Azamal Husen *Editor*

Harsh Environment and Plant Resilience

Molecular and Functional Aspects

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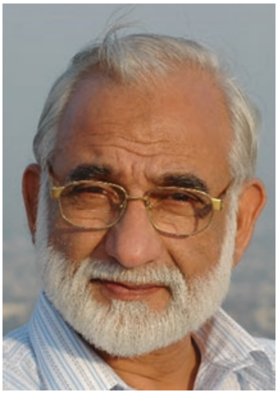
To My Mother

Foreword



Harsh Environment and Plant Resilience by Professor Azamal Husen presents an excellent collection of chapters covering almost all important aspects of environmental botany, as is evident from titles of chapters included in this edited volume. Physiological and molecular responses of plants to various environmental stresses are discussed in detail, on one hand, and the effects of growth-promoting and stimulating substances on plant performance and productivity are elucidated, on the other. Some chapters also deal with general topics such as biosensors for monitoring stress in plants, stress-responsive genes, genome editing, fast-breeding programs, recombinant DNA technique, plant growth–promoting rhizobacteria, and production of secondary metabolites under unfriendly environment. Overall, the book has enough to offer a reasonably useful, interesting, and informative reading to all concerned. I believe that, like his previous works *Nanomaterials and Plant Potential* and *Nanomaterials for Agriculture and Forestry Applications*, this new contribution by Dr. Husen will also be welcomed by the relevant section of readers and researchers with great interest and enthusiasm.

Muhammad Iqbal
(An old student of botany)

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Preface

Plant species play an important role in the sustainability of life on Earth. They provide food, clothing, and shelter to mankind, help maintain nutrient cycles and carbon storage, and stabilize the global climate system by abating environmental pollution and protecting the Earth from erosion. In the recent past, threats from climate change and unforeseeable environmental extremes to plant growth and productivity have consistently increased. The climate change-driven effects, especially from unpredictable environmental fluctuations, can result in an increased prevalence of abiotic and biotic stresses in plants. These stresses have slowed down the global yields of crop plants. On the other hand, food security for the rapidly growing human population in a sustainable ecosystem is a major concern of the present-day world. Thus, understanding the core developmental, physiological, and molecular aspects that regulate plant growth and productivity in a challenging environment is a pivotal issue to be tackled by the scientific community dealing with sustainable agricultural and horticultural practices. Plants are influenced by adverse environmental conditions at various levels, and their different and diverse responses play a significant role in determining their growth, production, and the overall geographical distribution.

Various chapters in this book focus on the biological mechanisms and fundamental principles that determine how different plant species grow, perform, and interact with a challenging and resilient environment. These articles cover a broad range of topics in plant science, including gene function, molecules, physiology, cell biology, and plant ecology, to understand the functioning of plants under harsh environmental conditions. They elucidate the physiological and molecular mechanisms in different plant species, ecophysiological interactions of plants, interplay between plant roots, arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria, biosensors for monitoring stress, production of secondary metabolites, stress alleviation processes, and so on. Accordingly, the book in hand is an attempt to meet knowledge requirements on these aspects. It comprises 20 chapters, and the vast coverage of diverse aspects of the subject reflects well from the table of contents. This book is primarily intended for graduate and postgraduate students and researchers in various fields of crop science, plant science, plant biotechnology, and plant ecology, and also for scientists, experts, and consultants in the agriculture sector.

I express my sincere thanks to the distinguished authors who have shared their knowledge and contributed chapters for this book. I feel indebted to Dr. Eric Stannard, senior editor (botany) at Springer, and all his associates for their sustained cooperation. I am grateful to Professor Khwaja Salahuddin Siddiqi (Department of Chemistry, Aligarh Muslim University, Aligarh, India), Dr. Mansur Osman (University of Gondar, Gondar, Ethiopia), Dr. Rakesh Kumar Bachheti (Addis Ababa Science and Technology University, Addis Ababa, Ethiopia), Dr. Sophie Mavrikou (Department of Biotechnology, Agricultural University of Athens, Athens, Greece), and Dr. Adalberto Benavides-Mendoza (Department of Horticulture, Autonomous Agricultural University Antonio Narro, Saltillo, Mexico) for their support and help in reviewing the chapters. I am also thankful to Dr. Muhammad Iqbal, former professor of botany, dean of science and vice chancellor at Jamia Hamdard, New Delhi, India, for writing the foreword to this volume. I shall be happy receiving comments and criticism, if any, from subject experts and general readers of this book.

Wolaita, Ethiopia Azamal Husen

October 2020

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About the Editor

Azamal Husen (BSc from Shri Murli Manohar Town Post Graduate College, Ballia, UP; MSc from Hamdard University, New Delhi; and PhD from Forest Research Institute, Dehra Dun, India) is a Foreign Delegate at Wolaita Sodo University, Wolaita, Ethiopia. He has served the University of Gondar, Ethiopia, as a Full Professor of Biology, and also worked as the Coordinator of MSc Program and the Head, Department of Biology. He was a Visiting Faculty of the Forest Research Institute, and the Doon College of Agriculture and Forest at Dehra Dun, India. He has a more than 20 years' experience of teaching, research and administration. Dr. Husen specializes in biogenic nanomaterials fabrication and their application, plant response to nanomaterials, plant production and adaptation to harsh environments at physiological, biochemical and molecular levels, herbal medicine, and clonal propagation and improvement of tree species. He has conducted several research projects sponsored by various funding agencies, including the World Bank, the Indian Council of Agriculture Research (ICAR), the Indian Council of Forest Research Education (ICFRE); and the Japan Bank for International Cooperation (JBIC), etc. He has published over 100 research papers, review articles and book chapters, edited books of international repute, presented papers in several conferences, and produced over a dozen of manuals and monographs. Husen received four fellowships from India and a recognition award from University of Gondar, Ethiopia, for excellent teaching, research and community service. An active organizer of seminars/conferences and an efficient evaluator of research projects and book proposals as he is, Dr. Husen has been on the Editorial board and the panel of reviewers of several reputed journals of Elsevier, Frontiers Media SA, Taylor & Francis, Springer Nature, RSC, Oxford University Press, Sciendo, The Royal Society, CSIRO, PLOS and John Wiley & Sons. He is included in the advisory board of Cambridge Scholars Publishing, UK. He is a Fellow of the Plantae group of American Society of Plant Biologists, and a Member of International Society of Root Research, Asian Council of Science Editors, and INPST, etc. Also, he is Editor-in-Chief of *American Journal of Plant Physiology*; and a Series Editor of 'Exploring Medicinal Plants' published by Taylor & Francis Group, USA.

Chapter 1
The Harsh Environment and Resilient Plants: An Overview

Azamal Husen

Contents

Abbreviations

ABA	Abscisic acid
ACC deaminase	1-Aminocyclopropane-1-carboxylate deaminase
APX	Ascorbate peroxidase
BRs	Brassinosteroids
CAT	Catalase
DHAR	Dehydrogenase ascorbic reductase
ET	Ethylene
IAA	Indole-3-acetic acid
JA	Jasmonic acid
NMs	Nanomaterials
PGPR	Plant growth-promoting rhizobacteria
POD	Peroxidase
ROS	Reactive oxygen species

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SA	Salicylic acid
SLs	Strigolactones
SOD	Superoxide dismutase

1 Introduction

Resilience is a skill to recover from tough conditions or to adjust easily to an adverse situation, change, or challenges. As sessile organisms in nature, plants have a self-organizing system with some limitations, for example, they have limits to adjust to high and low temperatures. Quite often, various anthropogenic activities, such as over exploitation of natural resources, land use, and pollution, adversely affect the resilience of flora and fauna in a system (Iqbal et al. 2000a). In the current scenario, it is quite challenging to accelerate plant growth and production under adverse environmental conditions. These adverse situations have increased owing to drastic fluctuations in the global climate conditions. For instance, the extreme temperature will trigger increased demand for water due to accelerated transpiration as well as evaporation by plants and will cause a faster soil moisture depletion. Therefore, these processes are adding significant uncertainty to water availability in future. Extreme climate variation will affect precipitation, runoff and snow/ice melt, water quality, and temperature, as well as the groundwater recharge. It will also affect the sea level with probable impacts on the surface and groundwater salinity especially in the coastal areas (Fig. 1.1).

Raftery et al. (2017) have suggested an increase in global average temperature from 2.0 to 4.9 °C by 2100. Thus, perhaps, in near future at the global level, the combination of three abiotic stresses (drought, salt stress, and extremes of temperature) may lead to a drastic reduction in plant fitness and their overall productivity (Aref et al. 2016). In the recent past, extreme meteorological and hydrological events have become more common and destructive. It has also been projected that about 90% of arable lands are prone to single or multiple stress conditions (dos Reis et al. 2012). Associations among weather, climate, and production risk are well documented (George et al. 2005). Effect of extreme actions on agriculture sectors, rangeland (grasslands, shrublands, woodlands, wetlands, and deserts), and forestry can be direct or indirect (Das 2003). Direct physical damage to crop plants, trees, and animals is caused by extreme hydrometeorological events, heat waves, cold waves, and so on. Indirect damage refers to potential production loss due to disturbed goods and services flow, reduced quality, yield and production ability of plants, and the enhanced production costs. UNISDR (2015) has projected that the economic loss associated with such disasters (extreme events) now ranges between USD 250 billion and USD 300 billion per year at the global level. In this regard, developed countries are able to manage the effects of variable climate in a better way in comparison to the developing countries, where extreme weather events cause disastrous consequences for agriculture sectors. FAO (2018) estimated that

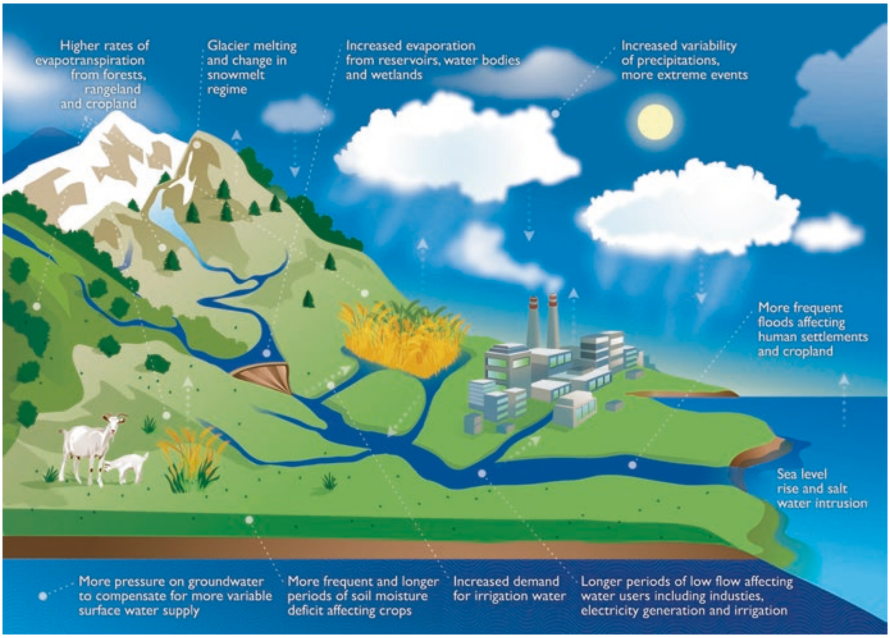

Fig. 1.1 Effect of climate change on various components of water cycle. (Adapted from FAO 2013)

there were 260 natural disasters (both climate- and weather-related as well as geophysical and biological) per year in the developing countries from 2005 to 2016; an 11% increase over the period of 1993–2004 when the average was 235 per year; and a more than two-fold increase in 1981–1992 when they averaged 122 per year. Zhu and Troy (2018) have also suggested that climate extremes can adversely affect the production of crop plants. According to Lobell et al. (2011), the global trends of temperature have led to a reduced wheat and maize production. Further, Challinor et al. (2014) have suggested that globally reduced production of wheat, maize, and rice will arise owing to climate change. It has been also realized that extreme environmental events are going to influence adversely the overall flora and fauna. Furthermore, according to an estimate (FAO 2009), the productivity of food crops needs to be increased by 70% for an extra 2.3 billion individuals up to 2050. Thus, to achieve this target under extreme environmental events is a key issue in the twenty-first century.

In brief, the abnormal or extreme environmental conditions affect plant potential in terms of growth and production mediated by an array of physiological, biochemical, and molecular changes (Husen 1997; Iqbal et al. 2015; Albaladejo et al. 2017; Negrão et al. 2017; Hussein et al. 2017; Husen et al. 2016, 2018, 2019; Rivero et al. 2014; Morales-Quintana et al. 2020; Elkelish et al. 2020a, b; Demirel et al. 2020). Thus, understanding the environmental signal sensing and the balance between defense and development in plants lays the foundation for the understanding of plant resilience. For instance, to mediate with adverse environment, plants have evolved the secondary metabolites as defense compounds to protect themselves from stress conditions (Zaynab et al. 2018; Berini et al. 2018; Isah 2019). Some of them also act as signaling chemicals to attract the pollinating insects as well as seed-dispersal animals (Wink 2015). Carbohydrates, lipids, and proteins (primary metabolites) are omnipresent in the plant kingdom and play an important role in the overall plant growth, development, and reproduction, and in other basic physiological/metabolic processes such as photosynthesis and respiration. However, the secondary metabolites facilitate the long-term plant survival, and even their low concentrations in the plant system avoid the instant plant death. Some reports have shown that the secondary metabolites are usually not available in a fixed amount in the plant system but rather transform and cycle through plant parts based on the activation of various secondary metabolite pathways in response to a number of temporal as well as environmental factors (Bednarek 2012; Siddiqi and Husen 2017, 2019; Bachheti et al. 2019). These secondary metabolites often produced in an appropriate amount only if they have the signal to do so based on interactions between their genetics, physiology, and prior history plus environmental stressors (Glynn et al. 2007; Zaynab et al. 2018; Isah 2019). Swift et al. (2004) have reported above 100,000 known secondary metabolites with diverse chemical structures and functions. Several other specific information related to secondary metabolites under adverse environmental conditions are discussed in detail in Chapters 18 and 19 of this book. Taken together, the goal of this chapter is to highlight the recent advances in our understanding of the challenges posed by harsh environment and the resilience of plants to survive under extreme environmental conditions.

