditions. Plant Cell Physiol 49:1711–1722

Corpas FJ, González-Gordo S, Cañas A, Palma JM (2019a) Nitric oxide and hydrogen sulfide in plants: which comes first? J Exp Bot. https://doi.org/10.1093/jxb/erz031

Corpas FJ, Barroso JB, González-Gordo S, Muñoz-Vargas MA, Palma JM (2019b) Hydrogen sulfide: a novel component in *Arabidopsis* peroxisomes which triggers catalase inhibition. J Integ Plant Biol Doi. https://doi.org/10.1111/jipb.12779

Da Silva AS, Suassuna JF, de Melo AS, Costa RR, de Andrade WL, da Silva DC (2017a) Salicylic acid as attenuator of drought stress on germination and initial development of sesame. Rev Bras Eng Agríc Ambient 21:156–162

Da Silva CJ, Fontes EPB, Modolo LV (2017b) Salinity-induced accumulation of endogenous H_2S and NO is associated with modulation of the antioxidant and redox defense systems in Nicotiana tabacum L. cv. Havana. Plant Sci 256:148–159

Dalal A, Bourstein R, Haish N, Shenhar I, Wallach R, Moshelion M (2019) Dynamic physiological Phenotyping of drought-stressed pepper plants treated with “productivity-enhancing” and “survivability-enhancing” biostimulants. Front Plant Sci 10:905

De Azevedo Neto AD, Prisco JT, Eneàs-Filho J, Medeiros JV, Gomes-Filho E (2005) Hydrogen peroxide pre-treatment induces salt-stress acclimation in maize plants. J Plant Physiol 162:1114–1122

Drazic G, Mihailovi CN (2005) Modification of cadmium toxicity in soybean seedlings by salicylic acid. Plant Sci 168:511–517

Drazic G, Mihailovi_ CN, Lojic M (2006) Cadmium accumulation in *Medicago sativa* seedlings. Biol Plant 50:239–244

Durner J, Wendehenne D, Klessig DF (1998) Defense gene induction in tobacco by nitric oxide, cyclic GMP, and cyclic ADP-ribose. Proc Nat Acad Sci U S A 95:10328–10333

El-Tayeb MA (2005) Response of barley grains to the interactive effect of salinity and salicylic acid. Plant Growth Regul 45:215–224

Fahad S, Bano A (2012) Effect of salicylic acid on physiological and biochemical characterization of maize grown in saline area. Pak J Bot 44:1433–1438

Fan QJ, Liu JH (2012) Nitric oxide is involved in dehydration/drought tolerance in *Poncirus trifoliata* seedlings through regulation of antioxidant systems and stomatal response. Plant Cell Rep 31:145–154

Fang H, Liu Z, Jin Z, Zhang L, Liu D, Pei Y (2016) An emphasis of hydrogen sulfide-cysteine cycle on enhancing the tolerance to chromium stress in *Arabidopsis*. Environ Poll 213:870–877

Farag M, Najeeb U, Yang J, Hu Z, Fang ZM (2017) Nitric oxide protects carbon assimilation process of watermelon from boron-induced oxidative injury. Plant Physiol Biochem 111:166–173

Fariduddin Q, Hayat S, Ahmad A (2003) Salicylic acid influences net photosynthetic rate, carboxylation efficiency, nitrate reductase activity, and seed yield in *Brassica juncea*. Photosynthetica 41:281–284

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA (2009) Plant drought stress: effects, mechanisms and management. In Sustainable agriculture (pp. 153–188). Springer, Dordrecht.

Fatma M, Masood A, Per TS, Khan NA (2016) Nitric oxide alleviates salt stress inhibited photosynthetic performance by interacting with sulfur assimilation in mustard. Front Plant Sci 7:521

Fayez KA, Bazaid SA (2014) Improving drought and salinity tolerance in barley by application of salicylic acid and potassium nitrate. J Saudi Soc Agr Sci 13:45–55

Feller U, Kingston-Smith AH, Centritto M (2017) Abiotic stresses in agroecology: a challenge for whole plant physiology. Front Environ Sci 5:13

Food and Agricultural Organization [FAO] (2009) How to feed the world in 2050. Food and Agriculture Organization, Rome, Italy. http://www.fao.org/fileadmin/templates/wsfs/docs/expert_paper/How_to_Feed_the_World_in_2050.pdf

Fu P, Wang W, Hou L, Liu X (2013) Hydrogen sulfide is involved in the chilling stress response in *Vitis vinifera* L. Acta Soc Bot Pol 82:295–302

García-Mata C, Lamattina L (2010) Hydrogen sulfide, a novel gasotransmitter involved in guard cell signalling. New Phytol 188:977–984

Gaupels F, Kuruthukulangarakoola GT, Durner J (2011) Upstream and downstream signals of nitric oxide in pathogen defense. Curr Opin Plant Biol 14:707–714

Gémes K, Poór P, Sulyok Z, Szepesi Á, Szabó M, Tari I (2008) Role of salicylic acid pre-treatment on the photosynthetic performance of tomato plants (*Lycopersicon esculentum* mill. L. Cvar. Rio Fuego) under salt stress. Acta Biol Szeg 52:161–162

Gill RA, Zhang N, Ali B, Farooq MA, Xu J, Gill MB, Bizeng Mao Zhou W (2016) Role of exogenous salicylic acid in regulating physio-morphic and molecular changes under chromium toxicity in black-and yellow-seeded *Brassica napus* L. Environ Sci Pollut Res 23:20483–20496

Gong J, Wang B, Zeng G, Yang C, Niu C, Niu Q, Zhou W, Liang Y (2009) Removal of cationic dyes from aqueous solution using magnetic multi-wall carbon nanotube nanocomposite as adsorbent. J Hazard Mater 164:1517–1522

Gotor C, García I, Crespo JL, Romero LC (2013) Sulfide as a signaling molecule in autophagy. Autophagy 9:609–611

Gunes A, Inal A, Alpaslan M, Eraslan F, Bagci EG, Cicek N (2007) Salicylic acid induced changes on some physiological parameters symptomatic for oxidative stress and mineral nutrition in maize (*Zea mays* L.) grown under salinity. J Plant Physiol 164:728–736

Hamada AM (1998) Effects of exogenously added ascorbic acid, thiamin or aspirin on photosynthesis and some related activities of drought-stressed wheat plants. In: Garab G (ed) Photosynthesis: mechanisms and effects, vol 4. Kluwer Academic Publisher, Dordrecht, pp 2581–2584

Hamada AM, Al-Hakimi AMA (2001) Salicylic acid versus salinity-drought-induced stress on wheat seedlings. Rostlinna Vyroba 47:444–450

Hamayun M, Khan SA, Khan AL, Shinwari ZK, Hussain J, Sohn EY, Lee IJ (2010) Effect of salt stress on growth attributes and endogenous growth hormones of soybean cultivar Hwangkeumkong. Pak J Bot 42:3103–3112

Hancock JT, Neill SJ, Wilson ID (2012) Nitric oxide and ABA in the control of plant function. Plant Sci 181:555–559

Hao GP, Xing Y, Zhang JH (2008) Role of nitric oxide dependence on nitric oxide synthase-like activity in the water stress signaling of maize seedling. J Integ Plant Biol 50:435–442

Hao L, Zhao Y, Jin D, Zhang L, Bi X, Chen H, Li G (2012) Salicylic acid-altering *Arabidopsis* mutants response to salt stress. Plant Soil 354:81–95

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Ann Rev Plant Biol 51:463–499

Hayat S, Fariduddin Q, Ali B, Ahmad A (2005) Effect of salicylic acid on growth and enzyme activities of wheat seedlings. Acta Agr Hung 53:433–437

Hayat S, Hasan SA, Fariduddin Q, Ahmad A (2008) Growth of tomato (*Lycopersicon esculentum*) in response to salicylic acid under water stress. J Plant Inter 3:297–304

He Y, Zhu ZJ (2009) Exogenous salicylic acid alleviates NaCl toxicity and increases antioxidant enzyme activities in *Lycopersicon esculentum*. Biol Plant 52:792–795

He H, Zhan J, He L, Minghua G (2012) Nitric oxide signaling in aluminum stress in plants. Protoplasma 249:483–492

He H, Li Y, He LF (2018) The central role of hydrogen sulfide in plant responses to toxic metal stress. Ecotoxicol Environ Saf 157:403–408

Horváth E, Pál M, Szalai G, Páldi E, Janda T (2007) Exogenous 4-hydroxybenzoic acid and salicylic acid modulate the effect of short-term drought and freezing stress on wheat plants. Biol Plant 51:480–487

Hossain MA, Bhattacharjee S, Armin S-M, Qian P, Xin W, Li H-Y, Burritt DJ, Fujita M, Tran L-SP (2015) Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from H_2O_2 detoxification and scavenging. Front Plant Sci 6:420

Hsu YT, Kao CH (2004) Cadmium toxicity is reduced by nitric oxide in rice leaves. Plant Growth Regul 42:227–238

Huang Z, Chen G, Zeng G, Chen A, Zuo Y, Guo Z, Tan Q, Song Z, Niu Q (2015) Polyvinyl alcohol-immobilized Phanerochaete chrysosporium and its application in the bioremediation of composite-polluted wastewater. J Hazard Mater 289:174–183

Hussain M, Malik MA, Farooq M, Ashraf MY, Cheema MA (2008) Improving drought tolerance by exogenous application of glycinebetaine and salicylic acid in sunflower. J Agr Crop Sci 194:193–199

IPCC Intergovernmental Panel on Climate Change (2007) Climate change 2007: impacts, adaptation and vulnerability. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Contribution of working group II to fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, p 1000

Ishibashi Y, Yamaguchi H, Yuasa T, Iwaya-Inoue M, Arima S, Zheng SH (2011) Hydrogen peroxide spraying alleviates drought stress in soybean plants. J Plant Physiol 168:1562–1567

Janda T, Szalai G, Leskó K, Yordanova R, Apostol S, Popova LP (2007) Factors contributing to enhanced freezing tolerance in wheat during frost hardening in the light. Phytochemistry 68:1674–1682

Janda K, Hideg E, Szalai G, Kovács L, Janda T (2012) Salicylic acid may indirectly influence the photosynthetic electron transport. J Plant Physiol 169:971–978

Jayakannan M, Bose J, Babourina O, Rengel Z, Shabala S (2015) Salicylic acid in plant salinity stress signalling and tolerance. Plant Growth Regul 76:25–40

Jin ZP, Shen JJ, Qiao ZJ, Yang GD, Wang R, Pei YX (2011) Hydrogen sulfide improves drought resistance in *Arabidopsis thaliana*. Biochem Biophys Res Commun 414:481–486

Jin ZP, Xue SW, Luo YN, Tian BH, Fang HH, Li H, Pei Y (2013) Hydrogen sulfide interacting with abscisic acid in stomatal regulation responses to drought stress in *Arabidopsis*. Plant Physiol Biochem 62:41–46

Jin Z, Wang Z, Ma Q, Sun L, Zhang L, Liu Z, Pei Y (2017) Hydrogen sulfide mediates ion fluxes inducing stomatal closure in response to drought stress in *Arabidopsis thaliana*. Plant Soil 419:141–152

Jorge TF, Tohge T, Wendenburg R, Ramalho JC, Lidon FC, Ribeiro-Barros AI, António C (2019) Salt-stress secondary metabolite signatures involved in the ability of *Casuarina glauca* to mitigate oxidative stress. Environ Exp Bot. https://doi.org/10.1016/j.envexpbot.2019.103808

Joshi R, Wani SH, Singh B, Bohra A, Dar ZA, Lone AA, Singla-Pareek SL (2016) Transcription factors and plants response to drought stress: current understanding and future directions. Front Plant Sci 7:1029

Jumali SS, Said IM, Ismail I, Zainal Z (2011) Genes induced by high concentration of salicylic acid in ‘Mitragyna speciosa’. Aus J Crop Sci 5:296

Kaur P, Ghai N, Sangha MK (2009) Induction of thermotolerance through heat acclimation and salicylic acid in brassica species. Afr J Biotechnol 8:619–625

Kaya C, Akram NA, Ashraf M (2019a) Influence of exogenously applied nitric oxide on strawberry (Fragaria× ananassa) plants grown under iron deficiency and/or saline stress. Physiol Plant 165:247–263

Kaya C, Akram NA, Sürücü A, Ashraf M (2019b) Alleviating effect of nitric oxide on oxidative stress and antioxidant defence system in pepper (*Capsicum annuum* L.) plants exposed to cadmium and lead toxicity applied separately or in combination. Sci Horticul 255:52–60

Kazemi M, Hadavi E, Hekmati J (2011) Role of salicylic acid in decreases of membrane senescence in cut carnation flowers. Am J Plant Physiol 6:106–112

Khan W, Prithiviraj B, Smith DL (2003) Photosynthetic responses of corn and soybean to foliar application of salicylates. J Plant Physiol 160:485–492

Khan MN, Siddiqui MH, Mohammad F, Naeem M, Khan MMA (2010) Calcium chloride and gibberellic acid protect linseed (*Linum usitatissimum* L.) from NaCl stress by inducing antioxidative defence system and osmoprotectant accumulation. Acta Physiol Plant 32:121

Khan MIR, Asgher M, Khan NA (2014) Alleviation of salt-induced photosynthesis and growth inhibition by salicylic acid involves glycinebetaine and ethylene in mungbean (*Vigna radiata* L.). Plant Physiol Biochem 80:67–74

Khan MIR, Fatma M, Per TS, Anjum NA, Khan NA (2015) Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. Front Plant Sci 6:462

Khan TA, Fariduddin Q, Yusuf M (2017) Low-temperature stress: is phytohormones application a remedy? Environ Sci Pollut Res 24:21574–21590

Khanam D, Mohammad F (2016) Effect of structurally different plant growth regulators (PGRS) on the concentration, yield, and constituents of peppermint essential oil. Int J Geogr Inf Syst 23:1–10

Khanam D, Mohammad F (2018) Plant growth regulators ameliorate the ill effect of salt stress through improved growth, photosynthesis, antioxidant system, yield and quality attributes in Mentha piperita L. Acta Physiol Plant 40:188

Khodary SFA (2004) Effect of salicylic acid on the growth, photosynthesis and carbohydrate metabolism in salt stressed maize plants. Inter J Agr Biol 6:5–8

Knutti R, Rogelj J, Sedláček J, Fischer EM (2016) A scientific critique of the two-degree climate change target. Nat Geosci 9:13

Kopriva S (2006) Regulation of sulfate assimilation in *Arabidopsis* and beyond. Ann Bot 97:479–495

Kosová K, Prášil IT, Vítámvás P, Dobrev P, Motyka V, Floková K, Trávničková A (2012) Complex phytohormone responses during the cold acclimation of two wheat cultivars differing in cold tolerance, winter Samanta and spring Sandra. J Plant Physiol 169:567–576

Krantev A, Yordanova R, Janda T, Szalai G, Popova L (2008) Treatment with salicylic acid decreases the effect of cadmium on photosynthesis in maize plants. J Plant Physiol 165:920–931

Kumari A, Pandey-Rai S (2018) Enhanced arsenic tolerance and secondary metabolism by modulation of gene expression and proteome profile in *Artemisia annua* L. after application of exogenous salicylic acid. Plant Physiol Biochem 132:590–602

Kunert KJ, Vorster BJ, Fenta BA, Kibido T, Dionisio G, Foyer CH (2016) Drought stress responses in soybean roots and nodules. Front Plant Sci 7:1015

Lai D, Mao Y, Zhou H, Li F, Wu M, Zhang J, Xie Y (2014) Endogenous hydrogen sulfide enhances salt tolerance by coupling the reestablishment of redox homeostasis and preventing salt-induced K+ loss in seedlings of *Medicago sativa*. Plant Sci 225:117–129

Larkindale J, Knight MR (2002) Protection against heat stress-induced oxidative damage in *Arabidopsis* involves calcium, abscisic acid, ethylene, and salicylic acid. Plant Physiol 128:682–695

Lee BR, Zhang Q, Park SH, Islam MT, Kim TH (2019) Salicylic acid improves drought-stress tolerance by regulating the redox status and proline metabolism in *Brassica rapa*. Horticul Environ Biotechnol 60:31–40

Lei Y, Yin C, Li C (2007) Adaptive responses of Populus przewalskii to drought stress and SNP application. Acta Physiol Plant 29:519–526

Li Z (2015) Synergistic effect of antioxidant system and osmolyte in hydrogen sulfide and salicylic acid crosstalk-induced heat tolerance in maize (*Zea mays* L.) seedlings. Plant Signal Behav 10:e1051278

Li ZG, Gong M, Xie H, Yang L, Li J (2012) Hydrogen sulphide donor sodium hydrosulfide induced heat tolerance in tobacco (*Nicotiana tabacum* L.) suspension cultured cells and involvement of Ca2C and calmodulin. Plant Sci 185–186:185–189