2 Drought Stress and Plant Potential

The natural reduction in the amount of precipitation over a prolonged duration leads to drought conditions. It has become a constant problem in many parts of the world. Drought affects the agriculture sector disproportionately, more than any other kind of climate extreme due to their large scale and everlasting nature. FAO (2011) have projected that drought affects severely on rainfed smallholder farming systems in highland areas and in the tropics, which account for 80% of the world's cropland and produce about 60% of global agricultural output. Another report of FAO (2018) revealed that 83% of all damage and loss caused by drought was absorbed by agriculture (Fig. 1.2).

Food crops and other higher plants including medicinal plants under drought-stress condition respond by a number of physiological mechanisms at the molecular, cellular, tissue, morphological, and whole-plant levels (Anjum et al. 2008a, b; Husen 2010; Prasch and Sonnewald 2013; Tripathi et al. 2014; Aref et al. 2016; Husen et al. 2014, 2017; Chaumont and Tyerman 2014; De Ollas et al. 2015; Elkelish 2020a). These responses vary with the species and genotype/cultivars, the length and severity of water stress, and the developmental stage of plants (Husen 2010). Reduction in soil water availability leads to a low plant water potential and a

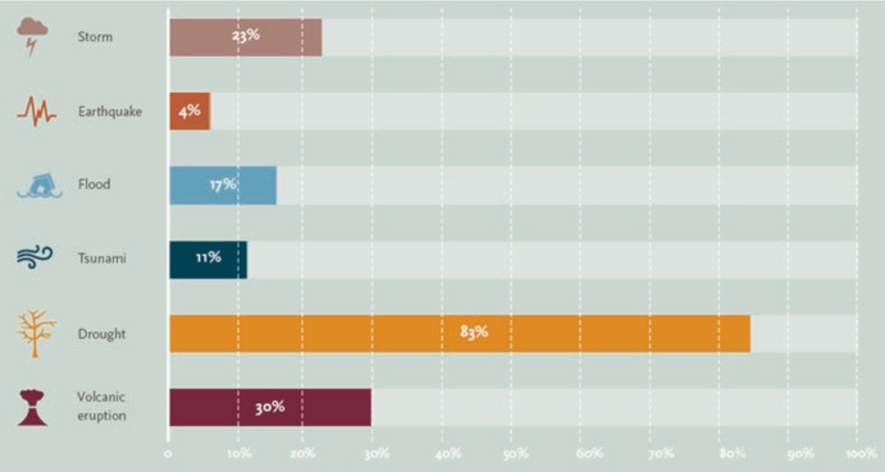

Fig. 1.2 Damage and loss in agriculture as share of total damage and loss across all sectors (2006–2016), by type of hazard. (Adapted from FAO 2018)

consequent loss of turgidity and inhibition of cell elongation in leaves. The effect of drought stress on the net photosynthesis has been traditionally studied in terms of "stomatal" and "nonstomatal" limitations, the former resulting from the resistance of CO_2 diffusion to intercellular leaf space and the latter being often completely assumed as a metabolic constraint (Chaves et al. 2009). Plants tend to avoid excessive transpiration by closing the stomata (Flexas et al. 2004). This reduces the gaseous exchange between leaf and the atmosphere, leading to a low intercellular CO_2 concentration (Flexas et al. 2004), reduced diffusion of CO_2 to chloroplasts, and a limited net CO_2-assimilation rate (Chaves et al. 2002), with ensuing negative feedback in photochemical efficiency (Ribeiro et al. 2008). Further, the water-stress condition also affects leaf-area expansion (Husen et al. 2014), water and chlorophyll contents (Aref et al. 2013), absorption of photosynthetically active radiation, and the leaf efficiency to carry out carbon fixation (Flexas et al. 2004; Umar et al. 2018). However, plants exhibit adaptive cellular responses like upregulation of oxidative-stress protectors and accumulation of protective solutes, besides leaf area adjustments that reduce water loss by transpiration (Anjum et al. 2008a, b, 2012). The efficiency of photosystem II (PSII), measured as chlorophyll fluorescence (maximum quantum yield *Fv/Fm*), has been used extensively as a diagnostic tool in studies of abiotic stresses (Baker and Rosenqvist 2004; Getnet et al. 2015; Embiale et al. 2016; Husen et al. 2014, 2016), genotypic variation (Husen 2010), altitudinal variation (Husen et al. 2004a), and species-specific diurnal changes (Husen et al. 2004b) on the PS II electron transfer process (Baker 2008), thus acting as an indicator of seedling-stock quality (Husen 2009; Hanachi et al. 2014; Getnet et al. 2015). Reduction in the quantum yield of photosystem is influenced not only by light intensity but also by the superimposition of other environmental stresses, such as high temperature, salinity, water availability, or CO_2 supply (Souza et al. 2004; Ribeiro et al. 2008;

Husen et al. 2014, 2016). Water stress inhibits photosynthetic activity in tissues due to an imbalance between light capture and its utilization (Foyer and Noctor 2004). Under these conditions, plants develop several strategies to avoid photoinhibition processes, for example, mechanisms to prevent or dissipate excessive light absorption or mechanisms to consume the reducing power generated by PSII (Demmig-Adams and Adams 1992). On the whole, extreme climatic conditions (higher frequencies of droughts and floods) are predicted to increase and be problematic for agriculture sectors especially in terms of food production. Thus, some of the recent strategies such as induction of smart growth and the photosynthetic efficiency acceleration have the potential to increase intrinsic yields. Further, new molecular markers confirmation and their efficient application in plant breeding will enhance food production and other required items under drought and other extreme climatic conditions. Many explanations related to the aforementioned subject are discussed in Chapters 2, 3, 4, 5, 6, 7, and 19 of this book.

3 Temperature Stress and Plant Potential

McGrath (2020) has reported that according to NASA, NOAA, and the UK Met Office, last year (2019) was the second warmest in a record dating back to 1850 (Fig. 1.3). It is clear from the observed records that there has been an increase in the global mean temperature. The extreme heat wave, worsened by the drought conditions, may lead to an increasing threat of widespread famine mainly in some developing countries. Heat waves/high temperatures have shown an adverse effect on the global agricultural production and posed a great risk for future food security.

It has been reported that like other extreme environmental-stress conditions, heat stress also influences a number of physiological mechanisms at the molecular, cellular, tissue, and whole-plant developmental levels (Bita and Gerats 2013; Hatfield and Prueger 2015; Wang et al. 2016a, b; Hussain et al. 2019; Noor et al. 2019; Guo et al. 2020; Hu et al. 2020; Paul et al. 2020). The extreme hot conditions may always damage plant at any developmental stage, that is, from seed germination to reproduction (Noor et al. 2019). During extreme hot summer season, an accelerated leaf-surface temperature may also have a substantial impact on plant metabolism and yields. For instance, Liu et al. (2016) have reported that for every unit increase of heat degree per day (over 30 °C), the grain-filling duration, total biomass (aboveground), and grain yield were decreased by 0.30–0.60%, 0.37–0.43%, and 1.0–1.6%, respectively, in rice plants. Garcia et al. (2015) have also suggested that the high night temperatures lead to decrease in wheat and barley grain yield. Similarly, low temperature (chilling and frost) stress adversely affected the plant growth, phenology, water and nutrient relations, anatomical, physiological, and molecular traits (Farooq et al. 2009; Theocharis et al. 2012; Ding et al. 2016, 2017; Hussain et al. 2020). Further, plant response to extreme temperatures (in both soil and air) in terms of increasing resilience and productivity has been discussed in detail in the chapters to follow.

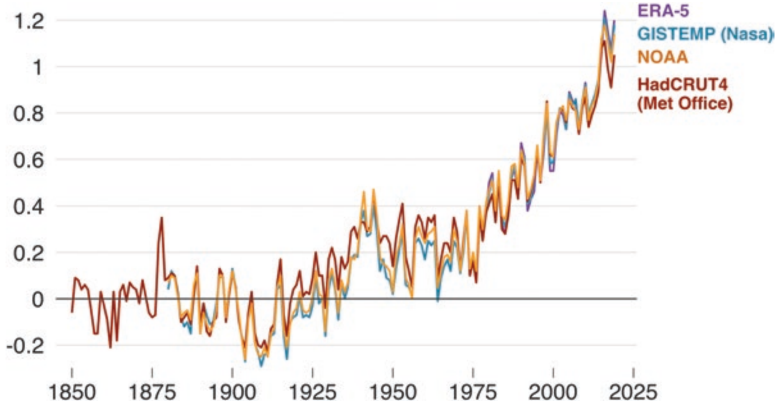

Fig. 1.3 Global temperature rise since 1980. (Adapted from McGrath 2020)

4 Salinity Stress and Plant Potential

Salinity problems arise under all climatic conditions, anthropogenic as well as natural. Not a single continent is free from salinity. With the help of FAO/UNESCO soil map of the world (1970–1980), FAO projected that, globally, the total area of saline soils was 397 million ha, and that of sodic soils 434 million ha. Of the then 230 million ha of irrigated land, 45 million ha (19.5%) were salt-affected soils; and of the almost 1500 million ha of dryland agriculture, 32 million (2.1%) were salt-affected (FAO 2020), and the influence of salinity is spreading consistently. Thus, like other environmental stresses, soil salinity is also considered as one of the major environmental factors that have reduced plant growth, yield, and distribution of plants worldwide (Bagheri et al. 2015; Alharby et al. 2019). In this situation, the maintenance of plant productivity on the saline land will be one of the greatest challenges in the coming years. Salinity stress normally causes a reduction in plant growth, which is interceded by an array of physiological, biochemical, and molecular changes (Park et al. 2016; Husen et al. 2016, 2017, 2019; Albaladejo et al. 2017; Negrão et al. 2017). Salinity hampers the uptake of water, and the consequent high accumulation of Na^+ and Cl^- together with a decline of K^+ leads to a nutrient imbalance (Munns and Tester 2008). In general, high salinity stress causes stomatal closure and lowers green pigments and photosynthesis (Arshi et al. 2002, 2006a; Hussein et al. 2017). Further, it increases the generation of reactive oxygen species (ROS), viz. hydrogen peroxide, superoxide, hydroxyl radical, and singlet oxygen, which cause damage to the cellular machinery (Qureshi et al. 2013; Srivastava et al. 2015; Zhang et al. 2016; Choudhury et al. 2017). The ROS production leads to chlorophyll deprivation and membrane lipid peroxidation (measured as malondialdehyde content), reducing the membrane fluidity and selectivity (Sekmen et al. 2007; Koyro et al. 2013). The most affected parameters include the photosynthetic rate and water-use efficiency, which ultimately restrict the plant growth rate (Husen et al. 2016, 2017, 2019; Hussein et al. 2017) and production of secondary metabolites (Arshi et al. 2006b; Qureshi et al. 2013). The decline in photosynthesis under salinity may be due to inhibition of photosystem II complex and a loss of chlorophyll pigments (Chen and Murata 2011). Plant resilience and tolerance mechanism to salinity stress are mainly managed in two ways. They have to limit the salt entry by the root system, and/or they have to control the salt concentration and its distribution. It has been noticed that nitrogen-fixing bacteria and arbuscular mycorrhizal fungi may also serve as an alternative and sustainable approach to upsurge plant growth and development in both drought and salt-stress conditions. In this connection, the identification of genetic resources with desired traits for improved salt tolerance is essential to develop improved cultivars. Several topics related to salinity tolerance mechanisms in plants have been discussed in Chapter 11 of this book.

5 Heavy Metal Stress and Plant Tolerance

Heavy metal toxicity in the environment is the result of natural and anthropogenic processes. Heavy metals are commonly found in the environment and interact with plant and human system. Normally, they have a high density (5 $g \cdot cm^{-3}$ or more specific gravity) and atomic mass more than 20, and are often toxic to living organisms, even at very low concentration (Hasanuzzaman and Fujita 2013). Environmental pollution due to heavy metals has been considered to affect the global as well as regional soil fertility, soil biomass, rhizosphere/soil health, and plant yields, leading to metals bioaccumulation in the food chain (Prasad 2004; Umar and Moinuddin 2005; Anasri et al. 2012) and therefore proving hazardous for the health of animals and humans (Iqbal et al. 2000a; Prasad 2008; Martin and Griswold 2009). The unavoidable expansion of industry and agriculture owing to population explosion, augmented use of chemical fertilizers in the agriculture sector, and the lack of adequate pollution-control measures have heavily contaminated agricultural soils, especially in developing countries (Aktar et al. 2009). However, remediation of contaminated sites is also being done now preferably by using appropriate plant species (Jabeen et al. 2009; Bhargava et al. 2012; Iqbal et al. 2015). Usually, at low or optimum concentrations, they are beneficial and improve the plant nutritional level. However, their requirement varies according to different plant species, cultivars, etc. (Saba et al. 2000; Arif et al. 2016). Moreover, they also participate in numerous mechanisms (biochemical and physiological tasks) important for the normal growth and development of plants (McCall et al. 2000; Ducic and Polle 2005; Hell and Stephan 2003; Siddiqi et al. 2018). At higher concentration, however, heavy metals become toxic or dangerous depending on the metal type, its oxidation state, concentration, pH, duration, etc., leading to the death of plants (Iqbal and Khudsar 2000). At higher concentrations, heavy metals such as cadmium (Khudsar and Mahmooduzzafar 2001; Anjum et al. 2008a, b; Bashir et al. 2015), chromium (Diwan et al. 2010, 2012), cobalt (Parmar and Chanda 2005;

Jayakumar and Vijayarengan 2006; Jayakumar et al. 2008; Khan et al. 2006; Khan and Khan 2010), copper (Ali et al. 1998, 1999; Anjum et al. 2015), lead (Qureshi et al. 2005, 2007), manganese (Ducic and Polle 2005), and mercury (Gauba et al. 2007; Ansari et al. 2009) normally become toxic for plants and damage their metabolic activities, photosynthetic machinery, and growth performance. Exposure to lower Co concentration (5 μg L^{-1}) caused an increase in seed germination, radical length, and plumule, whereas higher concentrations (25–100 μg L^{-1}) were inhibitory for these parameters in ragi (*Eleusine coracana)* and paddy (*Oryza sativa*) plants (Jayakumar et al. (2008). In chickpea (*Cicer arietinum*), exposure of Ni and Co at lower (0, 10, 50 ppm) and higher (100, 200, and 400 ppm) concentrations was examined by Khan and Khan (2010), who found that high concentration decreased the seed germination, plant growth and biomass, and chlorophyll content; triggered shoot and root injury, leaf chlorosis, suppression of root nodules; and caused an overall negative effect on the yield of *Cicer arietinum*. However, rooted sessile plants revealed a range of potential cellular mechanisms, which facilitate heavy metals detoxification, and thus plant tolerance to these elements (Hall 2002; Iqbal et al. 2015; El-Meihy et al. 2019; Jain et al. 2020; Ding et al. 2020; Lancíková et al. 2020). Of late, high-throughput sequencing has led to the identification of an increasing number of heavy-metal-responsive microRNAs in plants. For instance, Ding et al. (2020) have reported the metal-regulated microRNAs and their target genes are part of a complex regulatory network that controls many biological processes, including the heavy metal uptake and transport, protein folding and assembly, metal chelation, ROS scavenging, hormone signaling, and microRNA biogenesis.

Further discussion on heavy metal stress in terms of increasing plant resilience and productivity can be seen in Chapter 8 of this book.

6 Effect of Multiple Environmental Stresses

In the field condition, the plant also experiences a combination of multiple environmental stresses. The multiple stress also alters various physiological, biochemical, and molecular processes in the plant, and the responses of plants differ with timing, duration, and intensity of the stress (Iqbal et al. 2000b; Qureshi et al. 2006). In this situation, plants tailor their responses to combined stress factors and exhibit several unique responses, along with other common responses. For instance, in a study of the effect of heat shock and drought stress, individually and in combination, on the physiological activities of tobacco (*Nicotiana tabacum*) plants, a decreased rate of photosynthesis and respiration was noticed under drought-stress conditions, while in the case of heat shock, the rate of respiration was enhanced with an insignificant change in photosynthesis in comparison to control plants. The combined (heat and drought) stress decreased the stomatal conductance and rate of photosynthesis and increased the leaf temperature (Rizhsky et al. 2002). Prasch and Sonnewald (2013) have reported that the combined effect of heat, drought, and biotic (viruses) stresses induced molecular reprogramming and lead to a significant reorganization of defense response in *Arabidopsis*. Dehydrogenase ascorbic reductase (DHAR) enzyme helps in plant resistance to environmental stress. The full-length coding sequence of the *LcDHAR* plays a protective role in response to salt and drought stresses and provides a partial framework for *LcDHAR* gene regulation of dehydroascorbic acid and ascorbic acid contents in Chinese tulip tree *(Liriodendron chinense)* (Hao et al. 2019). However, the current understanding of the impacts of climate and related abiotic stresses on the molecular and physiological processes in woody tree species remains poor. Potato cultivars (Desiree, Unica, Agria, and Russett Burbank) were examined for multiple stress responses (Demirel et al. 2020). Physiological traits revealed that the cultivars Desiree and Unica were stress tolerant, while Agria and Russett Burbank were stress susceptible. Abiotic stress conditions have reduced photosynthetic carbon assimilation in susceptible cultivars which were associated with a lower leaf transpiration rate. Stress-tolerant cultivars have shown higher expression of genes associated with plant growth and development, hormone metabolism, and primary and secondary metabolism than the stress-susceptible cultivars. Demirel et al. (2020) have suggested that stress-tolerant cultivars suppress cell death and maintain growth and development through fine-tuning of hormone signaling, and the primary and secondary metabolisms. Further account of plant response to extreme multiple environmental stresses is produced in the chapters to follow.

7 Role of Beneficial Microbes

Sustainable use of arbuscular mycorrhizal fungi, *Rhizobium*, *Azotobacter*, *Azospirillum*, cyano-algae, phosphate-solubilizing bacteria such as *Pseudomonas* and *Bacillus* is considered as an environment-friendly approach to alleviate the undesirable effects of extreme ecological/environmental conditions. These microorganisms convert organic matter into simple compounds that facilitate vital nutrients, improve soil fertility, maintain the natural habitat of the soil, and increase plant productivity. Moreover, plant growth-promoting rhizobacteria (PGPR, a group of beneficial bacteria) are also known to improve plant resilience/tolerance, growth, and productivity by producing some hormones under stressful environments (see Chapters 15 and 16 for details). The chemical attractants (amino acids, inorganic acids, soluble sugar, vitamins, and growth factors) released by plant root system facilitate colonizing the diverse bacterial community. A large number of investigations have shown that PGPR inoculation or application of microbe-to-plant signal compounds increases the plant growth under adverse environmental conditions such as high temperature, droughts, and salinity (Saleem et al. 2007; Yang et al. 2009; Wang et al. 2012; Nadeem et al. 2014; Jochum et al. 2019; Chiappero et al. 2019; Khan et al. 2020; Mukhtar et al. 2020). It has been reported that PGPR enhances plant growth by boosting the nutrients uptake, mainly phosphorus (Glick 2014; Rafique et al. 2019). Also, in this concern, the production of hormones such as gibberellic acid, indole-3-acetic acid (IAA), cytokinins, abscisic acid (ABA), and antibiotics and siderophore have exhibited an important role (Compant et al. 2005; Warnita et al. 2019). It has been demonstrated that PGPR inoculation enhanced the processes of photosynthesis and electron transport, whereas it reduced stomatal resistance and xylem balancing pressure and accelerated biomass of pea (*Pisum sativum*) plants under salt stress (Wang et al. 2016a, b). Inoculation of *Enterobacter* sp. UPMR18 to okra (*Abelmoschus esculentus*) plants increased the antioxidant enzyme activities and transcription of ROS pathway genes when grown in 75 mM NaCl and exhibited augmented salt tolerance (Habib et al. 2016). It has been reported that 1-aminocyclopropane-1-carboxylate (ACC) deaminase-producing bacteria have the ability to supply nitrogen and energy to plants (Glick et al. 1998). Accordingly, inoculation of ACC-deaminase-producing bacteria encouraged longer roots and facilitated more amounts of water under stress conditions, which may have augmented growth and yield of wheat (*Triticum aestivum*) under salt-stressed conditions (Zahir et al. 2009). ACC-deaminase-producing strains of *Pseudomonas fluorescens* and *Enterobacter* spp. have also increased maize yield in salt-affected fields (Nadeem et al. 2009). In this study, higher K^+/Na^+ ratios and NPK uptake were also noticed in inoculated plants under salt-stressed conditions. Recently, Mukhtar et al. (2020) have demonstrated the role of heat-tolerant PGPR, ACC-deaminase, and extracellular polymeric substances producing *Bacillus cereus* strain. They have reported improvement in the physiological (shoot and root length, fresh and dry weight, and leaf surface area) and biochemical traits (chlorophyll contents, relative water content, protein, proline, and antioxidant activities) of two tomato varieties grown under heat-stressed conditions. Likewise, Asghari et al. (2020) have shown that PGPR inoculation reduced the adverse effects of water stress on physio-biochemical characteristics and secondary metabolites production in pennyroyal (*Mentha pulegium*) plants. Application of *Pseudomonas fluorescens* in soil, alone or in combination with mycorrhiza fungi, has also improved the growth of marigold (*Calendula officinalis*) plants under drought-stress conditions (Hasan et al. 2020). However, most of these studies were conducted under controlled laboratory conditions; therefore, to validate the current results, extensive field trials are still required. As it has been already predicted that the extreme environmental conditions, such as high temperature, droughts, and salinity, are likely to become more frequent as the climate change continues. Microbes as mentioned earlier thus serve as alternative and sustainable tools to upsurge plant growth and development under extreme ecological/environmental conditions.

8 Nanofertilizer and Plant Performance

Nanotechnology-assisted advancement in biotechnology has improved plant tolerance and resistance to abiotic as well as biotic stresses (Ocsoy et al. 2013; Chun and Chandrasekaran 2019; Singh and Husen 2019, 2020; Kumari et al. 2020). Potential applications of nanotechnology are increasing in every sector of science and technology (Wagay et al. 2019; Mishra et al. 2019; Husen and Iqbal 2019a, b; Husen 2020; Raja and Husen 2020; Porwal et al. 2020). In this regard, the use of nanofertilizer for smart plant growth and development is very innovative. In fact, nutrient management in food crops and other higher plants is a key challenge as it relies mainly on chemical fertilizers. It has been noticed that the traditional fertilizers are costly, bulky, and also harmful to human food chain and the environment. Thus, with the projected increase in human population and extreme climatic situations, the need of sustainable plant growth and production has led to the search for eco-friendly fertilizers, primarily those with high nutrient-use efficiency. In this context, nanofertilizer has emerged as a promising alternative (Husen and Siddiqi 2014; Husen and Iqbal 2019a, b; Iqbal et al. 2019; Husen and Jawaid 2020). Replacing the traditional methods of fertilizer application with nanofertilization is a way to release nutrients into the soil gradually and in a controlled way, thus preventing pollution of water resources (Moaveni and Kheiri 2011; Iqbal et al. 2019). Various formulated nanofertilizers (N, P, K, Cu, Fe, Mn, Mo, Zn, and carbon nanotubules) have revealed a remarkable control release for a targeted delivery efficiency. They are prepared by using organic and inorganic nanomaterials (NMs). Their fabrication processes also vary. The inorganic NMs include metals (Ag, Au, etc.) and/or metal oxides (ZnO, TiO_2, Al_2O_3, FeO, Fe_2O_3, etc.), while the organic NMs include lipids, polymers, fullerenes, and carbon nanotubules. Based on plant nutrient requirements, they can be classified into micronutrient nanofertilizers, macronutrient nanofertilizers, and nanoparticulate fertilizers. In addition to this, the concept of nano-biofertilization is also emerging fast, enabling an interaction between NMs and PGPR/blue-green algae/*Rhizobium* with reference to some food crops (Shukla et al. 2015). Such interactions may produce positive and negative effect on the crops, depending on the type of NMs. For instance, the interaction between Au-NPs and PGPR may promote growth, while Ag-NPs may not, because they adversely influence the biological processes of microbes. Thus, interaction between NMs and PGPR/blue-green algae/*Rhizobium* needs to be intensely investigated. Additionally, nanobiosensors can be effectively used for the sensing of fertilizers, herbicides, pesticides, insecticides, pathogens, moisture, soil, pH, etc., for sustainable plant production (Rai et al. 2012; Husen and Iqbal 2019a, b; Husen and Jawaid 2020). It has been suggested that the precision farming, with the help of smart sensors, could increase plant productivity, as this technology provides farmers with better fertilization management, low inputs, and better management of time and environment. Precision farming's technologies include satellite-positioning systems, geographic information systems, and remote-sensing devices that could remotely detect crop pests or the evidence of stress such as drought or salinity. Nanosensors dispersed in the field can also detect the presence of plant viruses and other pathogens and the level of soil nutrients (Shang et al. 2019; Kumar and Arora 2020; Li et al. 2020). Studies have shown that nanofertilizers cause an increase in the use efficiency of plant nutrients, reduce soil toxicity, minimize the potential adverse effects of excessive chemical fertilizer use, and reduce fertilizer application frequency (Husen and Siddiqi 2014; Husen and Iqbal 2019a, b; Iqbal et al. 2019; Husen and Jawaid 2020).

9 Hormonal Interactions

The net result of all the stresses experienced by the plant is the fall in production and a slow growth. Under adverse conditions (biotic and abiotic stresses), plants are forced to adapt to the stress and combat the ecological/environmental changes which lead to changes in their physiological, metabolic, and molecular functions (Cramer et al. 2011; Husen et al. 2014, 2017, 2018; Jeandroz and Lamotte 2017; Yurchenko et al. 2018; Chi et al. 2019; Wang et al. 2020). Hormones such as auxins, ABA, brassinosteroids (BRs), cytokinin, ethylene (ET), and gibberellins contribute significantly to plants. In addition, jasmonic acid (JA), salicylic acid (SA), plant peptide hormones, polyamines, nitric oxide, strigolactones (SLs), and karrikins are also recognized as important plant hormones (Heldt 2004; Umehara et al. 2008; Wang and Irving 2011; Smith and Li 2014; Koltai and Prandi 2016). They act alone or interact with other hormones, generate multiple signals, and regulate the growth and development of plant organs. They are known to protect and improve the physical development of plants even under harsh environmental conditions, such as water scarcity, soil salinity, temperature variation, and metal toxicity (Kagale et al. 2007; Siddiqi and Husen 2017, 2019; Podlešáková et al. 2019; Heidari et al. 2020; Nolan et al. 2020). For example, foliar application of JA on wheat seedlings for 3 days, followed by the application of NaCl solution, decreased plant height, root length, shoot and dry weight, chlorophyll b, and carotenoids content (Qiun et al. 2014). Activity of superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) was found to decrease under salt stress in wheat seedlings. The expression level of SOD, POD, CAT, and APX genes was significantly upregulated in wheat seedlings under salinity stress even when the seedlings were not pretreated with JA. It has been noted that exogenous JA treatment neutralizes NaCl-induced oxidative stress, as reflected by a decrease in MDA and H_2O_2 concentration and the production rate of peroxide radicals. Thus, JA helps in scavenging free radicals, preventing lipid peroxidation by excess ROS produced during salinity stress. Exogenous JA also enhanced APX, CAT, and POD activities in soybean under cadmium stress (Noriega et al. 2011). Enhancement in activity of these enzymes in soybean and wheat is a consequence of activation of defense mechanism under stressful conditions in general (Anjum et al. 2011). In another study, Ruiz-Lozano et al. (2016) have studied the role of SLs in *Solanum lycopersicum* and *Lactuca sativa* under drought stress. The abscisic acid levels, in addition to the expression of the corresponding marker genes, were affected by drought stress in the nonarbuscular mycorrhizal (*S. lycopersicum*) and arbuscular mycorrhizal plants (*L. sativa*). However, SL levels and the expression of corresponding marker genes were affected by both the arbuscular mycorrhizal symbiosis and the drought stress. Authors have suggested that the arbuscular mycorrhizal symbiosis alleviated drought stress by altering the hormonal profiles and improved growth rate and efficiency of photosystem II in the host plant. It has also been suggested that under stress conditions, plants increase SL production, which facilitates symbiosis and thus alleviates the adverse stress response. Plant responses to various biotic and abiotic stresses and the role of hormones in increasing resilience and productivity of plants have been discussed in detail in the chapters to follow.