Li ZG, Ding XJ, Du PF (2013) Hydrogen sulphide donor sodium hydrosulfide-improved heat tolerance in maize and involvement of proline. J Plant Physiol 170:741–747

Li J, Jia H, Wang J, Cao Q, Wen Z (2014) Hydrogen sulfide is involved in maintaining ion homeostasis via regulating plasma membrane Na^+/H^+ antiporter system in the hydrogen peroxide-dependent manner in salt-stress *Arabidopsis thaliana* root. Protoplasma 251:899–912

Li X, Lawas LMF, Malo R, Glaubitz U, Erban A, Mauleon R, Heuer S, Zuther E, Kopka J, Hincha DK, Jagadish KSV (2015a) Metabolic and transcriptomic signatures of rice floral organs reveal sugar starvation as a factor in reproductive failure under heat and drought stress. Plant Cell Environ 38:2171–2192

Li Z, Xie L, Li X (2015b) Hydrogen sulfide acts as a downstream signal molecule in salicylic acid-induced heat tolerance in maize (*Zea mays* L.) seedlings. J Plant Physiol 177:121–127

Li ZG, Min X, Zhou ZH (2016a) Hydrogen sulfide: a signal molecule in plant cross-adaptation. Front Plant Sci 7:1621

Li Z, Zhang Y, Zhang X, Peng Y, Merewitz E, Ma X, Huang L, Yan Y (2016b) The alterations of endogenous polyamines and phytohormones induced by exogenous application of spermidine regulate antioxidant metabolism, metallothionein and relevant genes conferring drought tolerance in white clover. Environ Exp Bot 124:22–38

Lisjak M, Srivastava N, Teklic T, Civale L, Lewandowski K, Wilson I, Wood ME, Whiteman M, Hancock JT (2010) A novel hydrogen sulfide donor causes stomatal opening and reduces nitric oxide accumulation. Plant Physiol Biochem 48:931–935

Lisjak M, Teklic T, Wilson ID, Wood M, Whiteman M, Hancock JT (2011) Hydrogen sulfide effects on stomatal apertures. Plant Signal Behav 6:1444–1446

Lisjak M, Teklic T, Wilson ID, Whiteman M, Hancock JT (2013) Hydrogen sulfide: environmental factor or signalling molecule? Plant Cell Environ 36:1607–1616

Liu HT, Liu YY, Pan QH, Yang HR, Zhan JC, Huang WD (2006) Novel interrelationship between salicylic acid, abscisic acid, and PIP2-specific phospholipase C in heat acclimation-induced thermotolerance in pea leaves. J Exp Bot 57:3337–3347

Liu Y, Wu R, Wan Q, Xie G, Bi Y (2007) Glucose-6-phosphate dehydrogenase plays a pivotal role in nitric oxide-involved defense against oxidative stress under salt stress in red kidney bean roots. Plant Cell Physiol 48:511–522

Liu S, Dong Y, Xu L, Kong J (2014) Effects of foliar applications of nitric oxide and salicylic acid on salt-induced changes in photosynthesis and antioxidative metabolism of cotton seedlings. Plant Growth Regul 73:67–78

Liu S, Yang R, Pan Y, Ma M, Pan J, Zhao Y, Cheng Q, Wu M, Wang M, Zhang L (2015) Nitric oxide contributes to minerals absorption, proton pumps and hormone equilibrium under cadmium excess in *Trifolium repens* L. plants. Ecotoxicol Environ Safety 119:35–46

Llusia J, Penuelas J, Munne-Bosch S (2005) Sustained accumulation of methyl salicylate alters antioxidant protection and reduces tolerance of holm oak to heat stress. Physiol Plant 124:353–361

Macomber L, Hausinger RP (2011) Mechanisms of nickel toxicity in microorganisms. Metallomics 3:1153–1162

Metwally A, Finkemeier I, Georgi M, Dietz KJ (2003) Salicylic acid alleviates the cadmium toxicity in barley seedlings. Plant Physiol 132:272–281

Mioto PT, Mercier H (2013) Abscisic acid and nitric oxide signaling in two different portions of detached leaves of *Guzmania monostachia* with CAM up-regulated by drought. J Plant Physiol 170:996–1002

Mishina TE, Lamb C, Zeier J (2007) Expression of a nitric oxide degrading enzyme induces a senescence programme in *Arabidopsis*. Plant Cell Environ 30:39–52

Mishra A, Choudhuri MA (1999) Effects of salicylic acid on heavy metal-induced membrane deterioration mediated by lipoxygenase in rice. Biol Plant 42:409–415

Miura K, Okamoto H, Okuma E, Shiba H, Kamada H, Hasegawa PM, Murata Y (2013) SIZ1 deficiency causes reduced stomatal aperture and enhanced drought tolerance via controlling salicylic acid-induced accumulation of reactive oxygen species in *Arabidopsis*. The Plant J 73:91–104

Montilla-Bascón G, Rubiales D, Hebelstrup KH, Mandon J, Harren FJ, Cristescu SM, Prats E (2017) Reduced nitric oxide levels during drought stress promote drought tolerance in barley and is associated with elevated polyamine biosynthesis. Sci Rep 7:13311

Moshelion M, Altman A (2015) Current challenges and future perspectives of plant and agricultural biotechnology. Trends Biotechnol 33:337–342

Mostofa MG, Rahman A, Ansary MM, Watanabe A, Fujita M, Tran LS (2015) Hydrogen sulfide modulates cadmium-induced physiological and biochemical responses to alleviate cadmium toxicity in rice. Sci Rep 5:14078

Munir M, Shabbir G (2018) Salicylic acid mediated heat stress tolerance in selected bread wheat genotypes of Pakistan. Pak J Bot 50:2141–2146

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Ann Rev Plant Biol 59:651–681

Mur LAJ, Mandon J, Persijn S, Cristescu SM, Moshkov IE, Novikova GV, Hall MA, Harren FJM, Hebelstrup KH, Gupta KJ (2013) Nitric oxide in plants: An assessment of the current state of knowledge. AoB Plants 5:pls052

Nabi RBS, Tayade R, Hussain A, Kulkarni KP, Imran QM, Mun BG, Yun BW (2019) Nitric oxide regulates plant responses to drought, salinity, and heavy metal stress. Environ Exp Bot 161:120–133

Nazar R, Umar S, Khan NA, Sareer O (2015) Salicylic acid supplementation improves photosynthesis and growth in mustard through changes in proline accumulation and ethylene formation under drought stress. South Afr J Bot 98:84–94

Nazar R, Iqbal N, Umar S (2017) Heat stress tolerance in plants: action of salicylic acid. In: Salicylic acid: a multifaceted hormone. Springer, Singapore, pp 145–161

Németh M, Janda T, Horváth E, Páldi E, Szalai G (2002) Exogenous salicylic acid increases polyamine content but may decrease drought tolerance in maize. Plant Sci 162:569–574

Ohtake Y, Takahashi T, Komed Y (2000) Salicylic acid induces the expression of a number of receptor-like kinase genes in *Arabidopsis thaliana*. Plant Cell Physiol 41:1038–1044

Pál M, Szalai G, Horváth E, Janda T, Páldi E (2002) Effect of salicylic acid during heavy metal stress. Acta Biol Szeged 46:119–120

Pancheva TV, Popova LP, Uzunova AM (1996) Effect of salicylic acid on growth and photosynthesis in barley plants. J Plant Physiol 149:57–63

Panda, SK, Patra HK (2007). Effect of salicylic acid potentiates cadmium-induced oxidative damage in Oryza sativa L. leaves. Acta Physiologiae Plantarum, 29(6): 567–575

Papenbrock J, Riemenschneider A, Kamp A, Schulz-Vogt HN, Schmidt A (2007) Characterization of cysteine-degrading and H_2S-releasing enzymes of higher plants - from the field to the test tube and back. Plant Biol 9:582–588

Pereira A (2016) Plant abiotic stress challenges from the changing environment. Front Plant Sci 7:1123. https://doi.org/10.3389/fpls.2016.01123

Poór P, Szopkó D, Tari I (2012) Ionic homeostasis disturbance is involved in tomato cell death induced by NaCl and salicylic acid. In Vitro Cell Dev Biol Plant 48:377–382

Qiao W, Li C, Fan LM (2014) Cross-talk between nitric oxide and hydrogen peroxide in plant responses to abiotic stresses. Environ Exp Bot 100:84–93

Qin L, Zeng G, Lai C, Huang D, Xu P, Zhang C, Cheng M, Liu X, Liu S, Li B, Yi H (2018) "Gold rush" in modern science: fabrication strategies and typical advanced applications of gold nanoparticles in sensing. Coord Chem Rev 359:1–31

Rai KK, Rai N, Rai SP (2018a) Response of *Lablab purpureus* L. to high temperature stress and role of exogenous protectants in mitigating high temperature induced oxidative damages. Mol Biol Rep 45:1375–1395

Rai KK, Rai N, Rai SP (2018b) Salicylic acid and nitric oxide alleviate high temperature induced oxidative damage in *Lablab purpureus* L plants by regulating bio-physical processes and DNA methylation. Plant Physiol Biochem 128:72–88

Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, Xu J (2019) Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. Plan Theory 8:34

Rodríguez-Serrano M, Romero-Puertas MC, Pazmino DM, Testillano PS, Risueño MC, Luis A, Sandalio LM (2009) Cellular response of pea plants to cadmium toxicity: cross talk between reactive oxygen species, nitric oxide, and calcium. Plant Physiol 150:229–243

Romero-Munar A, Baraza E, Gulías J, Cabot C (2019) Arbuscular mycorrhizal fungi confer salt tolerance in giant reed (*Arundo donax* L.) plants grown under low phosphorus by reducing leaf Na^+ concentration and improving phosphorus use efficiency. Front Plant Sci 10:843

Ruelland E, Vaultier MN, Zachowski A, Hurry V (2009) Cold signalling and cold acclimation in plants. Adv Bot Res 49:35–146

Sahar K, Amin B, Taher NM (2011) The salicylic acid effect on the *Salvia officianlis* L. sugar, protein and proline contents under salinity (NaCl) stress. J Stress Physiol Biochem 7:80–87

Sahay S, Gupta M (2017) An update on nitric oxide and its benign role in plant responses under metal stress. Nitric Oxide 67:39–52

Sahay S, Khan E, Gupta M (2019) Nitric oxide and abscisic acid protects against PEG-induced drought stress differentially in brassica genotypes by combining the role of stress modulators, markers and antioxidants. Nitric Oxide 89:81–92

Sakhabutdinova AR, Fatkhutdinova DR, Shakirova FM (2004) Effect of salicylic acid on the activity of antioxidant enzymes in wheat under conditions of salination. App Biochem Microbiol 40:501–505

Sami F, Faizan M, Faraz A, Siddiqui H, Yusuf M, Hayat S (2018) Nitric oxide-mediated integrative alterations in plant metabolism to confer abiotic stress tolerance, NO crosstalk with phytohormones and NO-mediated post translational modifications in modulating diverse plant stress. Nitric Oxide 73:22–38

Santisree P, Bhatnagar-Mathur P, Sharma KK (2015) NO to drought-multifunctional role of nitric oxide in plant drought: do we have all the answers? Plant Sci 239:44–55

Scuffi D, Alvarez C, Laspina N, Gotor C, Lamattina L, Garcíamata C (2014) Hydrogen sulfide generated by l-cysteine desulfhydrase acts upstream of nitric oxide to modulate abscisic acid-dependent stomatal closure. Plant Physiol 166:2065–2076

Sehar Z, Masood A, Khan NA (2019) Nitric oxide reverses glucose-mediated photosynthetic repression in wheat (*Triticum aestivum* L.) under salt stress. Environ Exp Bot 161:277–289

Senaratna T, Touchell D, Bunn T, Dixon K (2000) Acetyl salicylic acid (aspirin) and salicylic acid induce multiple stress tolerance in bean and tomato plants. Plant Growth Regul 30:157–161

Senaratna T, Merritt D, Dixon K, Bunn E, Touchell D, Sivasithamparam K (2003) Benzoic acid may act as the functional group in salicylic acid and derivatives in the induction of multiple stress tolerance in plants. Plant Growth Regul 39:77–81

Shakirova FM (2007) Role of hormonal system in the manisfestation of growth promoting and anti-stress action of salicylic acid. In: Hayat S, Ahmad A (eds) A plant hormone. Springer, Dordrecht

Shakirova FM, Sakhabutdinova AR, Bezrukova MV, Fatkhutdinova RA, Fatkhutdinova DR (2003) Changes in the hormonal status of wheat seedlings induced by salicylic acid and salinity. Plant science, 164(3):317–322

Shao R, Wang K, Shangguan Z (2010) Cytokinin-induced photosynthetic adaptability of Zea mays L. to drought stress associated with nitric oxide signal: probed by ESR spectroscopy and fast OJIP fluorescence rise. J Plant Physiol 167:472–479

Sharma A, Soares C, Sousa B, Martins M, Kumar V, Shahzad B, Thukral AK (2019) Nitric oxide-mediated regulation of oxidative stress in plants under metal stress: a review on molecular and biochemical aspects. Physiol Plant. doi:https://doi.org/10.1111/ppl.13004

Shen J, Xing T, Yuan H, Liu Z, Jin Z, Zhang L, Pei Y (2013) Hydrogen sulfide improves drought tolerance in *Arabidopsis thaliana* by microRNA expressions. PLoS One 8:e77047

Shi Q, Bao Z, Zhu Z, Ying Q, Qian Q (2006) Effects of different treatments of salicylic acid on heat tolerance, chlorophyll fluorescence, and antioxidant enzyme activity in seedlings of Cucumis sativa L. Plant Growth Regul 48:127–135

Shi H, Ye T, Zhu JK, Chan Z (2014) Constitutive production of nitric oxide leads to enhanced drought stress resistance and extensive transcriptional reprogramming in *Arabidopsis*. J Exp Bot 65:4119–4131

Siddiqui MH, Alamri SA, Al-Khaishany MY, Al-Qutami MA, Ali HM, Hala AR, Kalaji HM (2017) Exogenous application of nitric oxide and spermidine reduces the negative effects of salt stress on tomato. Hort Environ Biotechnol 58:537–547

Simontacchi M, Galatro A, Ramos-Artuso F, Santa-Maria GE (2015) Plant survival in a changing environment: the role of nitric oxide in plant responses to abiotic stress. Front Plant Sci 6:977

Singh B, Usha K (2003) Salicylic acid induced physiological and biochemical changes in wheat seedlings under water stress. Plant Growth Regul 39:137–141

Singh HP, Kaur S, Batish DR, Sharma VP, Sharma N, Kohli RK (2009) Nitric oxide alleviates arsenic toxicity by reducing oxidative damage in the roots of *Oryza sativa* (rice). Nitric Oxide 20:289–297

Suzuki N, Mittler R (2006) Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction. Physiol Plant 126:45–51

Szepesi Á (2005) Role of salicylic acid pre-treatment on the acclimation of tomato plants to salt- and osmotic stress. Acta Biol Szeg 49:123–125

Szepesi Á, Csiszár J, Gallé Á, Gémes K, Poór P, Tari I (2008a) Effect of long-term salicylic acid pre-treatment on tomato (*Lycopersicon esculentum* mill. L.) salt stress tolerance: changes in glutathione S-transferase activities and antocyanin contents. Acta Agron Hung 56:129–138

Szepesi Á, Poór P, Gémes K, Horváth E, Tari I (2008b) Influence of exogenous salicylic acid on antioxidant enzyme activities in the roots of salt stressed tomato plants. Acta Biol Szeg 52:199–200

Tahjib-Ul-Arif M, Siddiqui MN, Sohag AAM, Sakil MA, Rahman MM, Polash MAS, Tran LSP (2018) Salicylic acid-mediated enhancement of photosynthesis attributes and antioxidant capacity contributes to yield improvement of maize plants under salt stress. J Plant Growth Regul 37:1318–1330

Tang Y, Sun X, Wen T, Liu M, Yang M, Chen X (2017) Implications of terminal oxidase function in regulation of salicylic acid on soybean seedling photosynthetic performance under water stress. Plant Physiol Biochem 112:19–28

Tang H, Niu L, Wei J, Chen X, Chen Y (2019) Phosphorus limitation improved salt tolerance in maize through tissue mass density increase, Osmolytes accumulation, and Na^+ uptake inhibition. Front Plant Sci 10:856. https://doi.org/10.3389/fpls.2019.00856

Tanou G, Molassiotis A, Diamantidis G (2009) Hydrogen peroxide- and nitric oxide-induced systemic antioxidant prime-like activity under NaCl-stress and stress-free conditions in citrus plants. J Plant Physiol 166:1904–1913

Tari I (2002) Acclimation of tomato plants to salinity stress after a salicylic acid pretreatment. Acta Biol Szeg 46:55–56

Tari I, Simon LM, Deér KA, Csiszár J, Bajkán SZ, Kis GY, Szepesi A (2004) Influence of salicylic acid on salt stress acclimation of tomato plants: oxidative stress responses and osmotic adaptation. Acta Physiol Plant 26:237

Tari I, Kiss G, Deer AK, Csiszár J, Erdei L, Gallé Á, Simon LM (2010) Salicylic acid increased aldose reductase activity and sorbitol accumulation in tomato plants under salt stress. Biol Plant 54:677–683

Tester M, Davenport R (2003) Na^+ tolerance and Na+ transport in higher plants. Ann Bot 91:503–507

Thornton PK, Ericksen PJ, Herrero M, Challinor AJ (2014) Climate variability and vulnerability to climate change: a review. Glob Chang Biol 20:3313–3328

Tian X, Lei Y (2006) Nitric oxide treatment alleviates drought stress in wheat seedlings. Biol Plant 50:775–778

Uchida A, Jagendorf AT, Hibino T, Takabe T, Takabe T (2002) Effects of hydrogen peroxide and nitric oxide on both salt and heat stress tolerance in rice. Plant Sci 163:515–523

Uppalapati SR, Ishiga Y, Wangdi T, Kunkel BN, Anand A, Mysore KS, Bender CL (2007) The phytotoxin coronatine contributes to pathogen fitness and is required for suppression of salicylic acid accumulation in tomato inoculated with pseudomonas syringae pv. Tomato DC3000. Mol Plant-Mic Interac 20:955–965

Wahid A, Perveen M, Gelani S, Basra SM (2007) Pretreatment of seed with H2O2 improves salt tolerance of wheat seedlings by alleviation of oxidative damage and expression of stress proteins. J Plant Physiol 164:283–294

Wang LJ, Li SL (2006) Salicylic acid-induced heat or cold tolerance in relation to Ca^{2+} homeostasis and antioxidant systems in young grape plants. Plant Sci 170:685–694

Wang YS, Yang ZM (2005) Nitric oxide reduces aluminum toxicity by preventing oxidative stress in the roots of *Cassia tora* L. Plant Cell Physiol 46:1915–1923

Wang Y, Mopper S, Hasenstein KH (2001) Effects of salinity on endogenous ABA, IAA, JA, and SA in *Iris hexagona*. J Chem Ecol 27:327–342

Wang LJ, Fan L, Loescher W, Duan W, Liu GJ, Cheng JS (2010) Salicylic acid alleviates decreases in photosynthesis under heat stress and accelerates recovery in grapevine leaves. BMC Plant Biol 10:34–40

Wang GF, Seabolt S, Hamdoun S, Ng G, Park J, Lu H (2011) Multiple roles of WIN3 in regulating disease resistance, cell death, and flowering time in *Arabidopsis*. Plant Physiol 156:1508–1519

Wang H, Yuan X, Wu Y, Huang H, Zeng G, Liu Y, Wang X, Lin N, Qi Y (2013) Adsorption characteristics and behaviors of graphene oxide for Zn (II) removal from aqueous solution. Appl Surf Sci 279:432–440

Wang Y, Wen T, Huang Y, Guan Y, Hu J (2018) Salicylic acid biosynthesis inhibitors increase chilling injury to maize (*Zea mays* L.) seedlings. Plant Growth Regul 86:11–21

Wani W, Masoodi KZ, Zaid A, Wani SH, Shah F, Meena VS, Mosa KA (2018) Engineering plants for heavy metal stress tolerance. Rend Lin Sci Fis e Nat 29:709–723

Weast RC (1984) CRC handbook of chemistry and physics, 64th edn. CRC Press, Boca Raton

Xing H, Tan L, An L, Zhao Z, Wang S, Zhang C (2004) Evidence for the involvement of nitric oxide and reactive oxygen species in osmotic stress tolerance of wheat seedlings: inverse correlation between leaf abscisic acid accumulation and leaf water loss. Plant Growth Regul 42:61–68

Xu J, Wang W, Yin H, Liu X, Sun H, Mi Q (2010) Exogenous nitric oxide improves antioxidative capacity and reduces auxin degradation in roots of Medicago truncatula seedlings under cadmium stress. Plant Soil 326:321–330

Xu J, Wang W, Sun J, Zhang Y, Ge Q, Du L, Liu X (2011) Involvement of auxin and nitric oxide in plant cd-stress responses. Plant Soil 346:107

Yang ZM, Wang J, Wang SH, Xu LL (2003) Salicylic acid-induced aluminium tolerance by modulation of citrate efflux from roots of Cassia tora L. Planta 217:168–174

Yang Z, Cao S, Zheng Y, Jiang Y (2012) Combined salicyclic acid and ultrasound treatments for reducing the chilling injury on peach fruit. J Agr food Chem 60:1209–1212

Yang L, Ji J, Harris-Shultz KR, Wang H, Wang H, Abd-Allah EF, Luo Y, Hu X (2016) The dynamic changes of the plasma membrane proteins and the protective roles of nitric oxide in Rice subjected to heavy metal cadmium stress. Front Plant Sci 7:190. https://doi.org/10.3389/fpls.2016.00190

Ye S, Zeng G, Wu H, Zhang C, Dai J, Liang J, Yu J, Ren X, Yi H, Cheng M, Zhang C (2017) Biological technologies for the remediation of co-contaminated soil. Crit Rev Biotechnol 37:1062–1076

Yordanov I, Velikova V, Tsone V (2000) Plant response to drought, acclimation and stress tolerance. Photosynthetica 30:171–186

Yu CC, Hung KT, Kao CH (2005) Nitric oxide reduces cu toxicity and cu-induced NH4+ accumulation in rice leaves. J Plant Physiol 162:1319–1330

Yuan S, Lin HH (2008) Role of salicylic acid in plant abiotic stress. Zeits für Nat 63:313–320

Yuan S, Shen X, Kevil CG (2017) Beyond a Gasotransmitter: hydrogen sulfide and polysulfide in cardiovascular health and immune response. Antiox Redox Signal 27:634–653

Zaid A, Mohammad F, Wani SH, Siddique KM (2019) Salicylic acid enhances nickel stress tolerance by up-regulating antioxidant defense and glyoxalase systems in mustard plants. Ecotoxicol Environ Saf 180:575–587

Zanganeh R, Jamei R, Rahmani F (2018) Impacts of seed priming with salicylic acid and sodium hydrosulfide on possible metabolic pathway of two amino acids in maize plant under lead stress. Mol Biol Res Comm 7:83

Zhang WN, Chen WL (2011) Role of salicylic acid in alleviating photochemical damage and autophagic cell death induction of cadmium stress in *Arabidopsis thaliana*. Photochem Photobiol Sci 10:947–955

Zhang H, Hu LY, Hu KD, He YD, Wang SH, Luo JP (2008) Hydrogen sulfide promotes wheat seed germination and alleviates oxidative damage against copper stress. J Integr Plant Biol 50:1518–1529

Zhang H, Wang MJ, Hu LY, Wang SH, Hu KD, Bao LJ, Luo JP (2010a) Hydrogen sulfide promotes wheat seed germination under osmotic stress. Russ J Plant Physiol 57(4):532–539

Zhang H, Tan ZQ, Hu LY, Wang SH, Luo JP, Jones RL (2010b) Hydrogen sulfide alleviates aluminum toxicity in germinating wheat seedlings. J Integ Plant Biol 52:556–567

Zhang F, Zhang H, Xia Y, Wang G, Xu L, Shen Z (2011) Exogenous application of salicylic acid alleviates cadmium toxicity and reduces hydrogen peroxide accumulation in root apoplasts of Phaseolus aureus and Vicia sativa. Plant Cell Rep 30:1475–1483

Zhao HJ, Lin XW, Shi HZ, Chang SM (1995) The regulating effect of phenolic compounds on the physiological characteristics and yield of soybeans. Acta Agron Sin 21:351–355

Zhao Z, Chen G, Zhang C (2001) Interaction between reactive oxygen species and nitric oxide in drought-induced abscisic acid synthesis in root tips of wheat seedlings. Func Plant Biol 28:1055–1061

Zhao L, Zhang F, Guo J, Yang Y, Li B, Zhang L (2004) Nitric oxide functions as a signal in salt resistance in the calluses from two ecotypes of reed. Plant Physiol 134:849–857

Zhao MG, Chen L, Zhang LL, Zhang WH (2009) Nitric reductase-dependent nitric oxide production is involved in cold acclimation and freezing tolerance in *Arabidopsis*. Plant Physiol 151:755–767

Zhou C, Lai C, Zhang C, Zeng G, Huang D, Cheng M, Hu L, Xiong W, Chen M, Wang J, Yang Y, Jiang L (2018) Semiconductor/boron nitride composites: synthesis, properties, and photocatalysis applications. App Cata B 238:6–18

Zhu JK (2003) Regulation of ion homeostasis under salt stress. Curr Opin Plant Biol 6:441–445

Zhu M, Dai S, Chen S (2012a) The stomata frontline of plant interaction with the environment perspectives from hormone regulation. Front Biol 7:96–112

Zhu XF, Jiang T, Wang ZW et al (2012b) Gibberellic acid alleviates cadmium toxicity by reducing nitric oxide accumulation and expression of IRT1 in *Arabidopsis thaliana*. J Hazard Mater 239:302–307

Chapter 29
Biochemical and Molecular Mechanism of Abiotic Stress Tolerance in Plants

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Contents

Abstract Plants need to acclimatize with sudden changing environment for their adaptation. Plant community, as a whole, is the primary producer in our ecosystem, therefore versatile in nature. In its differential habitats, plants need to cope up with environmental (abiotic) stresses like heavy metals, heat, cold, drought, acidic soil, and various nutrient deficiencies. Plants have their genetic ability to overcome the challenges of different environmental stresses through complex metabolic processes. There are numerous reports in connection with biochemical and molecular mechanisms in response to abiotic stresses. However, it is difficult to correlate the different molecular mechanisms involved pertaining to abiotic stresses in plants. Therefore, in this article, an attempt has been made to draw a systematic relationships of different biochemical and molecular processes involved in plant system during environmental stresses.

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29.1 Introduction

Abiotic stress includes different nonliving factors such as metals/metalloid toxicity, drought, submergence, salinity, chilling/extreme temperature, acidic soil, oxidative stress, etc., that are sometimes termed as environmental insults and always has the negative impact upon flora and fauna, as a whole the biodiversity of the globe (Tuteja and Gill 2016). These are serious threat to the agriculture and deteriorate the environment. The exposure of plants to different abiotic factors induces disturbance in the plant metabolism, thereby disrupting physiological mechanism as well as its growth, ultimately leading to decrease in productivity (Rejeb et al. 2014). Plants to cope with the complex abiotic stress factors develop various mechanisms of tolerance that include both the physical adaption and integrated cellular or molecular responses (Bray et al. 2000). The mechanism of tolerance in plants is measured in relation to its survival against stress factors, which is the plant fitness to cope with an unfavorable environment (Gupta and Huang 2014). The crucial step in the mechanism of plant tolerance is the timely perception of the effect of abiotic factors in a rapid efficient manner. The initial step toward tolerance is the innate basal defense system which leads to further activation of different signaling cascades and expression of different genes responsible for induction of tolerance against the various stress factors (Rejeb et al. 2014).

In the recent years, researchers have undertaken different steps to understand the plant defense system from the perception of the stress stimulus to the phenotypic output and also the genetic reprogramming plants undergo to ameliorate the negative effect of stress. Different plants develop different defense systems in specific, varying from the biochemical factors released or secreted to the different genes or the molecular remodeling involved against the abiotic factors (Meena et al. 2017).

Plants to cope with the different abiotic environmental concern develop various mechanisms of tolerance which mainly include the biochemical and molecular mechanism of tolerance (Onaga and Wydra 2016). Biochemical mechanism of tolerance includes the cellular approaches that plants adapt to minimize the effect of abiotic stress. It comprises the adaptive approach of physical barrier or insulating layer formation, secretion of secondary metabolites or organic compounds, remodeling of the membrane constituents, and also some internal mechanisms of the increase in antioxidant capacity or internalization of the toxic compounds such as sequestration of Al^{3+} into the vacuoles (Wani 2018). Molecular mechanism of tolerance is based on the genetic approaches plants develop against abiotic stress. Genetic approaches include the expression of different tolerant genes that encodes the transcriptional regulation and development of proteins which helps in the maintenance and alleviation of stress effect. Various transcription factors incorporate or upregulate different genes, which initiate different signaling cascades and development of various stress alleviating factors which control or minimize the effect of abiotic stresses (Bechtold and Field 2018).

Based on the abiotic stress factors, plants develop different mechanisms of tolerance to cope with the effects of the stress, i.e., both biochemical and molecular mechanisms, and thus undergo the process of development and growth. In this article, few major and common abiotic stress factors have been targeted to analyze and correlate pertaining to different biochemical and molecular mechanisms of tolerance involved in plant under abiotic stresses.

29.2 Toxic Metal/Metalloid Stress

Different metals/metalloids such as aluminum (Al), arsenic (As), chromium (Cr), cadmium (Cd), and iron (Fe) are highly toxic and reactive in nature to living cells though some serve as an essential micronutrient in different physiological processes (Pradhan et al. 2019). But with the increase in concentration above the threshold level, they all become highly toxic, hampering the growth and development of plants or other living beings (Kalita et al. 2018). The toxicity of metal/metalloid to the plants includes the change or dysfunctioning of the different essential biomolecules by causing hindrance to its functional groups or by displacement of the essential cofactors like that of the metal ions (Kochian et al. 2015). In response to threshold levels of toxic metals, plants develop various mechanisms of tolerance like the development of different polypeptides with specific active metal binding site such as cysteine-rich peptides (e.g., C_2H_2 zinc finger protein), metallothioneins, phytochelatins, and various functional membrane transport systems that play important roles in maintaining the metal ion homeostasis and inactivation of the toxic metalloids like sequestration of metal ions into the vacuoles and thereby develop the phenomenon of tolerance (Hall and Williams 2003). In addition plants also release various secondary metabolites and other compounds such as organic acids. The primary mechanism mainly involves the different molecular genetic approaches, i.e., the activation of different tolerance genes against metal toxicity. Some of the major toxic metals and the various biochemical molecular mechanisms plants develop are discussed below.

29.2.1 Aluminum (Al) Toxicity

Al, the third most abundant element in the earth's crust, occurs in a nontoxic oxide form at the normal pH level, i.e., > 7.0, but due to the increase in acidic condition with the decrease in pH (< 5.0) mainly in the tropical areas due to heavy rainfall or leaching, Al gets oxidized to its most toxic form, i.e., Al^{3+}, causing severe toxicity to the growth and development of crops as well as other plants except to that of acid loving plants (Awasthi et al. 2017). The effect of the Al^{3+} is based on its interaction with plants with root inhibition being the initial symptom of Al toxicity.

The major factor for Al toxicity is the wide distribution of acid soils worldwide. Acid soils cover almost 50% of the total potential arable land, thereby leading to a severe threat of abiotic stress mainly Al toxicity to the crop plants and as a whole to agriculture (Von Uexkull and Mutert 1995). Under acidic condition, Al in its soluble form shows phytotoxicity, which rapidly inhibits the root elongation, subsequently leading to inhibition of water and nutrient uptake (Jayasundara et al. 1998) (Fig. 29.1).

Plants in response to Al toxicity show variable forms of tolerance mechanism with different plants showing different mechanisms of tolerance. As reported by Bona et al. (1993), the level of Al tolerance in cereal crops varied accordingly as follows: *Oryza sativa* > *Secale cereale* > *Avena sativa* > *Triticum aestivum* > *Hordeum vulgare*. But the different plants in majority share a common mechanism of tolerance varying on the type of compounds released or the genes responsible. Mainly, biochemical and molecular mechanism serve as the immediate form of tolerance.

The biochemical mechanism comprises of two different processes; the external mechanism, i.e., the exclusion of Al from entering the apex of root may be through symplasm or apoplasm, as well as the internal mechanism, i.e., detoxification and sequestration into the plant tissues, mostly vacuoles, through chelation or integration with various compounds released in response to Al toxicity in acidic condition (Kochian et al. 2015).