10 Conclusion

In the recent past, the extreme meteorological and hydrological events have become more common and destructive. These extreme ecological/environmental conditions are testing the plants' resilience and forcing them to tolerate and adapt to the adverse situations. As to the drought, salt stress, extremes temperature, heavy metal, and multiple stresses, careful studies of the complex tailored genetic performances and recognition of important genes, transcripts, protein, and metabolites as well as phenotypic performances may pave the way for designing food crops as well as medicinal plants with improved tolerance capability that could sustain growth and productivity under multiple environmental stress conditions. Nutrient management for optimum plant growth is also a key challenge as it relies mainly on traditional chemical fertilizers, although these are not eco-friendly. Thus, the use of beneficial microbes as biofertilizer and as the nanofertilizers or nano-biofertilizers can prove advantageous and eco-friendly. Further, plant hormones, mainly ABA, SA, JA, BR, IAA, and ET, are known to play major roles in mediating plant defense response against extreme environmental conditions, such as water scarcity, soil salinity, temperature variation, and metal toxicity. Thus, understanding of environmental stress signal sensing, and of the balance between defense and development in plants, is crucial for the improvement of plant resilience and ability to thrive under harsh environment.

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Chapter 2
Expression and Regulation of Stress-Responsive Genes in Plants Under Harsh Environmental Conditions

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Abbreviations

CDPKs	Ca-dependent protein kinases
G-type	Gap-type
HSE	Heat shock element
HSPs	Heat shock proteins
HSR	Heat shock response
LEA	Late embryogenesis proteins
MAPK/MPK	Mitogen-activated protein kinase
P-type	Perfect-type
S-type	Step-type
TFs	Transcription factors

1 Introduction

All living organisms are subjected to a set of conditions termed as ‘stress’, which makes them deviate from normal physiological conditions. In nature, plants are challenged by two major stresses; abiotic stress and biotic stress either simultaneously or singly. Abiotic stress is the one that is caused by fluctuation in the environment in which the plant is growing whereas biotic stress is a consequence of disturbances by living organisms such as fungi, bacteria, pests, etc. Plants often encounter these environmental stresses resulting in irreversible damage to their biological system which ultimately leads to lower yield and productivity of plants, in particular, crop plants’ decrease in yield by more than 50% annually has been observed (Boyer 1982; Ramegowda and Senthil-Kumar 2015).

Being sessile and devoid of a highly specialized immune system, plants have to constantly adapt intricate mechanisms to thrive under adverse biotic and abiotic stress conditions. These complex mechanisms to fight stress are categorized into avoidance mechanisms and tolerance mechanisms. Plants escape particular stress by employing avoidance mechanisms such as stomatal closure, early maturation, changes in membrane lipid compositions whereas tolerance mechanisms are used by plants to grow under stress and generate economic yield (Verslues et al. 2006; Yamamoto 2016). Major tolerance mechanisms include ‘expression and regulation of stress-responsive genes’ that encode some important metabolic proteins such as the late embryogenesis proteins and chaperones along with participation in the modulation of the genes involved in the stress signalling pathway. Upon exposure to stress, various external and internal signals are perceived by plants through various mechanisms that ultimately lead to the regulation of diverse responses incriminated in its tolerance development (Sun et al. 2018). An external stimulus generates signalling molecules and activates various transcription factors, hence playing a role in the activation of downstream stress-responsive genes (Guo et al. 2016; Jiang et al. 2017). Certain examples of signalling molecules produced by an external stimulus are Ca-dependent protein kinases (CDPKs), sugar (as signalling molecule), mitogen-activated protein kinase (MAPK/MPKs) and plant hormones (Ahmad et al. 2012; Hasanuzzaman et al. 2018). Stress-responsive gene expression is essential for the maintenance of cellular homeostasis.

Regulation of these stress-responsive genes befalls at three stages,namely, transcriptional, post-transcriptional and post-translational. Transcriptional regulation involves the interaction of chromatin with various proteins and RNAs, chromatin modification and remodelling. These changes are brought about by cis-regulatory elements such as enhancers and promoters and trans-regulatory elements such as transcription factors (TFs) (Singh and Laxmi 2015). Post-transcriptional regulation occurs at different stages related to mRNA maturation (such as processing, trafficking, translation, turnover and stability) (Fabian et al. 2010). Finally, post-translational regulation occurs via different processes such as phosphorylation, dephosphorylation, adenylation, SUMOylation and ubiquitinylation. All these regulations ensure the expression of an array of downstream genes to 'switch on' the adaptive response.

2 Impact of Challenging Environmental Conditions on Plants

Various stresses either simultaneously or sequentially affect plants by disturbing plant growth rate, productivity and plant cell homeostasis (Husen 2010; Husen et al. 2014, 2016, 2017; Getnet et al. 2015; Embiale et al. 2016; Hussein et al. 2017; Sinha et al. 2019). The response against particular stress is triggered by the modulation of gene expression important for stress response.

2.1 Cold Stress

Chilling injury and freezing injury caused by low temperatures contribute to cold stress. Chilling injury is caused by temperature below 20 °C whereas freezing injury is caused by a temperature less than 0 °C, affecting both growth and development of plants (Kasuga et al. 1999; Lang et al. 2005; Sharma et al. 2020). Some symptoms seen in plants growing under cold stress are decreased leaf enlargement, necrosis and wilting. Negative impact of cold stress is also observed in reproductive stage of plants, for example loss of floral sterility in rice plants (Jiang et al. 2002; Sharma et al. 2020). It also distresses germination, and leads to stunted plantlets, withering and lowered tillering. Delayed heading and pollen sterility leading to reduced grain yield are also evident due to cold stress (Suzuki et al. 2008). Cold stress-induced dehydration also leads to plasma membrane damage (Steponkus 1984; Steponkus et al. 1993; Sharma et al. 2020).

2.2 Heat Stress

With an outburst of the human population, there has been a rise in the emission of greenhouse gases resulting in temperature increase across the globe. Global warming directly or indirectly affects various life forms. Heat stress disturbs plant growth and crop harvest (Hasanuzzaman et al. 2012, 2013; Wassie et al. 2019). Heat stress results in surplus production of reactive oxygen species (ROS) causing another type of stress named oxidative stress (Hasanuzzaman et al. 2012, 2013; Ergin et al. 2016).

2.3 Salt Stress

Rise in salinity, mostly in arid and semiarid regions (Shanon 1986; Hussain et al. 2019), restricts the proliferation of plants in their natural habitat. An increase in sodium chloride relates to a decrease in growth as established by various experiments (Beltagi et al. 2006; Jamil et al. 2007; Houimli et al. 2008; Memon et al. 2010; Abdallah et al. 2016; Hussain et al. 2018). Leaf area is also negatively influenced by various concentrations of sodium chloride (Raul et al. 2003; Mathur et al. 2006; Chen et al. 2007; Yilmaz and Kina 2008; Hussain et al. 2018). The quantity of leaves also gets negatively influenced by a hike in salt concentration (Raul et al. 2003; Jamil et al. 2005; Ha et al. 2008; Natasha et al. 2019). Salt stress also increases osmotic stress as well as ion toxicity.

2.4 Drought Stress

Due to changes in climate because of global warming and increased CO_2 levels, the distribution of rainfall patterns has become uneven leading to an important stress called drought. Plant growth arrest is the first response during drought stress. Crop yield is reduced mainly because of three reasons: (i) lesser canopy absorption of photosynthetically active radiations (PAR), (ii) declined efficiency of use of radiation and (iii) reduced harvest index (Earl and Davis 2003; Charbonnier et al. 2017). Because of drought, there is a reduction in seed germination and plantlet stand (Kaya et al. 2006; Toscano et al. 2017). Rice plants growing under drought stress suffer repercussions on growth and overall development (Tripathy et al. 2000; Manikavelu et al. 2006; Zhang et al. 2018b).

3 Mechanisms Underlying Abiotic Stress Responses

Plants have different sensing mechanisms for different stresses. This sensing of the stress can be brought about by underground parts or above-ground parts. As perception is different, mechanism should also be different for different stress. Binding of a ligand to a specific membrane receptor is one of the most common models for sensing external stimuli (Verslues and Zhu 2005). This model only holds true for chemical stresses (e.g. heavy metal stress) and not for physical stresses (e.g. heat stress and cold stress) as they do not involve any type of chemical ligand. Stress in plants leads to a functional decline that involves a decline in photosynthetic activity, transport and agglomeration of metabolites and absorption and translocation of ions. These declines may lead to an acute damage or death if not counteracted in time. Rapidly imposed stress also results in the production of ROS (Cruz de Carvalho et al. 2012; Fichman and Mittler 2020).

Stress events and responses are marked by four phases: (i) the alarm phase, (ii) the resistance phase, (iii) the exhaustion phase and (iv) the regeneration phase. The phases are categorized on the basis of intensity and duration of the stressor (Lichtenthaler 1998; Kranner et al. 2010; Fig. 2.1). The four phases are discussed briefly below.

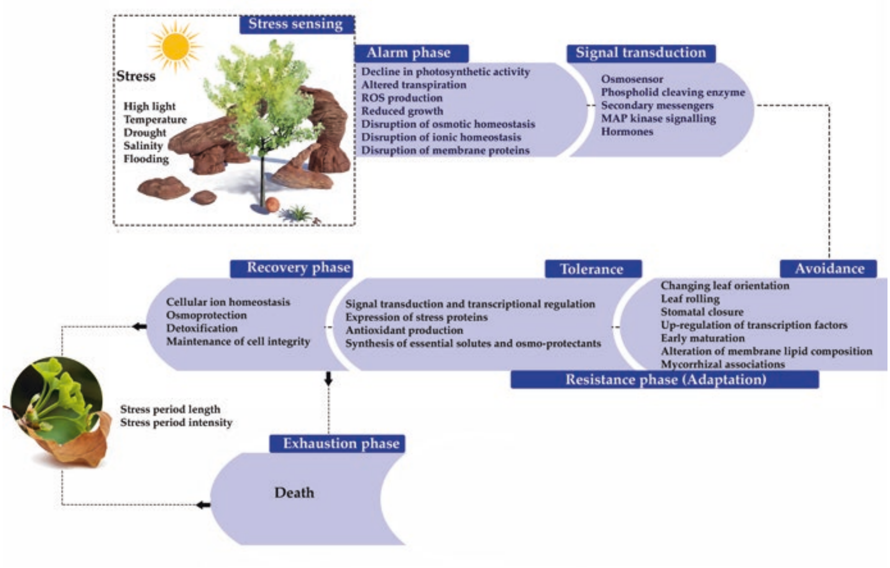

Fig. 2.1 Flow chart showing the different phases of stress responses in plants

3.1 *The Alarm Phase*

The alarm phase shows a functional decline known as stress reaction based on the changes in the optimum growth conditions. During this phase, a functional decline in terms of vitality and catabolism rate is observed (Lichtenthaler 1998). Stressors can act together and hence simultaneously activate the alarm phase. For example, plants growing in normal temperature when exposed to high temperature experience multiple stresses such as high temperature stress, drought stress and high light stress, triggering various responses (Kranner et al. 2010). Stress coping mechanisms or stress tolerance mechanisms are activated in this phase (Lichtenthaler 1998). The functional decline in this phase gets overcome by counter-reactions for functional restoration observed while transitioning to the resistance phase.

3.2 *The Resistance Phase*

This phase is also called the restitution phase, where plants grow and reproduce under stress through adaptation, repair and hardening process (Lichtenthaler 1998). Adaptation mechanisms include either tolerance mechanisms or avoidance mechanisms. Plants escape particular stress by employing avoidance mechanisms such as transcriptional cooling, stomatal exposure or early maturation whereas tolerance mechanisms are used by plants to grow under stress and provide economic yield (Verslues et al. 2006; Yamamoto 2016). Stress tolerance mechanisms triggered in the alarm phase and the mechanisms activated in the resistance phase are required to provide a physiological standard which are ideal for stress conditions. Moreover, a plant possesses particular resistance maximum; if breached by prolonged stress, the stress can make the plant to enter the next phase (Lichtenthaler 1998).