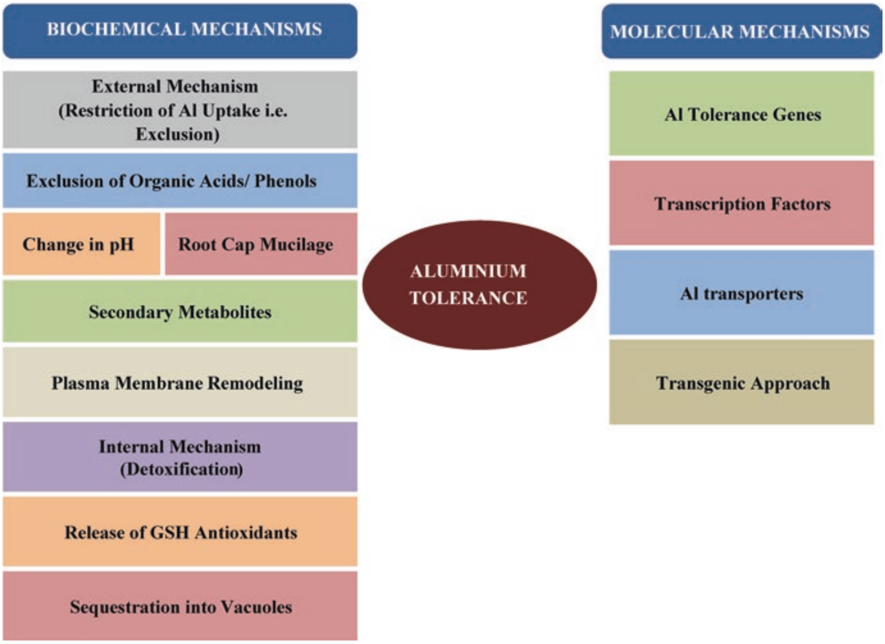

Fig. 29.1 Mechanism of aluminum tolerance in plants

External mechanism mainly includes the exclusion or restriction of Al uptake from entering into the plant through various processes. This mechanism reduces or protects the plants, mainly its sensitive sites such as the plasma membrane and cell wall, from the harmful interactions with the toxic forms of Al and, thereby, decreases the quantity of Al reaching the sensitive sites of nutrient uptake in the symplasm (Carver and Ownby 1995).

Al exclusion mechanism is mainly characterized based on the discharge of root exudates, mainly the organic acid (OA) anions into the rhizosphere, which form a strong complex with Al^{3+} ions, i.e., Al^{3+}-organic acid complex, which then serves to be a nontoxic compound that does not enter or remain attached to the sites of nutrient uptake or division in the root (Dong et al. 2004). Organic acids are potent chelators of Al with hydroxyl and carboxyl groups that form a stable ring structure with Al^{3+} consisting of five or six bonds, thereby conferring protection from Al toxicity. Plants have a selective approach toward the exclusion of Al mainly based on the choice of organic acids (such as malate, citrate, etc.), magnitude of organic acid secretion, and the time course of exudation after exposure to Al toxicity (Ma et al. 2002; Famoso et al. 2010; Tovkach et al. 2013). In addition to organic acids, some phenolic compounds though less potent chelators to Al^{3+} but its electrophilic nature provides a reasonable capacity of chelation (Ofei-Manu et al. 2001; Ma et al. 2014).

Besides the mechanism of organic acid secretion, other exclusion mechanisms include the maintenance of the rhizosphere pH change, thereby preventing from the acidic nature which aggravates the Al toxicity; the apices of the root being the primary target of Al toxicity, plants in response to Al^{3+} regulate a physiological mechanism of release of root cap mucilage, i.e., gelatinous polysaccharide with high affinity for Al, thereby forming a barrier (Puthota et al. 1991; Archambault et al. 1996; Miyasaka and Hawes 2001). In addition, plants to limit the entry of Al release various other compounds such as phosphates and polypeptides from the roots which altogether act as an insulator leading to exclusion of Al entry into the plant (Tang et al. 2002; Ryan et al. 2009).

The cell wall and plasma membrane of the plant root surface also serves as the immediate plant organ to cope with the Al toxicity, with its negative charge due to the phosphate group of phospholipid bilayer in plasma membrane and carboxyl group of pectin in the cell wall usually maintained or neutralized by calcium (Ca) ions. Al^{3+} binds to this negative charge in replacement of Ca causing the major toxic effect of root inhibition (Maejima and Watanabe 2014). The percentage of phospholipid bilayer serving to be an important constituent of the plasma membrane serves also to be an important factor toward Al tolerance. Thus to tolerate the effect of Al toxicity, plants undergo the mechanism of membrane remodeling decreasing the negative charge by replacement with glycolipid or decrease in carboxyl content.

The molecular mechanism of Al tolerance includes the transcriptional regulation of Al tolerance genes and its upregulation by the transcription factors (Delhaize et al. 2004). Plants to cope with the Al toxicity induce expression of different genes responsible for various mechanisms of Al exclusion or detoxification (Shandilya and Tanti 2019; Yokosho and Ma 2015).

The molecular tolerance mechanism of plants is based mainly on the genes responsible for exclusion of Al^{3+}, i.e., through organic acid secretion or other secondary metabolites, and also its detoxification by sequestration or transport into vacuoles or other plant parts. Based on the genes responsible plants vary from species to species with some specific genes responsible in only some plant species. Genes responsible for Al tolerance belong mainly to two major families, i.e., the ALMT (aluminum-activated malate transporters) and MATE (multidrug and toxic compound extrusion) families. The genes belonging to the ALMT family mainly encode the transport of malate organic acids related to detoxification and sequestration, with *ALMT1* as the first Al tolerance gene to be identified in *Triticum aestivum* responsible for secretion of malate under Al toxicity (Sasaki et al. 2004). Similarly homologs of *ALMT1* have also been identified in other plant species such as *Arabidopsis*, rye, soybean, oilseed rape, and barley (Hoekenga et al. 2006; Collins et al. 2008; Gruber et al. 2010). In addition to malate secretion for Al detoxification, some plants regulate different genes responsible for other organic acid secretions such as for citrate, *AACT1* (aluminum-activated citrate transporter 1), and *FRDL* (ferric reductase defective 3). For example, in rice *OsFRDL4* and in barley *HvAACT1* are activated under Al toxicity. MATE genes such as *SbMATE* in sorghum encode secretion of a broad range of metabolites (e.g., citrate) responsible for mechanism of Al tolerance (Magalhaes et al. 2004).

Besides the genes responsible for organic acid or secondary metabolite secretion, several genes have also been identified for both external and internal detoxification of Al especially in rice and *Arabidopsis*, which are considered to be the model plants in modern research. Rice considered as the most tolerant cereal crop upregulates different genes responsible for Al tolerance; some of the genes identified are *STAR1* and *STAR2* (sensitive to Al rhizotoxicity 1, 2) that transport UDP-glucose that helps in the modification of the cell wall, resulting in the fixation of Al with the root cell wall (Yamaji et al. 2009). *Nrat1* (Nramp aluminum transporter 1) is responsible for transport of Al^{3+} inside the cell for sequestration into vacuoles, with the help of *OsAlS1*gene (aluminum sensitive 1) (Xia et al. 2010). *OsMGT1* (magnesium transporter 1) induces Al tolerance by increasing the uptake of Mg. Similarly in *Arabidopsis*, *AtALMT1*, *AtMATE*, *AtSTAR1*, *ALS3*, and *ALS1* are involved in Al tolerance (Larsen et al. 2005; Shandilya and Tanti 2020; Tokizawa et al. 2015).

Transcription factors include the factors which regulate expression level of the different tolerance genes, thereby inducing the mechanism of plant tolerance against Al toxicity under acidic conditions. Different transcription factors have been identified in different species which are homolog to each other and regulate different genes related to Al tolerance. STOP1 (sensitive to proton rhizotoxicity 1), C_2H_2 zinc finger protein transcription factor was first identified in *Arabidopsis* mutant, sensitive to Al^{3+} under low pH, which specifically up-regulates the Al tolerance genes in Arabidopsis such as *AtALMT1, AtMATE, ALS3* (aluminum sensitive 3) along with different other 40 genes. The expression of STOP1 is based on its posttranslational activation when exposed to Al^{3+} and low pH; ART1 (Al resistance transcription factor 1), another transcription factor for Al tolerance in rice with exception to STOP1, is activated based on its insensitivity to low pH (Huang et al. 2009). ART1 upregulates the expression level of about 31 genes of which *STAR1*, *STAR2*, *Nrat1*, *OsALS1*, *OsFRDL4*, *OsMGT1*, and *OsCDT3* have functionally characterized. ASR5 (abscisic acid, stress, and ripening 5) is also a transcription factor for Al tolerance in rice. ASR5 is the Al-activated factor that binds to the *STAR1* promoter to enhance its expression. ASR5 and ART1 may cooperatively interact in the upregulation of Al tolerance genes in rice. WRKY46 belonging to the WRKY domain containing family is a transcription factor identified in *Arabidopsis* that serves as the negative regulator of *AtALMT1* gene in *Arabidopsis*. It regulates the expression level of the *AtALMT1* gene by binding to its promoter regions as a repressor.

Al transporters mainly serve in the mechanism of internal detoxification of Al based on the genes responsible for Al uptake. In rice, plasma membrane-localized *OsNrat1* (Nramp Al^{3+} uptake transporter) gene which serves in the uptake and detoxification of Al^{3+}, along with the interaction of vacuolar ABC transporter gene, i.e., *OsAlS1*, induces the mechanism of vacuolar sequestration of Al, thereby leading to internal detoxification. Therefore, Nrat1 serves an important Al resistance function by lowering the levels of Al in the root cell wall via transport into and sequestration within the root cell. ABC transporters which include the ATP-driven pump also help in the transport of different metabolites or others such as surface lipid deposition or hormone transport against the toxic conditions. ABC transporters serve in detoxification based on the genes encoding it. In rice, *OsSTAR1* and *OsSTAR2* encode the ABC transporter domain that functions in the transport of UDP-glucose into the cell wall causing modification of cell wall and thereby limiting the accumulation of Al. In *Arabidopsis*, *AtALS3* encodes the transporter domain which induces the redistribution and hindrance to Al^{3+} uptake from the sensitive root apex (Larsen et al. 2007).

Aquaporins also serve as an important transporter in the mechanism of Al tolerance mainly in the Al accumulators such as buckwheat, hydrangea, and tea. In hydrangea, two aquaporin genes, *HmPALT1* and *HmVALT*, belonging to aquaporin family of NIP (nodulin 26-like intrinsic protein) and tonoplast intrinsic protein (TIP) encode special membrane and vacuolar Al uptake transporters for detoxification.

The development of transgenic plants with the incorporation of genes responsible for Al tolerance also helps against the extreme toxic Al under acidic conditions. In 2004, Delhaize et al. reported a significantly improved Al tolerance in transgenic barley with the incorporation of wheat malate transporter gene, i.e., *ALMT1*. Similarly the overexpression of gene responsible for tolerance based on the efflux or secretion of metabolites showed an increase in secretion of metabolites, thereby leading to Al tolerance. De La Fuente et al. (1997) also reported enhanced citrate efflux in transgenic tobacco with the overexpression of citrate synthase gene leading to improved root Al tolerance.

29.2.2 Arsenic (As) Toxicity

Arsenic is a ubiquitous toxic metalloid (Sharma 2012; Barringer and Reilly 2013) with its natural sources varying from soil, air, water to living organisms including human beings. Insecticides, food additives, etc., are also considered as anthropogenic sources of arsenic (Mandal and Suzuki 2002; Barringer et al. 2013). The recommended value of arsenic in drinking water provided by WHO (1993) is 10 μg/L. Arsenite (As III), arsenate (As V), monomethyl arsenic acid (MMAA), dimethyl arsenic acid (DMAA), arsenobetaine, and arsenocholine are the major species of arsenic found in the environment (Sharma 2012). Arsenate is the predominant species under aerobic environment, whereas arsenite predominates under anaerobic condition (Huang et al. 2010). The organic (methylated) forms of arsenic can be the consequences of different microbial activities (Mandal and Suzuki 2002; Kalita et al. 2018). On entering the food chain through drinking water or crops, arsenic can cause cancer of the skin, lungs, or kidneys and affects circulatory as well as nervous system of human beings (Sharma 2012).

Arsenic toxicity causes several morphological and anatomical changes in plants like wilting of leaves, reduced root and shoot length, decrease of root hairs, lack of pith differentiation, damage to epidermal and cortical cells, or damage to thylakoid membrane leading to cell death.

29.2.2.1 Arsenic Tolerance Mechanism in Plants

Plants to withstand the arsenic toxicity acquire various biochemical as well as signaling processes which help in the detoxification and aggravation of arsenic content and its toxicity.

Hyperaccumulation, phytochelatin complexation, and production of antioxidants are some mechanisms which have a very important role in detoxification of arsenic in plants. Some plants accumulate high level of arsenic in their bodies to reduce the arsenic-induced toxicity. The first reported arsenic hyperaccumulator is *Pteris vittata* containing high amount of arsenic in their fronds (Ma et al. 2001).

One mode of detoxification of arsenic, adopted by plants, is the binding of the thiol (-SH) group of glutathione (GSH) with the arsenite ions (Chen et al. 2017). Phytochelatins (PC) are some peptides derived from GSH which have a tendency to bind with the heavy metals (Sharma 2012). Arsenic exposure induces the synthesis of these PCs in plants. Toxicity of arsenic is reduced in the cytoplasm by chelating with PC which are then sequestered in the plant vacuoles at an acidic pH (5.5) (Sharma 2012; Chen et al. 2017). Some enzymatic antioxidants like glutathione reductase (GR), superoxide dismutase (SOD), ascorbic acid peroxidase (APX), and catalase (CAT) are produced in ferns and in higher plants for diminishing the damages of arsenic-induced oxidative stress. Some antioxidants which are nonenzymatic in nature, as, for example, ascorbic acid (AsA), carotenoids (car), and glutathione (GSH), are also stimulated in plants to combat the toxicity caused by arsenic (Sharma 2012).

Reduction of As(V) into As(III) in plant roots and the removal of these ions in the outer medium is another way of arsenic detoxification found in plants. For example, in rice, As(III) is effluxed by the aquaporins Lsi1 (OsNIP2;1). PvTIP4;1 of *Pteris vittata*, LjNIP5;1 of *Lotus japonicas*, and AtNIP3;1 and AtNIP5;1 of *Arabidopsis* are some other examples of bidirectional aquaporins which facilitate the transportation of AsIII. This kind of movement of arsenic serves as a passive process as the flux direction of the arsenite ions is dependent upon the concentration gradient (Chen et al. 2017).

In rice root formation of iron plaque is found which can adsorb or coprecipitate arsenic that facilitates its sequestration. Iron plaques are the result of the oxidation of Fe^{2+} to Fe^{3+} by the oxygen molecules entered radially into the roots from the soil via aerenchyma or due to the various microbial activities (Chen et al. 2017).

The gene *PvACR3* responsible for arsenite efflux into vacuole was isolated from *P. vittata* which has been found to provide arsenic tolerability to the plants (Indriolo et al. 2010). Dasgupta et al. (2004) mapped a major gene, *AsTol*, in the chromosome 6 and revealed their involvement in the arsenic tolerance. Mosa et al. (2012) demonstrated the presence of three plasma membrane intrinsic proteins, namely, OsPIP2;4, OsPIP2;6, and OsPIP2;7, in rice and their relation to the effects of arsenic. These transporters when overexpressed in transgenic *Arabidopsis* resulted in an increased As(III) tolerance.

On exposure with heavy metals like arsenic in plants, some signaling molecules are stimulated that perceive the stress-induced stimulus and thereafter transduce and expand it to the whole plant (Islam et al. 2015). Signaling through protein, calcium ion, and plant growth factors are some of the important mechanisms related to arsenic detoxification which are induced in plants during arsenic stress (Fig. 29.2).

In protein signaling, mitogen-activated protein kinases (MAPK) are reported to be activated on arsenic exposure. These kinases involve in a signaling cascade that transduce the signals through reversible phosphorylation. MAPKKK, MAPKK, and MAPK are the three kinds of protein kinases to be activated during signal transduction in a sequential manner (Islam et al. 2015). In *Arabidopsis thaliana* H_2O_2-mediated activation of MAP kinase enzymes has been reported by Hancock et al. (2001). A direct relationship between arsenic stress and MAPK protein regulation has been found by Rao et al. (2011) and Huang et al. (2012). Upregulation of one

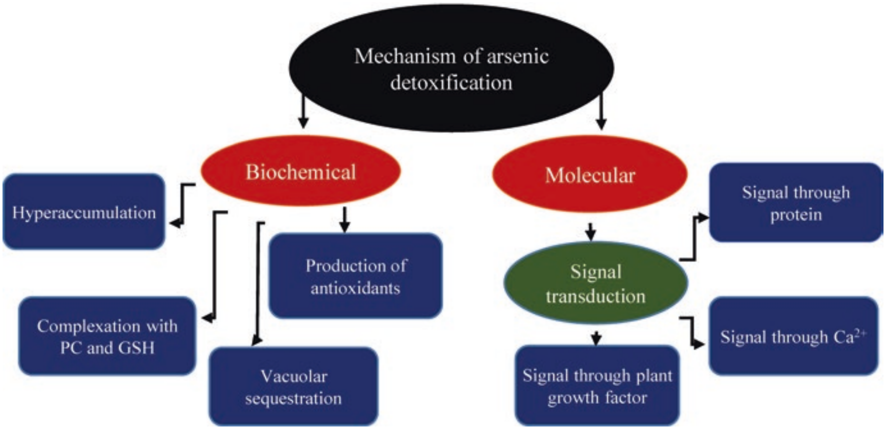

Fig. 29.2 Schematic representation of arsenic tolerance mechanism in plants

MAPK, eleven MAPKKKs, and ten PP2C after the application of arsenic was reported from rice (Huang et al. 2012).

Ca^{2+} ions play a role as secondary messengers in calcium signaling pathways in plant cells. As a response to the abiotic stresses, Ca^{2+} ion concentration varies which initiates a signaling pathway. In this pathway, the genes meant for the transportation of heavy metals and their tolerance are expressed after the interaction of Ca^{2+} ions and the calmodulin proteins (Islam et al. 2015). As reported by Das and Pandey (2010), on exposure with As(V), rice roots exhibited an increase in the Ca^{2+} ion concentration that can be a consequence of the regulation of proteins and kinases to detoxify arsenic. Similar kind of results also has been obtained in case of *Pteris vittata* (Li et al. 2006) and *Nicotiana plumbaginifolia* (Price et al. 1995).

Plant growth factors also participate in the signaling pathways as a response to the stress induced by arsenic. Synthesis of jasmonic acid is increased in plants during arsenic exposure which in turn induces the expression of genes responsive to stress like *CDC25* or *MAPK* or some other genes important in GSH metabolism (Xiang and Oliver 1998; Agrawal et al. 2003). In microarray studies of arsenic-stressed plants, upregulation of six JA, four ABA, and three ET signaling genes was reported (Huang et al. 2012).

29.3 Temperature Stress

Temperature stress is a major environmental stress that has devastating effect on various crop plants, thereby affecting the socioeconomic background and limiting the geographical distribution to a great extent. Based on the temperature condition it may be a cold/chilling or heat stress.

29.3.1 Effect of Cold/Chilling Stress on Plant

Cold stress may be of two different types, namely, chilling (0–15 °C) and freezing (<0 °C) (Sanghera et al. 2011). Plants growing in the subtropical regions are more sensitive to such stress than those grown in the temperate regions. Cold stress affects the photosynthetic ability of plants by interfering the fluorescence and chlorophyll content limiting crop yield and productivity. Moreover, there is an increased accumulation of reactive oxygen species (ROS) that weakens metabolism through oxidative damage. To establish and maintain a cell's overall integrity and functionality, enzymatic and nonenzymatic antioxidant defense system tends to increase to fight against such reactive oxygen species. ROS needs to be controlled by the cell as it can cause oxidative damage resulting into untimely death of the cell. Moreover, various transcriptional factors, proteins, and genes are responsible to induce tolerability during such stress conditions (Gill and Tuteja 2010) (Figs. 29.3 and 29.4).

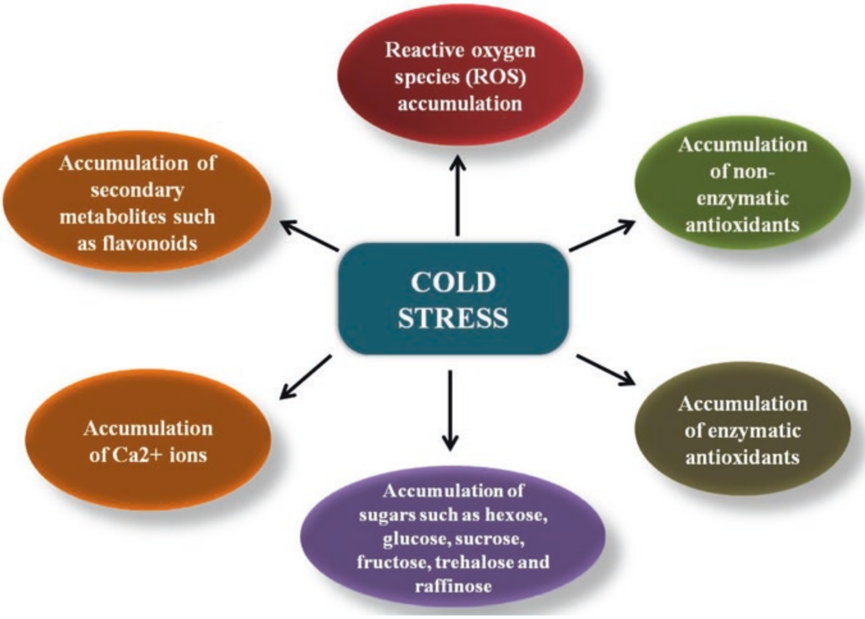

Fig. 29.3 Schematic diagram showing different biochemical changes that are induced as a result of plant acclimation during cold stress conditions

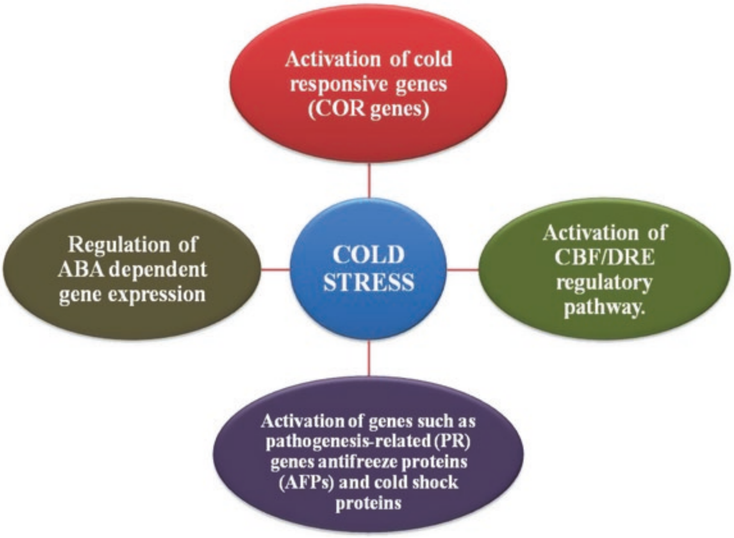

Fig. 29.4 Schematic diagram showing changes in plant body during cold stress acclimation at molecular level

The role of reactive oxygen species (ROS) is very crucial in cold stress acclimation of plants. ROS being chemically reactive molecules can readily react with various DNA, proteins, and lipids in the cell. ROS are produced through the activity of NADPH oxidases that trigger various downstream stress pathways and defense mechanisms (You and Chan 2015). They allow the signaling of various by-products including hydrogen peroxide production, lipid peroxidation and proline accumulation, and antioxidant enzymes such as catalase, superoxide dismutase, AsA peroxidase, GSH reductase, guaiacol peroxidase, etc. (Suzuki and Mittler 2006). Further, reports revealed that there was significant increase in the contents of soluble nonenzymatic antioxidants such as GSH and AsA. These by-products thus in return scavenge the activity of ROS in the cell. However, the exact mechanism of ROS, along with the enzymatic and nonenzymatic antioxidant defense machinery, is still not known. Yet according to some reports, proline acts as reservoirs of nitrogen and carbon and it prevents important enzymes of cells from degradation. It also removes the extra H^+ ions produced as a consequence of abiotic stress and maintains the overall optimum pH and oxidative respiration inside the cytosol (Zhang et al. 2014) (Fig. 29.5).

Apart from the reactive oxygen species, various enzymatic and nonenzymatic antioxidant mechanisms including different secondary metabolites also play a vital role during stress acclimation in plants. Secondary metabolites such as flavonoids have been reported to accumulate in the leaves and stems of plants during cold stress conditions. Chalcone synthase and phenylalanine ammonia-lyase are the precursors of flavonoid synthesis that are by-products of phenylpropanoid pathway,

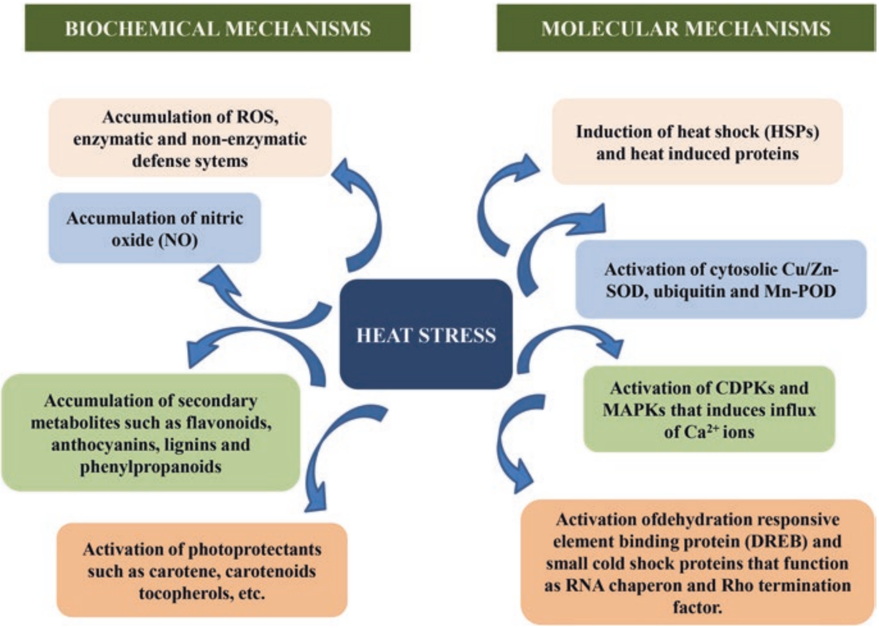

Fig. 29.5 Schematic diagram showing the mechanism of heat stress tolerance in plants

which gets triggered during such stress conditions. During cold stress conditions in plants, various soluble sugars such as raffinose, trehalose, hexose, sucrose, fructose, etc., get accumulated, thereby serving as osmoprotectants to maintain the osmotic potential in the plant (Theocharis et al. 2012).

Besides this, Ca^{2+} ions are one of those primary mechanisms that are associated with cold stress acclimation in plants. Calcium plays a very vital part as the mediator of plant growth regulation and their responses to various stimuli developed. They are in some way or the other known to be involved in the production of ROS. However, the exact mechanism is still unknown. Plasma membrane stiffening is induced by cold stress resulting in rearrangement of actin cytoskeleton. This leads to the influx of Ca^{2+} ions through the Ca^{2+} channels resulting in an increase in cytosolic Ca^{2+} ions which is a mechanism involving cold acclimation in plants. These may further activate a downstream cascade of cold sensing and response genes (Theocharis et al. 2012).

In addition to biochemical processes, various molecular mechanisms, such as change in gene expression patterns, role of various transcription factors, activation of various regulatory pathways, activity of RNA-binding proteins and cold shock proteins, and various posttranscriptional and posttranslational regulations, are prevalently occurred under cold stress. Some of the important molecular mechanisms of cold stress tolerance are discussed below.

During cold stress conditions, gene expression alteration occurs leading to the formation of proteins which confers cold tolerance to plants. This occurs through change in existing protein that will transduce signals of cold stress responses. One such example that can be cited is of HOS15 protein of *Arabidopsis*, which alters chromatin modification; thus controlling gene expression patterns is associated with cold stress tolerance (Shinozaki and Shinozaki 2006; Zhu et al. 2015).

According to reports, cold responsive genes (COR) are known to be expressed in plants during their acclimation process under cold stress (Yadav 2010). These genes have been cloned variously and can be categorized as cell protective proteins during environmental stress conditions, gene expression regulatory proteins during adaptive responses to environmental stimuli, and genes that mediate physiological and biochemical changes during cold stress condition. The products of such COR genes are known to have crucial roles in plant tolerance to cold stress conditions. However, these COR genes are activated as a result of overexpression of two CBF (C-repeat binding factor) genes, namely, *CBF1* and *CBF2* genes. This CBF gene gets accumulated in plants within just 15 min of exposure to cold stress. The CBFs bind to the *cis*-elements of COR genes at its promoter region and activate those (Chinnusamy et al. 2007). However, the activation is also associated with DREs (drought-responsive elements). Therefore, this mechanism or pathway of cold tolerability can also be termed as the CBF/DRE regulatory pathway (Suzuki and Mittler 2006). As discussed earlier, the accumulation of flavonoids during cold stress condition is also due to the result of molecular mechanism of stress tolerance. It is regulated through transcription factor PAP2 of MYB family. Under stress conditions in plants, transcription factors of MYB family are also known to regulate the ABA-dependent gene expression. Abscisic acid (ABA) offers its role as secondary signal in signal transduction process during cold stress. It has a vital role in ROS scavenging by enhancing the activity of antioxidant defense system. It also enhances the activity of the CBF genes. Some cold-induced genes such as pathogenesis-related (PR) genes and synthesis of antifreeze proteins (AFPs) are known to play vital roles as cryoprotectants in plants during cold stress conditions. However, the exact mechanism and the synthesis process is not known. Dehydrin is one of the well-known AFPs or cryoprotectant. Besides, certain cold shock proteins, such as *Arabidopsis* Cold Shock Domain Protein 3 (AtCSP3), are reported to involve during cold acclimation in plants under cold stress conditions (Theocharis et al. 2012).

29.3.2 Effect of Heat Stress on Plant

Heat stress like most other abiotic stresses is one of the most devastating stresses that alter plant's physiological and biochemical metabolism, germination, growth and development, reproduction, and ultimately yield loss (Setiyono et al. 2018). Usually temperatures exceeding above 35–40 °C are considered as heat stress for plants. During such stress conditions plants tend to show various changes such as impaired photosynthesis, generation of a large amount of reactive oxygen species (ROS), enzymatic and nonenzymatic antioxidants, and alterations of gene expressions. To overcome such stress conditions, plants undergo a cascade of mechanisms at their physiological, biochemical, and molecular levels (Hasanuzzaman et al. 2013). However, in the present day, application of protective such as proline, as osmoprotectants; plant hormones such as gibberellic acid, abscisic acid, brassinosteroids, jasmonic acids, etc.; signaling molecules such as nitric acid, polyamines, and trace elements; and various nutrients such as nitrogen, potassium, calcium, phosphorus, etc., has been found to be effective to the underlying damage caused to plants under heat stress.

High temperature responses vary with different plants, degree of temperature, and duration. Heat stress may be the reason of alteration of the structure and function of certain underlying proteins, RNA, enzymatic reactions, and also cytoskeleton structures (Upadhyaya et al. 2017). In this article, various phenomena that take place inside a plant body during stress conditions as a part of plant's defense system have been discussed at their biochemical and molecular levels.

29.3.2.1 Biochemical Mechanism of Heat Stress Tolerance in Plants

Heat stress might uncouple certain metabolic pathways and enzymes that lead to the accumulation of ROS such as singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet-}$), hydroxyl radical ($OH^\bullet$), and hydrogen peroxide (H_2O_2) which are harmful for the basic metabolism in a plant body. Generations of ROS occur in reaction centers, photosystem I (PSI), and photosystem II (PSII) and are considered as the primary sites of ROS activities. Besides, ROS generation also occurs in cell organelles such as mitochondria, chloroplast, or peroxisomes. To overcome the high rate of accumulation of these ROS, various antioxidant defense mechanisms are known to play a crucial role on this regard such as hydrogen peroxide production, lipid peroxidation, and proline accumulation. The antioxidant defense mechanisms include both enzymatic (catalase (CAT), AsA peroxidase (APX), superoxide dismutase (SOD), peroxidase (POX), and GSH reductase (GR) and nonenzymatic (synthesis of AsA and GSH) defense systems. However, according to reports, enzyme activity in plants was highest at temperatures ranging from 35 to 40 °C (tolerant varieties) and at 30 °C (susceptible varieties). Moreover, nitric oxide (NO) is known to activate the underlying ROS scavenging enzymes that induce thermo-tolerance.

During heat stress conditions, apart from ROS accumulation and scavenging activity, certain well-known secondary metabolites also get accumulated such as flavonoids, anthocyanins, lignins, and phenylpropanoids which are by-products of the phenylpropanoid pathway produced as a result of the enzymatic activity of phenylalanine ammonia-lyase. This is one of the major steps occurring in plant cells during acclimation process under heat stress.

Under heat stress, certain photoprotectants play vital roles in plants during its acclimation process. They may include carotene belonging to the xanthophylls group, tocopherols belonging to terpenoid group that helps in stabilizing the lipid phase of thylakoid membranes. Various hormones have vital roles to play in plant's growth and development under high temperature stress, some of which may include salicylic acid and ethylene.