3.3 *The Exhaustion Phase*

The exhaustion phase or the end phase is observed when stress coping mechanisms fail to protect the plant from prolonged or overloading stress dose (Lichtenthaler 1998). It may lead to severe damage and persistence of these stressful conditions ultimately leads to death. The severity of damage depends on various factors such as stress dose, plant species, organ and time (Lichtenthaler 1998; Fig. 2.1).

3.4 The Regeneration Phase

If the plant is removed before the strong influence of the stress, plants can regenerate and restore their physiological functions by entering into the regeneration phase (Lichtenthaler 1998; Kranner et al. 2010). The regeneration phase assures the survival of the plant except in cases where permanent damage has been caused by extended or overburdening stress.

4 Expression and Regulation of Stress-Responsive Genes

4.1 Expression of Stress-Responsive Genes

Different stresses such as high- or low-temperature stress, salinity stress and drought stress are all deviations from normal environmental conditions that negatively affect the quality and productivity of plants and animals. Plants being sessile cannot run away from these adverse conditions, so they adapt themselves to respond to these stresses thus managing their survival. Plants survive these abiotic stresses by employing either tolerance mechanisms or avoidance mechanisms (Verslues et al. 2006; Yamamoto 2016). Out of all, expression of stress-responsive genes is an essential tolerance mechanism that allows plants to grow under these stressful conditions. Genes activated during stress regulate other genes for stress signalling response in addition to encoding important metabolic proteins.

Preparation for stress responsiveness is known as priming (Conrath et al. 2006; Lal et al. 2018). It increases the defensive capacity of the plant and brings the plant to an alarming state of defence. Priming is also associated with the modification of chromatin of the promoter region of WRKY transcription factors. As reported, epigenetic mechanisms are also involved in response to environmental and multiple forms of abiotic stress (Pandey et al. 2016; Begcy and Dresselhaus 2018). Different abiotic stresses promote the modified methylation status of DNA and also the alteration of nucleosomal histones.

Genes induced by environmental stress are mainly categorized into two categories based on the protein products encoded by these genes: the first group includes genes, which includes protein products that are directly involved in providing resistance such as heat shock proteins (HSPs) or chaperones involved in protein folding, protein refolding and removal of unfolded protein, late embryogenesis proteins (LEA), some osmo-regulators, etc. The second group includes genes, whose coded protein product is further responsible in the regulation of expression of other genes and stress signalling pathways, usually the transcription factors.

In general, abiotic stresses are known to vary the amount of many transcripts and proteins by controlling gene expression and turnover of protein, implying an essential role of transcriptional and post-transcriptional regulations played in the protection of plants from various stresses at the cellular level. The generation of important metabolic proteins such as HSPs and of proteins participating in the modulation of stress signalling pathways, such as kinases such as mitogen-activated protein kinase (MAPK) or transcription factors (TFs), is required for responses to different abiotic stresses (Wimalasekera and Scherer 2018). To maintain a balance in stress adaptation, there is an instant production of new transcripts and, after some time, a steady state is reached.

4.2 Regulation of Expression of Stress-Responsive Genes

Regulation of a particular gene at the transcriptional level is directly governed by the action of the various TFs on transcription factor-binding sites (TFBS) (Chaves and Oliveira 2004; Singh and Laxmi 2015) found in the promoter region of various genes. Transcription factors are proteins having a DNA-binding domain that act on a particular gene by attacking on particular elements present in its promoter. Promoters are upstream regulatory regions of genes that bind transcription factors and components of the transcription machinery, aiding the employment of RNA polymerase II and initiation of the process of transcription (Juven-Gershon et al. 2008). Transcription factors are categorized into general transcription factors and additional transcription factors. General transcription factors attach to the promoter and result in the establishment of RNA polymerase II onto the promoter and initiate the transcription. The additional transcription factors act as either inducer (activators) or repressors of RNA polymerase. They enhance or reduce the ability of TFs to transcribe a particular gene by binding to regulatory elements such as enhancers and silencers, respectively, thus regulating gene expression.

Transcription factors are categorized into families grounded on different DNA-binding domains present in them (Riechmann et al. 2000). Whether the transcription regulating proteins such as transcription factors are present or absent, it regulates the gene transcription, which usually involves the entire process of signal transduction specified by the developmental stage, type of tissue, or environmental factor (Wyrick and Young 2002). Till now four different regulons are identified: (1) DREB (dehydration-responsive element-binding) or CBF (C repeat-binding factor); (2) the AREB/ABF (ABA-responsive element-binding protein/ABA-binding factor) regulon; (3) the NAC (N-acetylcysteine) proteins and ZF-HD (zinc-finger homeodomain) regulon; and (4) the MYC (myelocytomatosis oncogene)/MYB (myeloblastosis oncogene) regulon. Most of these TFs control the expression of the target gene by binding in promoters of stress-related genes to the associated cis-elements.

These families of TFs are repeatedly shown to be involved in response to various stresses (Table 2.1). Genes encoding WRKY factors are transcriptionally induced under stress conditions (Dong et al. 2003). For example, overexpression of the *OsWRKY11* gene increased drought tolerance (Wu et al. 2009). *OsNAC6* expression is induced by drought, high salinity, cold and ABA (Ooka et al. 2003). The environmental stress-responsive transcription factors of NAC type in pearl millet have also

Table 2.1 List of genes involved in the response to various stress conditions and their regulation mechanisms

Gene	Plant species	Function	Regulation	References
Mitogen-activated protein kinases (MAPKs)	Several	Salt and drought tolerance	Phosphorylation and de-phosphorylation	Zhu (2002)
OsNAC6	*Oryza sativa*	Drought tolerance	Induced by stress in drought, cold, high salinity and ABA	Ooka et al. (2003)
DREB2A	*A. thaliana; Triticum aestivum*	Transcripts DREB TF, providing drought and salinity stress tolerance	Post-transcriptional activation	Sakuma et al. (2006) and Egawa et al. (2006)
STABILIZED1 (STA1)	*A. thaliana*	Codes a pre-mRNA splicing factor, under cold stress and water deficiency	Alternative splicing	Lee et al. (2006)
COR; RD29B	*A. thaliana*	Cold stress tolerance	mRNA turnover by translation of putatively target genes by AtRZ-1a	Kim and Kang (2006)
XERICO	*A. thaliana*	Encodes an H2-type zinc-finger E3 ubiquitin ligase	Transcriptional upregulation of an ABA-biosynthesis gene, *AtNCED3*	Ko et al. (2006)
GRP2	*A. thaliana*	Encodes GRP2; salt and cold stress tolerance	Transcription anti-termination activity of GRP2	Kim et al. (2007)
OsWRKY11	*O. sativa*	Encodes a transcription factor with the WRKY domain	Controlled by Heat Shock Protein 101 (HSP101) promoter	Wu et al. (2009)
OsWRK45	*A. thaliana*	Altered drought and salt tolerance	Response to stress-related hormone abscisic acid (ABA)	Qiu and Yu (2009)
OsWRK72	*A. thaliana*	Controls auxin transport and ABA signal pathways	Stress factors such as NAA, ABA, NaCl and heat	Song et al. (2010)
LEA4–5, P5CS1 and HSFA3	*A. thaliana*	Ethylene (ET) and Jasmonate (JA) signalling during environmental stresses	Stress-specific binding of ERF1 to DRE elements in the promoter region	Cheng et al. (2013)

(continued)

Table 2.1 (continued)

Gene	Plant species	Function	Regulation	References
ER5, TAS14, Cat1, Cat2, ERF1, APX1, APX2, P5CS and GME2	*Solanum lycopersicum*	Drought and salinity tolerance	Transcriptional regulation by SlNAC TF	Zhu et al. (2014)
GmDREB1	*Glycine max*	Encodes GmDREB1s TF in various abiotic stress	Transactivation activities of TFs through DRE	Kidokoro et al. (2015)
PgNAC21	*Pennisetum glaucum*	Salinity tolerance	Codes for stress-responsive NAC Transcription Factor	Shinde et al. (2019)

shown control of tolerance against abiotic stresses such as drought (Shinde et al. 2019). In *Solanum lycopersicum*, various stress-related genes such as *ER5, TAS14, Cat1, Cat2, ERF1, P5CS, APX1, APX2* and *GME2* are regulated by the SlNAC4 transcription factor during salinity and drought stress conditions (Zhu et al. 2014). Ethylene Response Factor 1 (ERF1) can bind both GCC box and DRE elements (Gong et al. 2008). ERFs specifically bind DRE elements and GCC boxes in a fixed stress-specific manner. In JA-responsive genes, ERF1 binds to GCC boxes present in the promoter whereas, in *LEA4-5*, *P5CS1* and *HSFA3* abiotic stress-responsive genes, ERF1 binds to the DRE elements (Cheng et al. 2013). A few TFs can also downregulate the expression of *DREB* genes. For example, MYB15 protein attaches to the MYB recognition domains in the *DREB1s* promoter regions, decreasing the expression of the gene (Agarwal et al. 2006).

4.2.1 Role of Non-coding RNAs (ncRNAs) in Abiotic Stress

It has been revealed recently that non-coding RNAs (ncRNAs) are key players in the stress response mechanisms (Ahmed et al. 2020). Transcripts lacking long open-reading frames (usually >100 codons) and/or which do not show codon conservation are classified as ncRNAs. They occupy a major part of the transcriptome and participate in the management of transcriptional and post-transcriptional gene regulatory pathways (Dykes and Emanueli 2017). Based on the size, ncRNAs are of two types: small non-coding RNA (sncRNA, <200 nucleotides), which include miRNA, siRNA, piRNA etc., and long non-coding RNA (lncRNA, ≥200 nucleotides). Out of the many different types of ncRNAs, miRNA, siRNA and lncRNA are found to be vital regulatory factors in abiotic stress tolerance (Ahmed et al. 2020).

The siRNAs and miRNAs are produced within the cytoplasm when Dicer-like enzymes cleave the double-stranded RNA into smaller pieces. They further get attached with RNA-induced silencing complex (RISC) and hinder gene expression by degradation of target mRNA or by repression of translation or by methylation of target gene/histone. Stress regulates small RNAs positively which may target negative regulators for stress tolerance to enhance suppression whereas those which are suppressed at the time of stress are expected to enhance the positive regulators of stress tolerance, followed by gene product accumulation (Sunkar et al. 2007). The lncRNAs are transcribed by RNA Pol II from the intergenic or intronic regions, in anti-sense or both directions with respect to the target gene. They perform multiple functions such as guiding the chromatin-modifying enzymes to the promoter, acting as a scaffold for binding twa decoyteins together or as decoy. They can also mimic miRNA targets and protect them from degradation, act as precursors for various sncRNAs such as miRNA, siRNA and piRNA and help in chromatin looping, alternate splicing and protein localization (Wilusz et al. 2009; Liu et al. 2019). These ncRNAs also play other major roles such as regulation of cell cycle, fertility and flowering. The stress-responsive ncRNAs can be identified by RNA Seq and various bioinformatic tools. Qin et al. (2017) found that lncRNA (DRIR) in *Arabidopsis* functions as a positive regulator of stress responses such as salt stress and drought. They found a T-DNA mutant $drir^D$ that showed a higher expression of *DRIR* than wild type. They also generated *DRIR* overexpression lines through transgenic approach. All these plants showed higher tolerance to drought, salt and ABA treatments. Genome-wide transcriptome analysis showed that *DRIR* regulated gene expression that takes part in ABA signalling, water movement and various stress-relief processes. Zhang et al. (2018a) revealed that knocking down miR166 confers drought tolerance by altering gene expression involved in cell wall biogenesis or polysaccharide metabolism, which in turn led to morphological changes such as leaf rolling, reduction in size of vascular bundle in stem and reduced hydraulic conductivity. They also observed that the lines overexpressing *OsHB4* (a target gene of miR166) showed enhanced drought tolerance. This explains the mechanism by which miR166 imparts tolerance to drought stress.

The knowledge of different mechanisms through which ncRNAs regulate gene expression can unfold various targets for manipulating the responses to different abiotic stresses. By the advent of molecular biology techniques, it will be possible to develop abiotic stress-tolerant crops by overexpression or downregulation of target genes using transgenesis or genome-editing techniques.

4.2.2 A Case Study: Transcriptional Regulation of Heat Shock Proteins

Heat shock proteins are the proteins that are synthesized in large amounts in response to accumulation of unfolded proteins during various stresses such as heat stress, oxidative stress, heavy metal stress, etc. through heat shock response (HSR) (Heikkila et al. 1982; Courgeon et al. 1984; Yura et al. 1984; Michel and Starka 1986). These heat shock proteins are classified into seven different classes, among which the initially discovered class ‘molecular chaperone’ is the predominant class (Ellis et al. 1989). Chaperones bind to the hydrophobic patches or specific peptide or structural elements of non-native proteins, partially or globally unfolded proteins and result in the folding of these proteins through ATP hydrolysis.

Specific transcription factors contribute majorly in the expression regulation of heat shock proteins (Wu 1984; Wu et al. 1986). For example, in eukaryotes, Hsf1 is an important regulator whereas, in prokaryotes, σ32 is an important regulator that replaces σ70 under heat stress. In prokaryotes, heat shock proteins are maintained in low amounts under normal conditions through degradation of σ32 by a complex of DnaK (HSP70) and its cofactor DnaJ (Rodriguez et al. 2008). Similarly, in eukaryotes, heat shock proteins are maintained in substantial amounts by maintaining Hsf1 in an inactive state forming complexes with Hsp90 and Hsp70/Hsp40 chaperone systems. Monomeric heat shock factors such as Hsf1 in eukaryotes, upon stress, get converted into active homo-oligomers or hetero-oligomers and transported into the nucleus. Inside the nucleus, the activated heat shock factors further undergo various modifications such as phosphorylation, SUMOylation and oligomerization (Hietakangas et al. 2003; Prahlad and Morimoto 2009; Akerfelt et al. 2010). These heat shock factors being transcription factors are able to sit on a particular promoter region of stress-responsive genes. This region of the promoter is called as heat shock elements. There are three different types of HSE known to date: Perfect (P), Gap (G) and Step (S) (Yamamoto et al. 2005). Perfect (P)-type HSE comprises a contiguous array of three inverted repeats of nGAAn (nTTCnnGAAnnTTCn). Gap (G) type consists of two inverted repeats of nGAAn separated from a third unit by a gap of 5 base pairs (nTTCnnGAAn(5 bp)nGAAn). In Step (S) type, all the three units are separated by 5 base pairs (nTTCn(5 bp) nTTCn(5 bp)nTTCn). Heat shock factors after binding to this region have the ability to either upregulate or downregulate the transcription of stress-responsive genes (Fig. 2.2).