29.3.2.2 Molecular Mechanism of Heat Tolerance in Plants

Heat shock proteins (HSPs) and heat-induced proteins are induced as a result of heat stress in a plant body. There are three different classes of proteins induced under such unfavorable conditions. Of which two of them belong to HSPs, namely, HSP70 and HSP90, and proteins of lower molecular weight of about 15–30 kDa. Some of the HSPs are accumulated in the cytosol at low temperatures (27 °C) and some at high temperatures (43 °C). However accumulation of such proteins occurs in the chloroplast at moderate temperatures (~37 °C). These are nuclear-encoded HSPs and the gene for such HSPs is Hsa32, 32 kDa protein, which is cloned in tomatoes. Because of their thermo-tolerability, HSP expression is mediated by the action of heat treatment in association with the conserved HSEs (heat shock proteins), present in the promoter region of HSGs (heat stress granules), resulting in transcription in accordance to heat stress. They are cis-acting elements (HSE) which comprise of the nucleotide sequence (5'-AGAANNTTCT-3′), which is palindromic in nature that serves as binding site and recognition of transcription factors associated with heat shock or can be simply termed as heat shock factors (HSFs). HsfA1a and HsfA2 have been reported to be the major regulator heat stress factor respectively in plants induced during heat stress. HSPs are the most important factor associated with thermo-tolerance and reports suggest that nearly 19 and 14 heat shock factors have been identified in *Arabidopsis* and *Oryza sativa*, respectively. Apart from

HSPs, various other proteins such as cytosolic Cu/Zn-SOD, Mn-POD, and ubiquitin are activated under heat stress conditions in plants (Wahid et al. 2007).

Sometimes heat induces the influx of Ca^{2+} ions, which is regulated through the activity of CDPKs (calcium-dependent protein kinases) and MAPKs (mitogen-activated protein kinases), which in turn activates antioxidants and osmolytes that scavenge stress-induced accumulation of ROS species (Wahid et al. 2007). Some DREB proteins (dehydration-responsive element binding protein), such as DREB2A and DREB2B belonging to AP2/ERF family, are induced as a result of such stresses (Licausi et al. 2013). However, in some plants proteins such as glucose-1-phosphate adenylyltransferase that are associated with starch synthesis were downregulated under high temperature stress (Koussevitzky et al. 2008). Besides, some of the regulatory proteins, such as small cold shock proteins, are regulated in some under heat stress conditions which would function as RNA chaperons and Rho termination factor (Jagadish et al. 2010).

29.4 Submergence Stress

With the changing global climate its effect on crop production and yield has been considered as an important issue which increases the threat of water stress (Tuba and Lichtenthaler 2007). Whenever the ratio of soil water surface layer exceeds more than 20% than the field's carrying capacity, it leads to the waterlogging condition (Agrawal et al. 2003; Nilsen and Orcutt 1996). Submergence stress may develop due to several direct and indirect factors like improper irrigation practices, global warming and anthropogenic activities, and sometimes meteorological component which contribute to alteration of plant metabolism and ecogeographical distributions (Voesenek et al. 2006). Floods are the major constraints to crop production, affecting the availability of oxygen, i.e., increase in BOD, which leads to serious physiological damages within the cell as oxygen is the vital element for carrying out all the important physiological phenomena. A prolong or transient flash floods can also lead to partial or complete submergence that directly can inhibit crop normal growth and yield (Kato et al. 2014). In recent years, many reports have indicated that complete submergence reduces the fundamental component of a plant that plays a significant role in plant growth, viz., internal oxygen availability, sugar status, carbon dioxide, and light for photosynthesis that ultimately influences its survival (Bailey-Serres and Voesenek 2010; Winkel et al. 2013; Sakagami et al. 2013a, b). The major morphophysiological modifications shown under submergence stress are leaf elongation, reduction in chlorophyll content, low-carbohydrate reserve storage, alteration in relative water content, and a huge change in its biochemical profile (Ito et al. 1999; Ram 2002; Jackson and Ram 2003) (Fig. 29.6).

Quiescence and elongation were the two major strategies adapted by rice plants by which plants control their integrity depending upon the nature of flooding (Luo et al. 2011). Low-carbohydrate metabolism under submergence stress is an important trait in flash flood tolerance crops, and the "quiescence strategy" is characterized

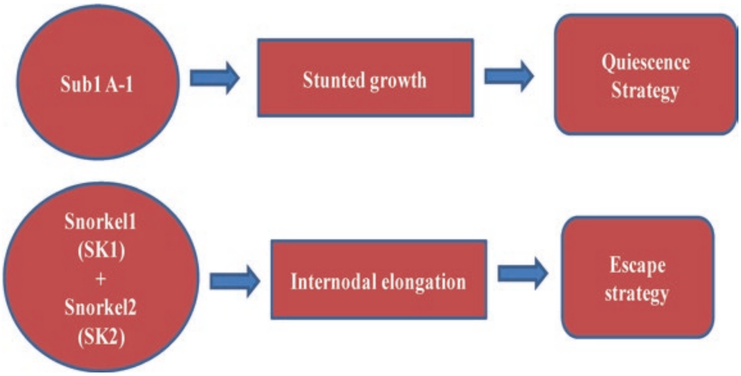

Fig. 29.6 Schematic diagram representing two major strategies adapted by rice plants under submergence

by slow growth that is supposed to conserve energy and carbohydrates (Singh et al. 2001). Some crops like rice cultivars show elevated shoot elongation in response to submergence which is termed as "escape strategy"; this enables rice plants to perform aerobic metabolism and photosynthetic fixation of CO_2 under long-term submergence in deep-water condition (Ram 2002; Jackson and Ram 2003). However, flash floods that cause short-term submergence rapid leaf elongation adversely affect submergence tolerance (Jackson 2008; Chaturvedi 1995; Setter and Laureles 1996, 1996; Kawano et al. 2009). Yamada (1959) reported that plants debilitated total carbohydrate in the leaves and roots during submergence and the carbohydrate metabolism during submergence correlates with flash flood tolerance (Palada 1972; Chaturvedi 1995).

Under submerged condition with low oxygen availability, photosynthesis and respiration are restricted, leading to an energy crisis, production of toxic products and the accumulation of reactive oxygen species (ROS) and peroxides singlet oxygen molecules in cells (Licausi and Perata 2009; Pucciariello et al. 2012; Yang and Hong 2015, b). Several studies have focused on the important role of ROS during hypoxia signaling under full submergence conditions (Baxter et al. 2014; Fukao et al. 2011; Liu et al. 2015; Yang and Hong 2015). Out of all the ROS, H_2O_2 is one of the foremost stable non-radical reactive oxidative species, produced in the compartment of chloroplast. Although peroxisomes were reported as the main site of intracellular H_2O_2 production, production of hydrogen peroxide in less amount is reported during photorespiration and in mitochondria by the process of electron transport (ETC) (Bhattacharjee and Saha 2014; Del Río et al. 2006). It was reported that there was an increase in hydrogen peroxide level in both biotic and abiotic stresses like pathogen attack, UV radiation, drought, submergence, chilling, and wounding (Sharma et al. 2012; Ślesak et al. 2007). Hydrogen peroxide along with the other ROS is a good indicator of oxidative stress. For the suppression of dangerous H_2O_2 level in cell H_2O_2 scavenging mechanism is vital through the balancing of GSH peroxidase (GPX), AsA peroxidase (APX), and catalase (CAT) activities (Apel and Hirt 2004).

The antioxidant protection mechanism system can be divided into two branches, enzymatic and nonenzymatic components. The enzymatic antioxidants include catalase (CAT), superoxide dismutase (SOD), guaiacol peroxidase (GPX), and enzymes of AsA-glutathione (AsA-GSH) cycle such as ascorbate peroxidase (APX), dehydro-AsA reductase (DHAR), mono-dehydro-AsA reductase (MDHAR) and GSH reductase (GR), etc. (Roy et al. 2009; Gill and Tuteja 2010). The nonenzymatic antioxidants are membrane-bound lipid or water-soluble molecules that include glutathione, proline, ascorbate, carotenoids, flavonoids, and tocopherols.

Genetic studies reported the major QTL (quantitative trait loci) submergence 1 (sub1) located on rice chromosome 9 is the key contributor for 70% of phenotypic variation that results in submergence tolerance of the rice genotypes. Sub1 is an ethylene responsive factor (ERF) like transcriptional regulator that induces internodal elongation of shoot; controls carbohydrate metabolism and degradation of chlorophyll, etc. (Fukao et al. 2006; Xu et al. 2006); and, thus, controls survival and recovery of the tolerant plants after the submergence (Pucciariello and Perata 2013; Perata and Voesenek 2007). In rice it has been reported that the Sub1 QTL consist of a group of three genes, Sub1A, Sub1B, and Sub1C (Xu et al. 2006). *SUB1A*, responsive transcription factor (AP2/ERF), plays a key role in “quiescent strategy” by decreasing the cellular gibberellin levels. On the other hand, another gene *SNORKEL 1* and *SNORKE 2*, encoding ethylene responsive transcription factors, plays a significant role in “elongation strategy” in deep-water or floating rice by enhancing gibberellin responses which induce rapid internode elongation (Xu et al. 2006; Hattori et al. 2009).

29.5 Drought Stress

With increased change in world global climatic condition drought stress pronounced as the most prevalent environmental factor limiting crop productivity. Water deficit condition affects the seed survivor rate and increases the post-pollination embryo abortion rate and as a whole decreases the yield. Morphological modification as a result of a prolonged water deficit condition that leads to its yield potential includes smaller leaves, premature flowering, and a long anthesis-silking interval (Bruce et al. 2002; Nahar et al. 2016, 2018a, b) and physiological modification like nutrient absorption capacity, crop growth and development, molecular alteration, distribution, etc. (Zhao et al. 2009). Plants growing under water stress environment also go through some important physiological responses, including decreased cell turgidity, leaf rolling, and decrease in CO_2 level which leads to a decrease in photosynthetic efficiency and lowering of chlorophyll contents. Photosynthetic and gas exchange responses are the most sensitive to water deficits (Chutia et al. 2012; Qin et al. 2007). The plant response against the stress can be varying depending on the speed and magnitude of stress. The level of adaptation and injuries during the stress condition and after the distress condition gives a good reference of the stress severity (Fig. 29.7).

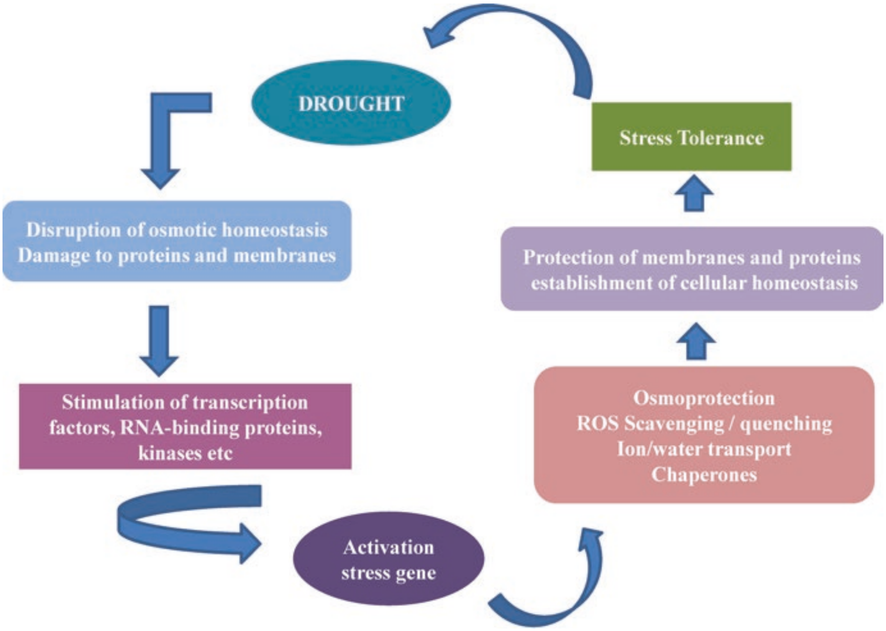

Fig. 29.7 Biochemical adaptation in response to drought stress in plants

To combat against the drought stress, plants adapt different mechanisms such as accumulation of high concentrations of osmoregulators in the cytoplasm against drought stress (Dennison et al. 2001; Egilla et al. 2001; Chemikosova et al. 2006), altered metabolic pathways of photosynthesis, respiration, sugar metabolism, hormone synthesis, and other necessary physiological processes as well as increased induction of metabolomic solutes, such as proline, betaine, sucrose, and fructose to fight against the drought stress (Wang et al. 2012; Yasar et al. 2006).

Under stress condition reactive oxygen species (ROS), also called active oxygen species (AOS) or reactive oxygen intermediates (ROI), are produced that are the result of the partial reduction of atmospheric O_2. Cellular ROS can be divided into different groups, singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\bullet-}$), and the hydroxyl radical ($HO^{\bullet}$), each with a distinct half-life. ROS are extremely reactive, especially singlet oxygen and the hydroxyl radical; they oxidize multiple cellular biocomponents that lead to cellular death (Mittler 2002; Nahar et al. 2018a, b). Although ROS also plays an important role in signaling pathway of different process, increase in the level of ROS than normal is injurious for the plant. Both abiotic and biotic stresses trigger oxidative stress in plants and their capacity to manage the level of oxidants is directly correlated with plant tolerability. Like other abiotic stresses drought also imposes the induction of reactive oxygen species which immediately changes plant redox potential (Noctor et al. 2002). It has been reported that chloroplast is the major site for ROS generation. Under stress condition the photosynthetic electron transport system becomes overactive that alters the reduction of oxygen to different ROS (Foyer et al. 1994; Foyer and Noctor 2003).

Adaptation of plants under water deficit condition is maintained under both the cellular and molecular level. Drought stress imposes release of a major phytohormone, i.e., abscisic acid (ABA), which is responsible for closing of stomata and expression of drought stress genes. It has been reported that the presence of two important transcriptional activator factors is abscisic acid (ABA)-dependent signaling pathway and ABA-independent regulatory pathway. ABA-dependent regulatory network consists of ABA-responsible cis-element binding factor (AREB/ABI). The AREB/ABF transcriptional factor has four conserved domains and a bZIP domain having snRK2 phosphorylation sites. AREB/ABF phosphorylation which is a master transcriptional activator triggers the binding of AREB/ABF to ABA-responsive cis-elements. A study conducted on maize reveals the genome-wide expression generated by drought stress includes various transcriptional factors, viz., NAC, WRKY and VQ, bZIP, and CCH-type zinc finger families (Ying et al. 2012; Bogamuwa and Jang 2014; Mao et al. 2015; Song et al. 2016).

29.6 Nutrient Deficiency

Plants require essential mineral nutrients in a definite amount for their proper growth and function. Elevation or depletion in the content of the essential nutrients may cause some abnormalities in plants. Nutrient deficiency occurs when the essential nutrient requirement is present in a lesser amount than the amount required (McCauley et al. 2009). The essential nutrients may be of two kinds: macronutrients and micronutrients. The concentration of macronutrients in plants is found to be more than 0.1% of the dry tissue weight. These nutrients include nitrogen (N), potassium (K), sulfur (S), phosphorus (P), calcium (Ca), and magnesium (Mg). On the other hand, micronutrients are present at a concentration less than 0.01% of the dry tissue weight. The micronutrients include boron (B), copper (Cu), iron (Fe), manganese (Mn), zinc (Zn), chlorine (Cl), molybdenum (Mo), and nickel (Ni). Plant growth and crop yields are affected by deficiency of these mineral elements, which include both the macro- and microelements (White and Brown 2010).

29.6.1 Phosphorus Deficiency

Phosphorus (P) is available to plants as orthophosphate ions ($HPO_4^{2\,-}$, H_2PO^{4-}). Phosphorus constitutes an important component of nucleic acids that plays a very important role in maintaining different developmental and metabolic processes of the plants. It helps to store energy in the form of ATP (adenosine triphosphate) in photosynthesis and respiration. Metabolically active sites of plants like young shoots and root tips contain highest concentration of phosphorus. The initial symptom of phosphorus deficiency is stunted growth. The first symptom of phosphorus deficiency is the dark to blue-green coloration of older leaves which may become purplish in severe cases. Low availability of phosphorus may result into poor seed production and affect fruit development (Uchida 2000; Hinsinger 2001).

Phosphorus utilization efficiency (PUE) is the capability of crops to survive in phosphorus-deficient condition (Aziz et al. 2014). Plants adopt several morphological, biochemical, and physiological modifications to overcome the challenge of phosphorus inefficiency. As an adaptation to the phosphorus deficiency, plants may develop various morphological changes in the root architecture (Trachsel and Kaeppler 2011; Aziz et al. 2014). Under P-deficient condition for the better absorption of limited available P, plants increase their root surface area (Gahoonia and Nielsen 1998; Aziz et al. 2014). Accumulation of more assimilate in the region which is involved in the phosphorus absorption is another important adaptation adopted by plants. Mollier and Pellerin (1999) demonstrated an increase in root/shoot ratio of maize under P-deficient condition which results in more translocation of carbohydrates in roots.