The next level in gene expression modulation is post-transcriptional regulations, which include processes divided into four groups: processing of transcript (mRNA) after transcription that includes capping, splicing and polyadenylation; nucleocytoplasmic trafficking of mRNA, its turnover as well as stability and translation of mRNA into the amino acid sequence. These processes affect transcript sequence, stability and intracellular localization of protein products (Haak et al. 2017). The event of splicing resulting in excision of introns occurs in the nucleus after the

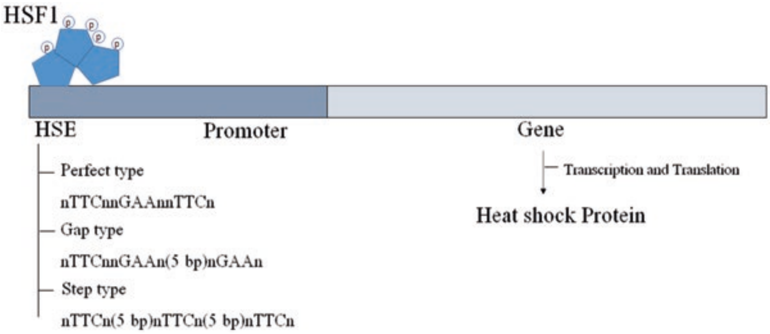

Fig. 2.2 Transcriptional regulation of heat shock proteins by heat shock factors

transcription of a particular gene, at the spliceosomal complex. Specific splicing factors (SF) are involved in the splicing process (Carvalho et al. 2010). For example, in *Arabidopsis*, the *DREB2A* encodes stress-related DREB/CBF transcription factors induced during stresses like drought stress and salinity stress. DREB2A protein modification could be necessary for its activation under stress conditions (Sakuma et al. 2006). A similar post-transcriptional regulation of *DREB* gene is also reported in common wheat as well in soybean (Kidokoro et al. 2015). *STABILIZED1* (*STA1*) is a gene that codes for a pre-mRNA splicing factor in the nucleus, which is important for cold tolerance in Arabidopsis. Alternative splicing was also observed in plants in deficiency of water (Lee et al. 2006). Two of the Arabidopsis glycine-rich proteins, GRP2 and AtRZ-1a, have been observed to play a part in abiotic stress tolerance as RNA chaperones. Both the proteins increase seed germination and plantlet growth under cold stress and enhance tolerance under low-temperature conditions. AtRZ-1a alters the translation of putatively targeted genes, together with stress-responsive genes and genes responsible in RNA and protein metabolism (Kim and Kang 2006), whereas, by possessing transcription antitermination activity, GRP2 regulates the expression of various genes that are mitochondrial encoded (Kim et al. 2007).

Post-translational-level regulation includes processes of phosphorylation, SUMOylation and ubiquitination of proteins which modulate plant response under abiotic stress. During times of water deprivation and osmotic stress, many signal transduction cascades processed by SNF-1-related protein kinases (SnRKs) and mitogen-activated protein kinases (MAPKs) are activated through phosphorylation and dephosphorylation of specific residues (Zhu 2002). The XERICO gene is upregulated, which encodes an H2-type zinc-finger E3 ubiquitin ligase and results in the enhancement of tolerance during drought due to frequent stomatal closure that is ABA induced. XERICO modulates the ABA level by increasing the transcription of *AtNCED3,* the key ABA biosynthetic gene (Ko et al. 2006). Sumoylation processes participate in phosphate starvation responses and to tolerate different temperature stresses (Catala et al. 2007). In ubiquitination, mostly the 26S proteasome recognizes the ubiquitinated proteins for degradation while the proteins are modified via a chain of multi-Ubs that is connected through one of 7 lysine (K) residues of Ub, primarily K48 and K11 (Kim et al. 2013). Mono-ubiquitination or polyubiquitination through other lysine residues of Ub, such as K63, can control the localization of a ubiquitination substrate as well as its activity to serve as a degradation signal (Komander and Rape 2012). SnRK1, an important ABA-related protein kinase is regulated by SR45, a splicing factor, which binds RNAs that are coded during stress and for other hormone-related genes (Carvalho et al. 2016).

4.2.3 A Case Study: Post-translational Regulation of MAP Kinase

MAPKs are serine/threonine kinases that can phosphorylate particular protein at specific serine/threonine residue, thereby being a part of the protein kinase cascade and playing a key role in growth and defence in plants (Zhang et al. 2018c). MAPKs either function by moving inside the nucleus and phosphorylating a particular transcription factor or by staying in the cytoplasm and passing a signal to cytoskeletal-binding proteins or certain enzymes such as protein kinases, phosphatases, phospholipases, further contributing to the downstream signal transduction pathway. MAPKs are present downstream to Receptor Tyrosine Kinase (RTK) and a monomeric G-protein named RAS protein. After the activation of RTK in response to particular stimulus such as light, RAS also gets activated by exchanging the GDP present already with GTP using GEF (Guanine nucleotide Exchange Factor), SOS. The interaction of RTK with GEF occurs through an adaptor protein, GRB2. Activated RAS initiates a downstream kinase cascade that includes the activation of MAP Kinase. The first kinase being a part of downstream kinase cascade is RAF, a serine/threonine kinase (Morris 2001). RAF then phosphorylates two serine residues and thereby activates MEK (MAP-Kinase-Kinase). MEK is a dual specificity enzyme that phosphorylates threonine and tyrosine and activates MAP kinase. In this way, MAP kinase gets regulated post-translationally.

5 Conclusion

Because of an increase in the human population and associated activities, the rate of change in the environment has accelerated resulting in a deviation from normal environmental conditions and accumulation of stressful conditions. The increase in different stresses, such as high-temperature stress, low-temperature stress, drought stress, salinity stress, throughout the globe, has a severe effect on the agricultural crop plants as reported by IPCC 2012 (Field et al. 2012). Crop plants, being the major plants for intake purpose, are very important in order to provide adequate amounts of food to increasing human population. That is why, the improvement of these crop plants by plant breeding is necessary at this point of time. All these plant breeding techniques are only possible if either the marker associated with a particular stress-responsive gene or the stress-responsive genes are known along with those genes/proteins that are essential for stress-responsive gene regulation.

Techniques such as traditional breeding, molecular breeding based on markers, transgenic approach prove beneficial for the development of improved crop variety. Plants obtained by these approaches are first grown under controlled conditions, acclimatized to field conditions and finally grown under the field conditions. There have been many cases where stress-responsive genes from one plant are dissected and transferred to another plant by either plant breeding technique or transgenic approach, for example a salt and drought-tolerant transgenic tobacco plant is obtained by an apple transcription factor, MdDREB76 (Sharma et al. 2019). Many other plants such as *Arabidopsis thaliana, Nicotiana tabacum* are made abiotic stress tolerant using various previously discussed approaches.

By understanding the different regulatory mechanisms of stress-responsive genes, it becomes easy to artificially regulate a stress-responsive gene already present in a particular plant and hence produce an improved crop variety. For example, regulation by miRNA such as miR398 has been known to produce abiotic stress-tolerant plants. So, by learning about different stress-responsive genes and various methods of regulation of these stress-responsive genes, approaches and methodology can be simplified that are used in the development of plants efficient in stress tolerance.

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Chapter 3
Genome Editing: A Tool from the Vault of Science for Engineering Climate-Resilient Cereals

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Abbreviations

CRISPR	Clustered regularly interspaced short palindromic repeats
HDR	Homologous DNA directed repair
HR	Homologous recombination
NHEJ	Non-homologous end joining
TALEN	Transcription activator-like effector nucleases
ZFN	Zinc finger nucleases

1 Introduction

From the time of understanding of cropping, humans have continuously been focusing on the yield and quality of plant products via various traditional approaches until the green revolution. On the other hand, the human population is increasing continuously, but arable land is constant in dimensions. So, to feed the world population, it is imperative to make efficient use of non-cultivable lands such as pH imbalanced, salt-stressed, drought areas, and marshy lands (Singh et al. 2018; Mehta et al. 2019a). Gene revolution has been possible due to technological revolutions in the field of biotechnology. However, despite countless benefits and qualities in cereal plants, there are a few problems which need to be addressed such as cultivation issues, selective nutrient enrichment, overall nutritional content, and stress tolerance using genetic engineering of genes in the genome of affected cereal crops. GM crops can fight poverty and malnutrition by increasing yield, bio-fortification, reuse of salt-affected areas, overcome energy crisis, pest resistance, pesticide and herbicide tolerance, drought tolerance, efficient CO_2 use, nitrogen use efficiency, and phytoremediation. ISAAA report March 2020 reported an increase in GM crops planting area. In 1996, 1.7 million hectares of land cover were utilized for GM plants, while in 2018, it was 191.7 million hectares. Genetic engineering techniques for cutting and introducing the desired gene sequence involves the use of DNA-based biomolecules such as transcription activator-like effector nuclease (TALEN), zinc finger domain nucleases (ZFNs), CRISPR/Cas9, CRISPR/Cpf1 most importantly, and non-DNA based biomolecules such as guide RNA-based gene editing (Mehta et al. 2020). These genome-editing tools have advantages as well as limitations (Mehta et al. 2020). Both TALENs and CRISPR/Cas9 allow precise alterations by target specificity. TALENs provides greater freedom in target site selection compared to CRISPR/Cas9. However, the popularity of CRISPR is due to its capability for modifying chromosomal targets at higher frequencies. Simplicity in design and usage makes CRISPR/Cas9 an attractive tool. However, TALENs designing gets streamlined by modules with repeated combinations, thus reducing the cloning time. TALENs is sensitive to cytosine methylation, expensive and targets one site at a time. ZFNs are another class of nucleases that can edit/modify any targeted genomic sequence. However, they have low efficacy and is time consuming. Here, we highlight various targets in cereals to fight biotic and abiotic stresses using gene-editing techniques to boost the productivity and nutrient content of cereals to fight world hunger in an eco-friendly manner.

2 Genetic Engineering Tools for Crop Resiliency

There are various DNA and non-DNA-based techniques for editing the crop's genome, which includes insertion, deletion, or modification of a gene of interest. Many classical techniques are available for the transformation of the edited genes of interest into crops, such as electroporation, *Agrobacterium*-mediated, and nanoparticle-mediated transformation. *The Agrobacterium*-based technique is the most widely accepted because of its simplicity, and a higher integration probability even for low-copy DNA fragments with minimum problems to the host genome (Sindhu et al. 2019). The genetically modified crops created using gene-editing tools have desired characteristics (Griffiths et al. 2005). The transgene may have its origin from any organism having a beneficial trait. It can be from prokaryotes such as bacteria and viruses, or eukaryotes such as fungi and animals. Apart from this, there are other popular modern breeding techniques such as genome-wide association studies (GWAS), genome selection (GS), and marker-assisted selection (MAS) that are being employed by scientists for incorporating useful traits into the crops.

However, the current trend in life sciences is genome engineering using methods such as ZFN, TALEN, and CRISPR with variants such as CRISPR/Cas9, and CRISPR/Cpf1. These are well-known approaches which have been used to develop crops that can tolerate climate variabilities and biological stresses (Liu et al. 2013; Ali et al. 2015; Andolfo et al. 2016; Wang et al. 2016; Li et al. 2017; Kumar et al. 2018). There are other approaches such as RNA silencing using microRNA, trans-acting siRNA, hairpin RNA, and virus-induced gene suppression which reduce the translated product of marked genes (Bernstein et al. 2001). ZFNs, TALENs and CRISPR technologies create dsDNA cuts at particular genomic sequences which are further repaired using either NHEJ (non-homologous end-joining) or HR (homologous recombination). ZFNs and TALENs use engineered proteins along with DNA binding regions, and DNA endonuclease enzymes, whereas CRISPR/Cas utilizes laboratory synthesized sgRNA (synthetic guide RNA) targeted to precise

DNA sequences by base pairing. As far as ZFNs and TALENs are concerned, protein engineering is expensive, laborious, and time consuming, which limit their usage in high-throughput studies. On the other hand, CRISPR/Cas9 technique has circumvented these problems by being cheaper, versatile, less laborious, precise, and most importantly, efficient in genome-editing purposes at multiple levels (Mehta et al. 2020).

2.1 DNA-Based Genetic Engineering Approaches

2.1.1 Transcription Activator-Like Effector Nucleases (TALENs)

These are a variety of DNA-cutting proteinic enzymes especially designed to cleave at specific target DNA sequences. They are formed of the TAL effector DNA-binding domain with DNA cleaving sphere acting as nuclease which is taken from restriction endonuclease FokI. DNA-binding domain has various tandem DNA repeats ranging from 1.5 to 33.5 characteristically. Every repeat has 34 aa stretch with deviation at 12–13th amino acid named repeat variable residues, that is, RVD. These repeats recognize one nucleotide specifically. There are unique RVDs such as IN (Ile Asn), NN (Asn Asn), DH (Asp His) and GN (Gly Asn) which recognize A, G, C, and T, nucleotide bases respectively. Double-strand breaks after nicks are mended by HDR or NHEJ. These repairs result in deletions, insertions, duplications, inversions, transversions, translocations, or point mutations (Wei et al. 2013). The key features are explained in Table 3.1.

2.1.2 Zinc Finger Nucleases (ZFNs)

ZFNs are a type of DNA-cutting enzymes used for genome-editing applications such as duplication, addition, deletion, or substitution of gene sequences, with more precision than conventional plant breeding techniques for improvement of various crop attributes. They also include a DNA-sticking domain (Zinc finger class) and DNA cleavage sphere. DNA binding part of a molecule usually has 3–4 zinc finger proteins conjugated with di-cysteine and di-histidine motifs. These motifs recognize nucleotide triplets based on the residues from the alpha helix. DNA cleaving domain comes from FoKI restriction endonuclease. It dimerizes for DNA cutting in a non-sequence-specific manner and induces dsDNA cuts. The DSBs (double-stranded breaks) are mended by two paths, namely (1) HDR using homologous DNA as a model sequence to reinstate the DSBs for accurate and controllable repairs and (2) NHEJ machinery leads to additions, deletions, or substitutions in the broken dsDNA of host genome (Miller et al. 2007). ZFNs' key attributes are well-documented in Table 3.1.

Table 3.1 Key features of different genetic engineering approaches used nowadays for enhancing crop resiliency

S. No.	Features	ZFNs	TALENs	CRISPR/Cas9
1	Cleavage basis	Protein-based	Protein-based	RNA-based
2	Size	Considerably smaller than Cas9 (+)	Larger than ZFNs (++)	Considerably larger than ZFNs and TALENs (+++)
3	Constituents	Zinc-finger domains, nonspecific FokI nuclease domain	TALE DNA-binding domains, nonspecific FokI nuclease domain	Cas9 protein, crRNAs
4	Catalytic domains	FokI endonuclease domain	FokI endonuclease domain	HNH, RUVC
5	Structural parts	Dimeric	Dimeric	Monomeric
6	Target nucleotide length	18–36	24–59	20–22
7	gRNA requirement	No	No	Yes
8	Forms of action	Induce DSBs in target DNA	Induce DSBs in target DNA	Induce DSBs or ssDNA nicks in target DNA
9	Restriction size	High G	5′T and 3′A	PAM sequence
10	Recognition efficiency of target site	High	High	Very High
11	Mutation rate	High	Low	Very Low
12	Off-target effects	Yes	Yes	Yes, but can be minimized by the selection of unique crRNA sequence
13	Cleavage of methylated DNA	No	No	Yes, but it will be explored more
14	Multiplexing enabled	Highly difficult	Highly difficult	Yes
15	Laboriousness	Yes	Yes	No
16	Technology cost	Very high (£1000–£3000)	High (£40–£350)	Low (£30–£300)
17	First report in plants	Durai et al. (2005)	Christian et al. (2010)	Feng et al. (2013)

2.1.3 CRISPR/Cas9 Approach

CRISPR usage in plants has promised precise and accurate gene editing for targeted crop trait improvements (Arora and Narula 2017). They have been used versatility in almost all model organisms of different origins including plants (Sander and Joung 2014). It has been showcased and used for various attributes in rice, tomato, maize, wheat, woody plants such as apple, poplar, etc., to extended level for alleviating biotic, abiotic, and other climatic stress issues (Osakabe and Osakabe 2017; Mehta et al. 2020). It involves induction of dsDNA breaks at selective sites in genomic sequences with the help of guided RNA complementary sequences that bind with DNA and Cas endonucleases of CRISPR/Cas system targets and cuts genomic loci of DNA and pair using Watson-Crick base pairing. The breaks are mended by the cell's inner restoration mechanisms involving NHEJ and HR. Cas9 or Cpf1 plays molecular scissor role and RNA marks the address at genomic sequence level, thus guaranteeing precise and accurate cutting for further action. The entire process can be conceptualized as effective designing of Cas nucleases, assemblage of gRNA cassettes, Cas and RNA vector's delivery, screening, selection, efficient gene-editing detection, and plant regeneration with selective traits. Thus, a characteristic trait is extensively utilized in a variety of model cells and organisms for targeted mutagenesis. Thus, it has been widely accessed for achieving functional annotation of various biotic and abiotic stress resilience in genetic elements. However, the efficient delivery of gene-editing tools and components via transformation is a key bottleneck in gene-editing techniques. There is low transformation efficiency in *Agrobacterium*-mediated and particle bombardment-mediated transformation. Alternative strategies such as ex vitro plant composite development can help in efficient functioning of CRISPR/Cas9 and thus help in the elucidation of gene function, generation of valuable traits for yield, and quality improvement which usually gets affected with biotic stresses such as pests and pathogens (bacterial, viral, and fungal) and abiotic stresses. Biological stresses are usually coded by solo gene and gene erasure using CRISPR/Cas9-targeted modification or inactivation of susceptible genes gives protection against pathogens and has proven to produce resistant plants against bacterial, fungal, and viral pathogens (Borrelli et al. 2018). Further, CRISPR/Cas has the ability to edit multiple genes simultaneously (Sasano et al. 2016). Abiotic stress responses are usually controlled by multiple genes because of their complex nature. CRISPR/Cas-based unique allele variants for a non-biological stress-related gene (s) (Shi et al. 2017; Osakabe and Osakabe 2017) or clubbing multiples genes via HDR-induced gene aiming (Devkota 2018) has been used to develop resistance against abiotic stresses. The mutants failed to develop nodules when inoculated with *Sinorhizobium sp.* strain NGR234. Moreover, clubbing CRISPR/Cas with the expression of morphogenic regulators such as BBM/WUS may improve gene-edited plant's regeneration capacity with reduced tissue and genotype dependency.

Programming of CRISPR/Cas9 can be changed using sgRNA sequences and more than one sgRNA can work concurrently using similar Cas9 protein for diverse targets (Wu et al. 2014). However, there is a problem of off-target effects of CRISPR/Cas9, which must be minimized so that new mutants for abiotic and biotic stress response would be generated. One approach is to use optimized sgRNA designing (Montagne et al. 2014). CRISPR-P web software has been exploited for optimized designing of sgRNA as used for more than 20 plant species including cereals (Jain 2015). Numerous vectors and toolkits were also developed to facilitate plant genome editing using CRISPR/Cas9 (Xing et al. 2014). Thus, CRISPR/Cas9 usage in genetic engineering, genomic screening, and transcriptional intonation for dichotomizing molecular origin behind biotic and abiotic strain response and generating stress-tolerant cereal crop can be used by accessibility of the aforementioned attributes and knowledge. Key features of CRISPR/Cas9 are explained in Table 3.2.

2.1.4 CRISPR/Cpf1

One other budding variant of CRISPR is CRISPR/Cpf1 which is CRISPR (Prevotella and Francisella 1) and was recently found to be a unique RNA-mediated site-specific class 11 type V nuclease. It was first used to engineer a mammalian cell (Mahfouz 2017). Cpf1 endonuclease has a RuvC-type nuclease domain but it does not have the HNH domain as in Cas9. Cpf1 produces double-stranded breaks with sticky or staggered ends, not blunt ends as in Cas9. Thus, it enables gene expurgation, inclusions, or substitution via HDR-homology-directed repair (Zetsche et al. 2015; Mehta et al. 2020). Cpf1 provides multiple rounds of cutting as opposite to Cas9 where a single cleavage occurs, and it cuts DNA at a specific distance from protospacer adjacent motif (PAM). Cpf requires shorter CRISPR RNA and utilizes a T-rich PAM instead of G-rich PAM as in the Cas9 system. So, Cpf1 can explore better and increase the number of plant genome editions (Stella et al. 2017). Cpf1 has increased target specificity than Cas9 in plants compared to animals (Tang et al. 2017).

2.1.5 CRISPRi

This variant of CRISPR utilizes catalytically inactive Cas9 (dCas9) which disrupts the gene's function via gene intercession (Qi et al. 2013). CRISPRi technology essays the role of a perturbation tool for sequence-specific suppression of transcription in small prokaryotic organisms as well as complex eukaryotic organisms (Huang et al. 2016). Earlier, it was invented for transcriptional interference to silent gene expression, but nowadays, it is being exploited for transcriptional activation and epigenetic modifications such as exploiting the functionality of gene methylation or chromatin modifications for abiotic stress responses. It is highly specific and precise in nature along with a little off-target effects (Domingue et al. 2016). It was found that when dCas9 gets merged with Kruppel associated box (KRAB), the gene expression level was reduced equal to approximately 99% in human cells (Gilbert et al. 2013). Hence, this technique can be well applied in plants for stress-responsive genes using CRISPR-mediated and synthetically driven transcriptional activator or repressor molecules (Piatek et al. 2015). Transcriptional activation got enhanced if dCas9 was fused with a transcriptional activator (Gilbert et al. 2013). CRISPRi can regulate a particular target gene's efficiency along with enhancing its effect (Lo and Qi 2017).

Table 3.2 Review of literature highlighting the key examples of genome editing in improving resistance to various biotic stresses in cereals

Cereals	Targeted gene	Genome-editing technique	Molecular function related to disease	Promotor used	Efficiency/ mutations	Type of editing	Cultivar	References
Rice	*11N3/SWEET14*	TALENs	Bacterial blight	Ubi1, CaMV35S	13.5%	Disruption in promoter region	Kitake	Li et al. (2012)
	SWEET11 and *SWEET14*	CRISPR/Cas9	Bacterial blight	*Os*U6	–	Promoter disruption	–	Jiang et al. (2013)
	OsMPK5	CRISPR/Cas9	Fungal blast, bacterial blight	U3 or U6	3–8%	Indel	Nipponbare	Xie and Yang (2013)
	SWEET13	TALENs	Bacterial blight	–	–	Knock-out	IR24	Zhou et al. (2015)
	ERF922	CRISPR/ Cas 9	Fungal blast disease	*Os*U6a	42%	Indels in ORF	Kuiku131	Wang et al. (2016)
	SWEET14	TALENs	Bacterial blight	Ubi1	Up to 51%	Gene disruption	Kitaake	Blanvillian-Baufum et al. (2017)
	09g29100	TALENs	Bacterial leaf streak	Ubi and 35S	–	Base editing	–	Cai et al. (2017)
	Xa10-Ni and *Xa23-Ni*	TALENs	Bacterial blight	–	–	Knock-out	Nipponbare	Wang et al. (2017)
	SEC3A	CRISPR/Cas9	Fungal blast disease	*Os*U3/U6	–	–	–	Ma et al. (2018)
	BSR-k1	CRISPR/Cas9	Bacterial blight		–	–	–	Zhou et al. (2018)
	eIF4G	CRISPR/Cas9	Rice tungro spherical virus (RTSV)	*Ta*U6	36–86.6%	–	IR64	Macovei et al. (2018)

Cereals	Targeted gene	Genome-editing technique	Molecular function related to disease	Promotor used	Efficiency/ mutations	Type of editing	Cultivar	References
	USTA ustiloxin and UvSLT2 MAP kinase	CRISPR/Cas9	False smut	U6	–	Knockout	–	Liang et al. (2018)
	ALB1, *SDI1* and *RSY1*	CRISPR/Cas9 (RNP)	Rice blast fungus	–	–	–	CO-39	Foster et al. (2018)
	SWEET11, *SWEET13* and *SWEET14*	CRISPR/Cas9	Bacterial blight	*Zm*Ubi	–	5 mutations in promoter region	Kitaake, IR64 and Ciherang-Sub1	Oliva et al. (2019)
	TMS5, *Pi21*, and *Xa13*	CRISPR/Cas9	Bacterial blight	–	47%	Homozygous frame-shift mutations	Pinzhan	Li et al. (2019)
Wheat	*MLO*	CRISPR/Cas9	Powdery mildew	*Ta*U6	28.5%	Knock-out	Kenong199	Shan et al. (2013)
	MLO-A1, *MLO-B1* and *MLO-D1*	TALENs and CRISPR/Cas9	Powdery mildew	*Ta*U6	5.6%	Gene disruption	Kenong199	Wang et al. (2014)
	ABCC6	CRISPR/Cas9	Fusarium head blight	*Ta*U6	6.6–13%	Knock-out	Fielder	Cui (2017)
	LTP9.4	CRISPR/Cas9	Fusarium head blight	*Ta*U6	0–11.9%	Knock-out	Fielder	Cui (2017)
	NFXL1	CRISPR/Cas9	Fusarium head blight	*Ta*U6	0–42.2%	Knock-out	Fielder	Cui (2017)
	EDR1	CRISPR/Cas9	Powdery mildew	*Ta*U6	5 mutants	Knock-out	Bread wheat KN199	Zhang et al. (2017)

(continued)

Table 3.2 (continued)

Cereals	Targeted gene	Genome-editing technique	Molecular function related to disease	Promotor used	Efficiency/ mutations	Type of editing	Cultivar	References
	Lpx-1/MLO	CRISPR/Cas9	Fusarium head blight, Powdery mildew	*Ta*U6	22 mutants	Knock-out	Bobwhite	Wang et al. (2018b)
	ALA and *ACC*	CRISPR/Cas9	Herbicide resistance	*Ta*U6	33–75%	Base editing	PI653509	Zhang et al. (2019b)
Maize	*glossy2* (*gl2*) locus	TALEN	Glossy phenotype	CaMV 35S	10%	Small bp deletions	Hi-II, B104	Char et al. (2015)
	bW2 and *bE1*	CRISPR/Cas9	Corn smut	U6 snRNA	70–100%	Gene disruption	–	Schuster et al. (2016)
	NLB 18	CRISPR/Cas9	Northern Leaf Blight	–	–	–	–	USDA (2017)
	DsRed	CRISPR/Cas9	Wheat dwarf virus	*Zm*UBI	Comparatively more efficient	Mutation		Kis et al. (2019)
	GA20ox3	CRISPR/Cas9	Transgene-Free Semidwarf Maize	*Ta*U3	–	Base editing	Inbred line Cal	Zhang et al. (2020)

2.2 DNA-Free Genome Engineering

DNA based and non-DNA based CRISPR/Cas approaches have been implemented in recent scenarios. DNA-based approach usually involves *Agrobacterium*-based transformation, whereas non-DNA-based approach involves PEG-mediated protoplast fusion method. In the classical CRISPR/Cas method, T-plasmid is constructed along with the required sgRNA and Cas9/Cpf1/Cas variant coding sequence. During transformation, RNA and Cas sequences get incorporated into the host genome. Guide RNA and Cas9 get translated inside the host cell and in vivo gRNA-Cas9 RNP (ribonucleic protein complex) is formed. As the target DNA sequence is detected, double-strand DNA breaks are induced and mutations are generated by the cell's internal DNA repair mechanisms. Here, the CRISPR/Cas complex is continuously getting expressed and actively produces desired mutations in host cells.