Plants may excrete various organic compounds like acetic acid, lactic acid, fumaric acid, succinic acids, and oxalic acid to acquire soluble phosphorus during the challenge of phosphorus deficiency (Wissuwa 2003; Grierson 1992). Organic anions compete with Pi and form complexes with elements like Fe, Al, Ca, etc., which help to increase the amount of free inorganic phosphorus in soil (Aziz et al. 2014). Increased exudation of citric acid in rice and *Brassica napus* was reported by different workers (Kihara et al. 2003; Aziz et al. 2014). In the root zone of *B. napus* increased malic acid secretions were also reported (Hoffland et al. 1989, Aziz et al. 2014). Mycorrhiza can enhance the soil volume which in turn enhances the uptake of phosphorus (P) acquisition of plant roots (Gerke et al. 2000; Richardson and Simpson 2011; Lambers et al. 2015).

Along with the various physiological and biochemical mechanisms associated with the process of P deficiency, several transcription factors and genes are also associated in the mitigation of the problem of phosphorus starvation. Phosphorus starvation responsive (PSR) micro-RNAs are involved in the signaling mechanism and regulation of homeostasis of inorganic phosphate under deficient condition (Kuo and Chiou 2011). Ribonuclease (RNS) enzymes are responsible for the release of phosphorus from organic sources and make them available for the plants for absorption. During phosphorus starvation upregulation of the genes encoding RNS1 is upregulated (Bariola et al. 1994). Phosphorus uptake 1 (Pup1), an important quantitative trait loci associated with the stimulation of root growth, increasing P-uptake and grain yield is located on the chromosome 12 of rice. This helps in improving the tolerability of plants to soil phosphorus insufficiency and increasing the PUE (Wissuwa and Ae 2001; Shane et al. 2006; Li et al. 2008; Ramaekers et al. 2010; Chin et al. 2010; Gamuyao et al. 2012; Aziz et al. 2014).

29.7 Conclusion

Plants being the terrestrial living organisms undergo a series of environmental changes due to various abiotic factors. Therefore, plants to confront or cope with the various stress factors develop various mechanisms of tolerance including both the biochemical and molecular strategies. As discussed above, various genes undergo expression in different levels and various biochemical compounds get released to confront the changes. The natural metabolic pathways occurring in plant undergo changes producing different low molecular weight metabolites which serve as an important factor for plants to escape stress. Understanding the level of gene expression and localization of genes expressing under a particular environmental stress factor may serve a significant role to cope stress. In the present days, metabolomics has served to be an important subject of study for the plant tolerance as the metabolites released and the pathways it undergo may provide a detailed information on the plant ability to tolerate sudden environmental changes that are increasing at an alarming rate. As such compounds may be introduced to plants externally for future ability of tolerance. In addition to study of various biochemical and molecular mechanisms in a particular plant species, understanding the landrace diversity and its tolerance capability, it would change the scenario of plants against environmental factors for tolerance.

References

Agrawal GK, Tamogami S, Iwahashi H, Agrawal VP, Rakwal R (2003) Transient regulation of jasmonic acid-inducible rice MAP kinase gene (*OsBWMK1*) by diverse biotic and abiotic stresses. Plant Physiol Biochem 41:355–361

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399

Archambault DJ, Zhang G, Taylor GJ (1996) Accumulation of Al in root mucilage of an Al-resistant and an Al-sensitive cultivar of wheat. Plant Physiol 112:1471–1478

Awasthi JP, Saha B, Regon P, Sahoo S, Chowra U, Pradhan A, Panda SK (2017) Morpho-physiological analysis of tolerance to aluminum toxicity in rice varieties of north East India. PLoS One 12(4):e0176357. https://doi.org/10.1371/journal.pone.0176357

Aziz T, Sabir M, Farooq M, Maqsood MA, Ahmad HR, Warraich EA (2014) Phosphorus deficiency in plants: responses, adaptive mechanisms, and signaling. In: Hakeem K, Rehman R, Tahir I (eds) Plant signaling: understanding the molecular crosstalk. Springer, New Delhi, pp 133–148

Bailey-Serres J, Voesenek LA (2010) Life in the balance: a signaling network controlling survival of flooding. Curr Opin Plant Biol 13(5):489–494

Bariola PA, Howard CJ, Taylor CB, Verburg MT, Jaglan VD, Green PJ (1994) The *Arabidopsis* ribonuclease gene *RNS1* is tightly controlled in response to phosphate limitation. Plant J 6(5):673–685

Barringer JL, Reilly PA (2013). Arsenic in Groundwater: a summary of sources and the biogeochemical and hydrogeologic factors affecting arsenic occurrence and mobility. In: Current perspectives in contaminant hydrology and water resources sustainability. Chapter 4

Baxter A, Mittler R, Suzuki N (2014) ROS as key players in plant stress signalling. J Exp Bot 65(5):1229–1240

Bechtold U, Field B (2018) Molecular mechanisms controlling plant growth during abiotic stress. JExp Bot 69:2753–2758

Bhattacharjee S, Saha AK (2014) Plant water-stress response mechanisms. In: Gaur RK, Sharma P (eds) Approaches to plant stress and their management. Springer, India, pp 149–172

Bogamuwa SP, Jang JC (2014) Tandem CCCH zinc finger proteins in plant growth, development and stress response. Plant Cell Physiol 55(8):1367–1375

Bona L, Wright RJ, Baligar VC, Matuz J (1993) Screening wheat and other small grains for acid soil tolerance. Landsc Urban Plan 27(2–4):175–178

Bray EA, Bailey-Serres J, Weretilnyk E (2000) Responses to abiotic stress. In: Gruissem W, Jones R (eds) Biochemistry & molecular biology of plants. American Society of Plant Physiologists, Rockville, pp 1158–1203

Bruce WB, Edmeades GO, Barker TC (2002) Molecular and physiological approaches to maize improvement for drought tolerance. J Exp Bot 53(366):13–25

Carver BF, Ownby JD (1995) Acid soil tolerance in wheat. Adv Agron 54:117–172

Chaturvedi GS (1995) Physiological basis and screening for tolerance for flash flooding. In: Ingram KI (ed) Rainfed lowland rice agriculture research for high risk environment. IRRI) PP, Manila, pp 79–96

Chemikosova SB, Pavlencheva NV, Gur'yanov OP, Gorshkova TA (2006) The effect of soil drought on the phloem fiber development in long-fiber flax. Russ J Plant Physiol 53:656–662

Chen Y, Han Y-H, Cao Y, Zhu Y-G, Rathinasabapathi B, Ma LQ (2017) Arsenic transport in rice and biological solutions to reduce arsenic risk from rice. Front Plant Sci 8:268

Chin JH, Lu X, Haefele SM, Gamuyao R, Ismail A, Wissuwa M, Heuer S (2010) Development and application of gene-based markers for the major rice QTL phosphorus uptake 1. Theor Appl Genet 120:1073–1086

Chinnusamy V, Zhu J, Zhu JK (2007) Cold stress regulation of gene expression in plants. Trends in Plant Sci 12(10):444–451

Chutia J, Borah SP, Tanti B (2012) Effect of drought stress on protein and proline metabolism in seven traditional rice (Oryza sativa Linn.) genotypes of Assam, India. J Res Biol 2(3):206–214

Collins NC, Shirley NJ, Saeed M, Pallotta M, Gustafson JP (2008) An ALMT1 gene cluster controlling aluminum tolerance at the Alt4 locus of rye (*Secale cereale* L.). Genetics 179:669–682

Das R, Pandey G (2010) Expressional analysis and role of calcium regulated kinases in abiotic stress signaling. Curr Genomics 11:2–13

Dasgupta T, Hossain SA, Meharg AA, Price AH (2004) An arsenate tolerance gene on chromosome 6 of rice. New Phytol 163:45–49

De la Fuente JM, Ramı́rez-Rodrı́guez V, Cabrera-Ponce JL, Herrera-Estrella L (1997) Aluminum tolerance in transgenic plants by alteration of citrate synthesis. Science 276(5318):1566–1568

Del Río LA, Sandalio LM, Corpas FJ, Palma JM, Barroso JB (2006) Reactive oxygen species and reactive nitrogen species in peroxisomes. Production, scavenging, and role in cell signaling. Plant Physiol 141:330–333

Delhaize E, Ryan PR, Hebb DM, Yamamoto Y, Sasaki T, Matsumoto H (2004) Engineering high-level aluminum tolerance in barley with the ALMT1 gene. Proc Natl Acad Sci 101(42):15249–15254

Dennison KL, Robertson WR, Lewis BD, Hirsch RE, Sussman MR, Spalding EP (2001) Functions of AKT1 and AKT2 potassium channels determined by studies of single and double mutants of Arabidopsis. Plant Physiol 127(3):1012–1019

Dong D, Peng X, Yan X (2004) Organic acid exudation induced by phosphorus deficiency and or aluminium toxicity in two contrasting soybean genotypes. Physiol Plant 122(2):190–199

Egilla JN, Davies FT, Drew LMC (2001) Effect of potassium on drought resistance of *Hibiscusrosasinensis* CV. Leprechaun: plant growth, leaf macro-and micronutrient content and root longevity. Plant Soil 229:213–224

Famoso AN, Clark RT, Shaff JE, Craft E, McCouch SR, Kochian LV (2010) Development of a novel aluminum tolerance phenotyping platform used for comparisons of cereal aluminum tolerance and investigations into rice aluminum tolerance mechanisms. Plant Physiol 153:1678–1691

Foyer CH, Noctor G (2003) Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. Plant Physiol 119:355–364

Foyer CH, Descourvieres P, Kunert KJ (1994) Protection against oxygen radicals: an important defence mechanism studied in transgenic plants. Plant Cell Environ 17:507–523

Fukao T, Xu K, Ronald PC, Bailey-Serres J (2006) A variable cluster of ethylene responsive-like factors regulates metabolic and developmental acclimation responses to submergence in rice. Plant Cell 18:2021–2034

Fukao T, Yeung E, Bailey-Serres J (2011) The submergence tolerance regulator SUB1A mediates crosstalk between submergence and drought tolerance in rice. Plant Cell 23(1):412–427

Gahoonia TS, Nielsen NE (1998) Direct evidence on participation of root hairs in phosphorus (^{32}P) uptake from soil. Plant Soil 198:147–152

Gamuyao R, Chin JH, Pariasca-Tanaka J, Pesaresi P, Catausan S, Dalid C, Slamet-Loedin I, Tecson-Mendoza EM, Wissuwa M, Heuer S (2012) The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. Nature 488:535–539

Gerke J, Lutz B, Romer W (2000) The quantitative effect of chemical mobilization by carboxylate anions on P uptake by a single root I. The basic concept and determination of soil parameters. J Plant Nutr Soil Sci 163:207–212

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 48:909–930

Grierson PF (1992) Organic acids in the rhizosphere of *Banksiaintegrifolia* L.f. Plant Soil 144:259–265

Gruber BD, Ryan PR, Richardson AE, Tyerman SD, Sunita R, Hebb DM, Howitt SM, Delhaize E (2010) HvALMT1 from barley is involved in the transport of organic anions. J Exp Bot 61:1455–1467

Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. Int J Genom 701596:18

Hall JL, Williams LE (2003) Transition metal transporters in plants. J Exp Bot 54(393):2601–2613

Hancock JT, Desikan R, Neill SJ (2001). Role of reactive oxygen species in cell signalling pathways. Biochem Soc Trans 29(2):345–349

Hasanuzzaman M, Nahar K, Alam M, Roychowdhury R, Fujita M (2013) Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci 14:9643–9684

Hattori Y, Nagai K, Furukawa S, Song X-J, Kawano R, Sakakibara H, Wu J, Matsumoto T, Yoshimura A, Kitano H, Matsuoka M, Mori H, Ashikari M (2009) The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. Nature 460:1026–1030. 2009

Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation? Trends Plant Sci 11(12):610–617

Hinsinger P (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant Soil 237:173–195

Hoekenga OA, Maron LG, Piñeros MA, Cancado GM, Shaff JM, Kobayashi Y, Ryan PR, Dong B, Delhaize E, Sasaki T, Kochian H, Yamamoto Y, Koyama H, Kochian LV (2006) AtALMT1, which encodes a malate transporter, is identified as one of several genes critical for aluminum tolerance in Arabidopsis. Proc Natl Acad Sci U S A 103:9738–9743

Hoffland E, Findenegg GR, Nelemans JA (1989) Solubilization of rock phosphate by rape. Plant Soil 113:155–160

Huang CF, Yamaji N, Mitani N, Yano M, Nagamura Y, Ma JF (2009) A bacterial-type ABC transporter is involved in aluminum tolerance in rice. Plant Cell 21:655–667

Huang JH, Hu KN, Decker B (2010) Organic arsenic in the soil environment: speciation, occurrence, transformation and adsorption behavior. Water Air Soil Pollut 219:401–415

Huang TL, Nguyen QTT, Fu SF, Lin CY, Chen YC, Huang HJ (2012) Transcriptomic changes and signalling pathways induced by arsenic stress in rice roots. Plant Mol Biol 80(6):587–608

Indriolo E, Na G, Ellis D, Salt DE, Banks JA (2010) A vacuolar arsenite transporter necessary for arsenic tolerance in the arsenic hyperaccumulatingfern *Pterisvittata*is missing in flowering plants. Plant Cell 22:2045–2057

Islam E, Khan MT, Irem S (2015) Biochemical mechanisms of signaling: perspectives in plants under arsenic stress. Ecotoxicol Environ Saf 114:126–133

Ito O, Ella E, Kawano N (1999) Physiological basis of submergence tolerance in rainfed lowland rice ecosystem. Field Crops Res 64:75–90

Jackson MB (2008) Ethylene-promoted elongation: an adaptation to submergence stress. Ann Bot 101:229–248

Jackson MB, Ram PC (2003) Physiological and molecular basis of susceptibility and tolerance of rice plants to complete submergence. Ann Bot 91:227–241

Jagadish SVK, Muthurajan R, Oane R, Wheeler TR, Heuer S, Bennett J, Craufurd PQ (2010) Physiological and proteomic approaches to address heat tolerance during anthesis in rice (*Oryza sativa* L.). J Exp Bot 61(1):143–156

Jayasundara HPS, Thomson BD, Tang C (1998) Responses of cool season grain legumes to soil abiotic stress. Adv Agron 63:77–151

Kalita J, Pradhan AK, Shandilya ZM, Tanti B (2018) Arsenic stress responses and tolerance in rice: physiological, cellular and molecular approaches. Rice Sci 25(5):235–249

Kato Y, Collard BC, Septiningsih EM, Ismail AM (2014) Physiological analyses of traits associated with tolerance of long-term partial submergence in rice. AoB Plants 6:plus058

Kawano N, Ito O, Sakagami J (2009) Morphological and physiological responses of rice seedlings to complete submergence (flash flood). Ann Bot 103:161–169

Kihara T, Wada T, Suzuki Y, Hara T, Koyama H (2003) Alteration of citrate metabolism in cluster roots of White Lupin. Plant Cell Physiol 44(9):901–908

Kochian LV, Pineros MA, Liu J, Magalhaes JV (2015) Plant adaptation to acid soils: the molecular basis for crop aluminum resistance. Annu Rev Plant Biol 66:571–598

Koussevitzky S, Suzuki N, Huntington S, Armijo L, Sha W, Cortes D, Shulaev V, Mittler R (2008) AsA peroxidase 1 plays a key role in the response of Arabidopsis thaliana to stress combination. J Biol Chem 283:34197–34203

Kuo HF, Chiou TJ (2011) Therole of microRNAs in phosphorus deficiency signaling. Plant Physiol 156:1016–1024

Lambers H, Martinoia E, Renton M (2015) Plant adaptations to severely phosphorus-impoverished soil. Curr Opin Plant Biol 25:23–31

Larsen PB, Geisler MJ, Jones CA, Williams KM, Cancel JD (2005) ALS3 encodes a phloem-localized ABC transporter-like protein that is required for aluminum tolerance in Arabidopsis. Plant J 41:353–363

Larsen PB, Cancel J, Rounds M, Ochoa V (2007) *Arabidopsis* ALS1 encodes a root tip and stele localized half type ABC transporter required for root growth in an aluminum toxic environment. Planta 225:1447–1458

Li WX, Chen TB, Huang ZC, Lei M, Liao XY (2006) Effect of arsenic on chloroplast ultrastructure and calcium distribution in arsenic hyperaccumulator *Pteris vittata* L. Chemosphere 62:803–809

Li H, Chen Y, Gu G (2008) The effect of propionic to acetic acid ratio on anaerobic–aerobic (low dissolved oxygen) biological phosphorus and nitrogen removal. Bioresour Technol 99:4400–4407

Licausi F, Perata P (2009) Low oxygen signaling and tolerance in plants. Adv Bot Res 50:139–198

Licausi F, Ohme-Takagi M, Perata P (2013) APETALA 2/ethylene responsive factor (AP 2/ERF) transcription factors: mediators of stress responses and developmental programs. New Phytol 199(3):639–649

Liu B, Rennenberg H, Kreuzwieser J (2015) Hypoxia induces stem and leaf nitric oxide (NO) emission from poplar seedlings. Planta 241(3):579–589

Luo F-L, Nagel KA, Scharr H, Zeng B, Schurr U, Matsubara S (2011) Recovery dynamics of growth, photosynthesis and carbohydrate accumulation after de-submergence: a comparison between two wetland plants showing escape and quiescence strategies. Ann Bot 107(1):49–63

Ma LQ, Komar KM, Tu C, Zhang W, Cai Y, Kennelley ED (2001) A fern that hyperaccumulates arsenic. Macmillan Magazines Ltd. Nature, Vol 409

Ma JF, Shen R, Zhao Z, Wissuwa M, Takeuchi Y, Ebitani TYM (2002) Response of rice to Al stress and identification of quantitative trait loci for Al tolerance. Plant Cell Physiol 43:652–659

Ma JF, Chen ZC, Shen RF (2014) Molecular mechanisms of Al tolerance in gramineous plants. Plant Soil 381(1–2):1–12

Maejima E, Watanabe T (2014) Proportion of phospholipids in the plasma membrane is an important factor in Al tolerance. Plant Signal Behav 9:e29277

Magalhaes JV, Garvin DF, Wang Y, Sorrells ME, Klein PE, Schaffert RE, Li L, Kochian LV (2004) Comparative mapping of a major aluminum tolerance gene in sorghum and other species in the Poaceae. Genetics 167:1905–1914

Mandal BK, Suzuki KT (2002) Arsenic round the world: a review. Talanta 58:201–235

Mao H, Wang H, Liu S, Li Z, Yang X, Yan J, Li J, Tran LS, Qin FA (2015) Transposable element in a NAC gene is associated with drought tolerance in maize seedlings. Nat Commun 6:8326

McCauley A, Jones C, Jacobsen J (2009) Plant nutrient functions and deficiency and toxicity symptoms. Nutrient Management Module 9:1–16

Meena KK, Sorty AM, Bitla UM, Choudhary K, Gupta P, Pareek A, Singh HB (2017) Abiotic stress responses and microbe-mediated mitigation in plants: the omics strategies. Front Plant Sci 8:172

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Miyasaka SC, Hawes MC (2001) Possible role of root border cells in detection and avoidance of aluminum toxicity. Plant Physiol 125:1978–1987

Mollier A, Pellerin S (1999) Maize root system growth and development as influenced by phosphorus deficiency. J Exp Bot 50:487–497

Mosa KA, Kumar K, Chhikara S, Mcdermott J, Liu Z, Musante C, White JC, Dhankher OP (2012) Members of rice plasma membrane intrinsic proteins subfamily are involved in arsenite permeability and tolerance in plants. Transgenic Res 21(6):1265–1277

Nahar S, Kalita J, Sahoo L, Tanti B (2016) Morphophysiological and molecular effects of drought stress in rice. Ann Plant Sci 5(9):1409–1416

Nahar S, Sahoo L, Tanti B (2018a) Screening of drought tolerant rice through morpho-physiological and biochemical approaches. Biocatal Agri Biotechnol 15:150–159

Nahar S, Vemireddy LR, Sahoo L, Tanti B (2018b) Antioxidant protection mechanisms reveal significant response in drought-induced oxidative stress in some traditional rice of Assam, India. Rice Sci 25(4):185–196

Nilsen E, Orcutt DM (1996) The physiology of plants under stress – abiotic factors. Wiley, New York, p 689

Noctor G, Veljovic-Jovanovic S, Driscoll S, Novitskaya L, Foyer CH (2002) Drought and oxidative load in the leaves of C3 plants: a predominant role for photorespiration? Ann Bot 89:841–850

Ofei-Manu P, Wagatsuma T, Ishikawa S, Tawaraya K (2001) The plasma membrane strength of the root-tip cells and root phenolic compounds are correlated with Al tolerance in several common woody plants. Soil Sci Plant Nutr 47:359–375

Onaga G, Wydra K (2016) Advances in plant tolerance to abiotic stresses. In plant genomics. Intech Open. https://doi.org/10.5772/64351

Palada MC (1972) Environmental effect on the resistance of rice seedlings to complete submergence. Crop Sci 12:209–212

Perata P, Voesenek LACJ (2007) Submergence tolerance in rice requires Sub1A, an ethylene-response-factor-like gene. Trends Plant Sci 12:43–46

Pradhan AK, Shandilya ZM, Lahkar L, Hasnu S, Kalita J, Borgohain D, Tanti B (2019) Comparative metabolomics approach towards understanding chemical variation in rice under abiotic stress. In: Advances in rice research for abiotic stress tolerance, pp 537–550, Woodhead Publishing

Price GD, Evans JR, von Caemmerer S, Yu JW, Badger MR (1995) Specific reduction of chloroplast glyceraldehyde-3-phosphate dehydrogenase activity by antisense RNA reduces CO_2 assimilation via a reduction in ribulosebisphosphate regeneration in transgenic tobacco plants. Planta 195(3):369–378

Pucciariello C, Perata P (2013) Quiescence in rice submergence tolerance: an evolutionary hypothesis. Trends Plant Sci 18(7):377

Pucciariello C, Banti V, Perata P (2012) ROS signaling as common element in low oxygen and heat stresses. Plant PhysiolBioch 59:3–10

Puthota V, Cruz-Ortega R, Jonson J, Ownby J (1991) Anultrastructural study of the inhibition of mucilage secretion in the wheat root cap by aluminum. In: Wright RJ, Baligar VC, Murrmann RP (eds) Plant-soil interactions at low pH. Kluwer, Dordrecht, pp 779–789

Qin F, Kakimoto M, Sakuma Y, Maruyama K, Osakabe Y, Tran LS, Shinozaki K, Yamaguchi-Shinozaki K (2007) Regulation and functional analysis of ZmDREB2A in response to drought and heat stresses in *Zea mays* L. Plant J 50(1):54–69

Ram PC (2002) Submergence tolerance in rainfed lowland rice: physiological basis and prospects for cultivar improvement through market-aided breeding. Field Crop Res 76:131–152

Ramaekers L, Remans R, Rao IM, Blair MW, Vanderleyden J (2010) Strategies for improving phosphorus acquisition efficiency of crop plants. Field Crop Res 117:169–176

Rao KP, Vani G, Kumar K, Wankhede DP, Misra M, Gupta M, Sinha AK (2011) Arsenic stress activates MAP kinase in rice roots and leaves. Arch Biochem Biophys 506:73–82

Rejeb IB, Pastor V, Mauch-Mani B (2014) Plant responses to simultaneous biotic and abiotic stress: molecular mechanisms. Plants (Basel, Switzerland) 3(4):458–475

Richardson AE, Simpson RJ (2011) Soil microorganisms mediating phosphorus availability. Plant Physiol 156:989–996

Roy R, Mazumder PB, Sharma GD (2009) Proline, catalase and root traits as indices of drought resistance in bold grained rice (*Oryza sativa*) genotypes. Afr J Biotechnol 8:6521–6528

Ryan PR, Raman H, Gupta S, Horst WJ, Delhaize E (2009) A second mechanism for aluminum resistance in wheat relies on the constitutive efflux of citrate from roots. Plant Physiol 149:340–351

Sakagami JI, John Y, Sone C (2013a) Complete submergence escape with shoot elongation ability by underwater photosynthesis in African rice, *Oryza glaberrima* Steud. Field Crop Res 152:17–26

Sakagami J-I, Joho Y, Sone C (2013b) Complete submergence escape with shoot elongation ability by underwater photosynthesis in African rice, *Oryza glaberrima* Steud. Field Crops Res 152:17–26

Sanghera GS, Wani SH, Hussain W, Singh NB (2011) Engineering cold stress tolerance in crop plants. Current Genom 12:30–43

Sasaki T, Yamamoto Y, Ezaki B, Katsuhara M, Ahn SJ, Ryan PR, Delhaize E, Matsumoto H (2004) A wheat gene encoding an aluminum-activated malate transporter. Plant J 37:645–653

Setiyono TD, Barbieri M, Prasadini P, Maunahan A, Gatti L (2018) Spatial assessment of heat stress impact on rice production in two districts of Andhra Pradesh, India. World J Agric Res 6(1):10–14

Setter TL, Laureles EV (1996) The beneficial effect of reduced elongation growth on submergence tolerance of rice. J Exp Bot 5:1551–1559

Shandilya ZM, Tanti B (2019) Hydroponic screening of traditional rice varieties in Assam, India to estimate their potential resistance to Al toxicity under P deficiency. Acta Agrobot 72(4). https://doi.org/10.5586/aa.17

Shandilya ZM, Tanti B (2020). Comparative biochemical, histochemical and expression analysis of SOD gene in a few traditional rice varieties under aluminium toxicity and phosphorous deficiency in Assam, India. Vegetos. https://doi.org/10.1007/s42535-019-00092-7

Shane MW, Cawthray GR, Cramer MD, Kuo J, Lambers H (2006) Specialized ‘dauciform’ roots of Cyperaceae are structurally distinct, but functionally analogous with ‘cluster’ roots. Plant Cell Environ 29:1989–1999

Sharma I (2012) Arsenic induced oxidative stress in plants. Biologia 3:447–453

Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Botany 2012:217037. https://doi.org/10.1155/2012/217037

Shinozaki KY, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. Annu Rev Plant Biol 57:781–803

Singh H, Singh BB, Ram PC (2001) Submergence tolerance of rainfed lowland rice: search for physiological marker traits. J Plant Physiol 158:883–889

Ślesak I, Libik M, Karpinska B, Karpinski S, Miszalski Z (2007) The role of hydrogen peroxide in regulation of plant metabolism and cellular signalling in response to environmental stresses. Acta Biochim Pol 54:39–50

Song W, Zhao H, Zhang X, Lei L, Lai J (2016) Genome-wide identification of VQ motif-containing proteins and their expression profiles under abiotic stresses in maize. Front Plant Sci 6:1177

Suzuki N, Mittler R (2006) Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction. Physiol Plant 126:45–51

Tang Y, Garvin DF, Kochian LV, Sorrells ME, Carver BF (2002) Physiological genetics of aluminum tolerance in the wheat cultivar atlas 66. Crop Sci 42:1541–1546

Theocharis A, Clement C, Barka EA (2012) Physiological and molecular changes in plants grown at low temperatures. Planta 235:1091–1105

Tokizawa M, Kobayashi Y, Saito T, Kobayashi M, Iuchi S, Nomoto M, Tada Y, Yamamoto YY, Koyama H (2015) Sensitive to proton rhizotoxicity1, calmodulin binding transcription activator2, and other transcription factors are involved in aluminum-activated malate transporter1 expression. Plant Physiol 167:991–1003

Tovkach A, Ryan PR, Richardson AE, Lewis DC, Rathjen TM, Ramesh S, Tyerman SD, Delhaize E (2013) Transposon mediated alteration of TaMATE1B expression in wheat confers constitutive citrate efflux from root apices. Plant Physiol 161:880–892

Trachsel S, Kaeppler SM, Kathleen MB, Lynch JP (2011) Shovelomics: high throughput phenotyping of maize (*Zea mays* L) root architecture in the field. Plant Soil 341:75–87

Tuba Z, Lichtenthaler HK (2007) Long-term acclimation of plants to elevated CO2 and its interaction with stresses. Ann N Y Acad Sci 1113:135–146

Tuteja N, Gill SS (eds) (2016) Abiotic stress response in plants. Wiley-VCH Verlag GmbH & Co. KGaA, Weinheim

Uchida R (2000) Essential nutrients for plant growth: nutrient functions and deficiency symptoms. Plant Nutrient Management in Hawaii's Soil 4:31–55

Upadhyaya H, Tanti B, Panda SK (2017) Molecular physiology of dehydration stress responses in plant: a review. Advances in Plant Physiology 17:1–24

Voesenek LACJ, Colmer TD, Pierik R, Millenaar FF, Peeters AJM (2006) How plants cope with complete submergence. New Phytol 170:213–226

Von Uexku¨ll HR, Mutert E (1995) Global extent, development and economic impact of acid soils. Plant Soil 171:1–15

Wahid A, Gelani S, Ashraf M, Foolad MR (2007) Heat tolerance in plants: an overview. Environ Exp Bot 61:199–223

Wang L, Chen W (2012) Characteristics of multi-timescale variabilities of the drought over last 100 years in Southwest China. Adv Meteorol Sci Technol 2(4):21–26

Wani SH (Ed.) (2018) Biochemical, physiological and molecular avenues for combating abiotic stress in Plants. Academic Press

White PJ, Brown PH (2010) Plant nutrition for sustainable development and global health. Ann Bot 105:1073–1080

WHO (1993) Guidelines for drinking-water quality. World Health Organization, Geneva

Winkel A, Colmer TD, Ismail AM, Pedersen O (2013) Internal aeration of paddy field rice (*Oryza sativa*) during complete submergence - importance of light and floodwater O_2. New Phytol 197(4):1193–1203

Wissuwa M (2003) How do plants achieve tolerance to phosphorus deficiency? Small causes with big effects. Plant Physiol 133:1947–1958

Wissuwa M, Ae N (2001) Further characterization of two QTLs that increase phosphorus uptake of rice (*Oryza sativa* L.) under phosphorus deficiency. Plant Soil 237:275–286

Xia J, Yamaji N, Kasai T, Ma JF (2010) Plasma membrane-localized transporter for aluminum in rice. Proc Natl AcadSci USA 107:18381–18385

Xiang C, Oliver DJ (1998) GSHmetabolic genes coordinately respond to heavy metals and Jasmonic acid in *Arabidopsis*. Plant Cell 10:1539–1550

Xu K, Xu X, Fukao T, Canlas P, Maghirang-Rodriguez R, Heuer S, Ismail AM, Bailey-Serres J, Ronald PC, Mackill DJ (2006) Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. Nature 442:705–708

Yadav SK (2010) Cold stress tolerance mechanisms in plants. A review. Agron Sustain Dev 30(3):515–527

Yamada N (1959). Physiological basis of resistance of rice plant against overhead flooding. Bull Nat Inst Agric Sci. In: Plant physiology, genetics and crops in general D8:1–112

Yamaji N, Huang CF, Nagao S, Yano M, Sato Y, Nagamura Y, Maa JF (2009) A zinc finger transcription factor ART1 regulates multiple genes implicated in aluminum tolerance in rice. Plant Cell 21:3339–3349

Yang CY, Hong CP (2015) The NADPH oxidase Rboh D is involved in primary hypoxia signalling and modulates expression of hypoxia-inducible genes under hypoxic stress. Environ Exp Bot 115:63–72

Yasar F, Ellialtioglu S, Kusvuran S (2006) Ion and lipid peroxide content in sensitive and tolerant eggplant callus cultured under salt stress. Eur J Hortic Sci 71(4):169

Ying S, Zhang D, Fu J, Shi Y, Song Y, Wang T, Li Y (2012) Cloning and characterization of a maize bZIP transcription factor, Zmb ZIP72, confers drought and salt tolerance in transgenic Arabidopsis. Planta 235(2):253–266

Yokosho K, Ma JF (2015) Transcriptional regulation of Al tolerance in plants. In: Aluminum stress adaptation in plants. Springer, Cham, pp 37–46

You J, Chan Z (2015) ROS regulation during abiotic stress responses in crop plants. Front Plant Science 6:1092

Zhang Q, Chen Q, Wang S, Hong Y, Wang Z (2014) Rice and cold stress: methods for its evaluation and summary of cold tolerance-related quantitative trait loci. Rice 7:24

Zhao YJ, Weng BQ, Wang YX, Xu GZ (2009) Plant physio-ecological responses to drought stress and its research progress. Fujian Science and Technology of Rice and Wheat 27:45–50

Zhu J, Jeong JC, Zhu Y, Sokolchik I, Miyazaki S, Zhu JK, Hasegawa PM, Bohnert HJ, Shi H, Yun DJ, Bressan RA (2015) Involvement of Arabidopsis HOS15 in histone deacetylation and cold tolerance. Proc Natl Acad Sci U S A 105:4945–4950

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