DNA-free CRISPR/Cas9 approach is getting wider acceptance, as it can create safer and ethically accepted GMO products. In one approach, in vitro-synthesized Cas protein and in vitro-translated gRNA are used to generate the RNP complex in vitro and delivered inside the host cell protoplast using the PEG-mediated fusion method. Since the complex is already formed in a tube, it is active and once inside the cells, it detects the target sequence and induces dsDNA breaks/nicks. The cellular repair mechanisms lead to the generation of mutations in the host genome at desired target sequences and do not add any foreign DNA in the host genome. With time, the CRISPR/Cas9 complex gets degraded inside the cell and their availability is decreased over time. A suitable screening process is required to identify stable cells for further growth (Metje-Sprink et al. 2019). Other DNA-free approaches include momentarily expressed CRISPR/Cas9 plasmid DNA (TECCDNA), and CRISPR/Cas9 in vitro transcripts (IVTs). All these techniques do not allow integration of foreign DNA into the host genomic DNA and hence, they diminish off-target effects. These techniques are comparatively faster and less costly than the CRISPR/Cas cassettes already available in the global market. The most suitable methods for the delivery of these CRISPR cargos are the polyethylene glycol (PEG), electroporation, biolistic bombardment, or cationic lipid-based method (Zhang et al. 2016; Yin et al. 2017).

The most advanced CRISPR/Cas variant in the market is CRISPR base editors which create single-nucleotide changes at the target loci. The dsDNA breaks or template DNA sequences are not required here. This approach for the generation of a single-nucleotide mutant is widely used in monocot and dicot plants. This variant utilizes dCas9 (dead/inactive cas9), nCas9 (Cas9 nickase), and adenine or cytidine deaminase enzymes. Deaminases convert cytosine to thymine via uracil and adenine to guanine via inosine (Monsur et al. 2020). They are more advanced, effective, and efficient in editing. *Sp*Cas9, Sacas9, *Sp*VQR-Cas9, *Sp*EQR-Cas9, *Sa*KKH-Cas9, and *Sp*VRER-Cas9 are a few variants which are available in the market having differential specificity toward PAM (protospacer-adjacent motif). They provide product purity at a high level and have low off-target editing efficiency.

3 Role of Genome Editing Tools in Biotic Stress Management

The factors eliciting biological stress in plants are a major threat to cereal crops causing substantial yield losses annually on a global scale (Langner et al. 2018). Cereal crops are attacked by numerous pathogens and pests, including myriad bacteria, virus, fungal entities, insects, and parasites (Rahman et al. 2019; Singh et al. 2019; Mehta et al. 2019b). These biotic stressors generally harm the host plant by directly or indirectly depriving its host of its vital nutrients and become a major cause of pre- and post-harvest crop damage. The native defense mechanisms of plants protecting against biotic stresses are diverse and dynamic, which are genetically governed by resistance genes encoded within the plant genome (Diaz 2018). Numerous methods such as traditional breeding, molecular breeding, and genetic modulation tools have been deployed with the ultimate goal of enhanced food security by enabling the crops to combat pathogenic infections. In recent years, gene-editing technology has appeared to be an opportunistic strategy that serves to improve resistance in crops toward biotic stress-inducing agents through targeted gene manipulation. Numerous pioneer studies reporting the application of gene-editing tools to improve resistance in various cereal crops towards bacterial and fungal diseases are presented in Table 3.2.

3.1 Resistance Against Fungal Diseases

Shan et al. 2013 was the first to report the successful application CRISPR/Cas9 technology to enhance resistance against *Blumeria graminis* F. sp. *tritici* which causes powdery mildew disease in wheat plants leading to significant yield losses. CRISPR/Cas9-mediated knock-out of *TaMLO* (MILDEW-RESISTANCE LOCUS) in wheat, imparted disease resistance, wherein 28.5% mutational frequency was observed in *TaMLO* for protoplasts (Shan et al. 2013). Further, Wang and his team demonstrated the use of CRISPR/Cas9 and TALENs systems for the concurrent expurgation of three homoalleles of *TaMLO* gene in hexaploid bread wheat and reported similar mutation frequency (5.6%) by both the editing methods (Wang et al. 2014). More recently, the feasibility of CRISPR/Cas9 in wheat for achieving fungal resistance was confirmed by Zhang and his colleagues, who targeted the *TaEDR1* gene which negatively regulates powdery mildew resistance (Zhang et al. 2017). They were able to simultaneously knock-down the three homologs of *EDR1* generating *Taedr1* wheat lines tolerant to mildew-induced cell death. Similarly, a group of researchers targeted lipoxygenase genes (*TaLpx1* and *TaLox2*) for enhancing wheat resistance to fusarium, the causative agent of one of the most destructive fungal diseases. Lipoxygenases stimulate jasmonic acid-mediated defense mechanism in plants by hydrolyzing polyunsaturated fatty acids and initiating oxylipin biosynthesis. *TaLpx-1* gene silencing has been reported to render wheat plant resistant towards *Fusarium graminearum* (Nalam et al. 2015). The mutation frequency of 9% and 45% was achieved for *TaLpx1* and *TaLox2* genes, respectively (Shan et al. 2014; Wang et al. 2018b). Hexaploid wheat plants carrying mutated *TaLOX2* were developed with a frequency of 9.5%, accounting for 44.7% homozygous mutants (Zhang et al. 2016). Similarly, three genes earlier reported to be linked with disease susceptibility (*TaNFXL1, TaABCC6*) and resistance (*TansLTP9.4*) toward *fusarium* head blight (FHB) (Ouellet et al. 2013; Balcerzak et al. 2016) were also targeted in wheat to confer resistance against FHB (Cui 2017) (Table 3.3).

Fungal blast has been associated with extensive losses in rice yields worldwide. Therefore, various techniques are being explored to develop blast-resistant cultivars using advanced gene-editing techniques. In an attempt to develop resistance in japonica rice, Wang et al. performed CRISPR/Cas9-targeted knockout of *OsERF922,* a negative regulator of fungal blast resistance (Wang et al. 2016). Additionally, Cas9/sgRNAs-mediated multiplex targeting of two or three sites within the *OsERF922* gene was also shown to increase mutagenic frequency (Wang et al. 2016). Agronomic traits of the mutant lines were significantly consistent with those of wild-type plants, indicating no negative effect on plant growth and sustainability. Likewise, blast resistance in rice plants was achieved through the disruption of genes *OsERF922* and *OsSEC3A* using the CRISPR/Cas9 system (Ma et al. 2018). *OsSEC3A* mutation was found to be associated with enhanced resistance against *Magnaporthe oryzae*, elevated concentrations of salicylic acid, as well as upregulation of defense responsive genes and salicylic acid synthesis (Ma et al. 2018). CRISPR/Cas9-based knock-out of a stress-responsive gene “mitogen-activated Protein Kinase5” (*Os*MPK5) using three sgRNAs, reportedly enhanced fungal as well as bacterial disease resistance in rice plants by showing constitutive expression of pathogenesis-related (PR) genes. The mutation frequency ranging from 3% to 8% was observed in Nipponbare rice protoplasts (Xie and Yang 2013). DuPont Pioneer is exploring the CRISPR/Cas9-mediated approach to generate improved disease-resistant maize cultivar by targeting the NLB-sensitive allele.

The development of multiplex genome-editing methods further increases the application of CRISPR system in cereal crops to confront more challenging attributes encompassing multiple genes by utilizing a single CRISPR construct (Wang et al. 2018a). A study adapting CRISPR/Cas9 technology to disrupt bE1 and bW2 genes in *Ustilaginoidea maydis* with efficiency of 70% and 100% in progeny from a single transformant provided proof of concept for developing resistance against corn smut. In more recent reports, the use of CRISPR-based multiplexed genome-editing method has been attempted in hexaploid wheat by employing three sgRNA to target three genes viz. *TaGW2, TaLpx-1,* and *TaMLO* to achieve resistance toward FHB and powdery mildew (Wang et al. 2018b). Further, Liang et al. successfully demonstrated an approach which employed CRISPR/Cas9 for efficient gene replacement or editing in *Ustilaginoidea virens* for imparting resistance against rice false smut, one of the major fungal diseases of rice (Liang et al. 2018). Additionally, a novel co-editing and counter-selection strategy presented by Foster and his colleagues allows precise editing in fungal strains to generate completely isogenic lines with no foreign DNA. The study demonstrated rapid plasmid-free CRISPR/Cas9-mediated editing in *Magnaporthe oryzae* with improved precision and speed of

Table 3.3 Review of literature summarizing the reports of genome editing for enhancing tolerance to abiotic stresses

Cereals	Targeted gene	Genome-editing technique	Molecular function	Promotor used	Delivery method	Efficiency/ mutations/ modified plants/ HR	Type of editing	Cultivar	Effect	References
Wheat	*LOX2*	CRISPR/ Cas9	Carotenoid biosynthesis	*TaU6*	Biolistic mediated	55–70% mutation rate efficiency	Base Editing	Bobwhite	Improved Carotene content	Zong et al. (2017)
	AHAS	ZFN	Role in branched amino acid formation	–	Particle bombardment	1.2% gain of function, 2.9% loss of function	Insertion and replacement	Bobwhite MBP26RH	Resistance against herbicide	Ran et al. (2018)
	EPSPS	CRISPR/ Cas9	Role in shikimate biosynthesis pathway	*TaU6*	PEG mediated transformation	0–20% Mean indels of which 8.5% were large insertions	Insertions	WT	Resistance against Glyphosate herbicide	Arndell et al. (2019)
	IPK1	ZFNs	Phytate formation (Intracellular signaling)	–	Cell-penetrating peptide-mediated transfection	–	Deletion	Bread wheat	Removal of anti-nutritional phytate, mineral accumulation against abiotic stress (Fe, Zn)	Bilichak et al. (2020)
Rice	*LG1*	ZFNs	Metal binding (Zinc)	–	Transfection	39%	Deletion, Insertions	Wild type	Improves seed shattering, metal binding	Gao et al. (2010)
	PDS, IPK1A, IPK, MRP4	TALENs	Phytic acid biosynthetic pathway genes	35S promoter	PEG/ Agrobacterium-mediated	9.1% mutation rate efficiency	Deletion 2–17 bp	Hi-II	Recovery from various biotic stresses	Liang et al. (2014)

Cereals	Targeted gene	Genome-editing technique	Molecular function	Promotor used	Delivery method	Efficiency/ mutations/ modified plants/ HR	Type of editing	Cultivar	Effect	References
	ALS2	CRISPR Cas9/ gRNA	Target for sulfonylurea and imidazolinone herbicides	UBI or MDI promoter	Agrobacterium-mediated	2.23% target mutation	Point mutation P165S	Hi -II	Recovery from Herbicide sensitivity	Svitashev et al. (2015)
	AOX1a, *AOX1b*, *AOX1c*,*BEL*	CRISPR sgRNA	Multiple abiotic stress regulators	U6	–	35.3%	Knockout	Wild type	Multiple abiotic stresses regulation	Xu et al. (2015)
	CENH3	CRISPR/ Cas9	Centromere segregation during cell division	*ZmU*3	Agrobacterium-mediated	55–70% mutation rate efficiency	Base Editing	Inbred line Zong31	Improvement in cellular division process	Zong et al. (2017)
	SAPK2	CRISPR/ Cas9	Drought response	SAPK2 promoter	PEG mediated	81–100% (germination), 6.5 to 9.1% (Water stress survival),36–38% (stomatal closure), 36–38% (stomatal opening)	Deletion mutants	*O. sativa* L. *japonica*	Improved drought tolerance, ROS detoxification	Lou et al. (2017)
	Ann3	CRISPR/ Cas9	Cold response	–	Agrobacterium mediates	8.3, 5.5, 55.5% survival	Knockout	Wildtype	Cold stress tolerance, lesser electrical conductivity	Shen et al. (2017)

(continued)

Table 3.3 (continued)

Cereals	Targeted gene	Genome-editing technique	Molecular function	Promotor used	Delivery method	Efficiency/ mutations/ modified plants/ HR	Type of editing	Cultivar	Effect	References
	CDC48	CRISPR/ Cas9	Prevention of senescence and plant death	*OsU3*	Agrobacterium-mediated	43.48%	Base Editing	*Japonica* rice variety Nipponbare	Prevention of senescence	Zong et al. (2017)
	NRT1.1B	CRISPR/ Cas9	High yield and early maturation	*OsU3*	Agrobacterium-mediated	43.48%	Base Editing	*Japonica* rice variety Nipponbare	Increased grain yield	Zong et al. (2017)
	RR22	CRISPR/ Cas9	Salinity tolerance	pUbi	Agrobacterium-mediated	64.3%	Deletion, Insertion, substitution	Japonica rice WPB106	Agronomic traits and Salt Tolerance	Zhang et al. (2019a)
	AOC	CRISPR/ Cas9	Jasmonic acid synthesis pathway involvement	–	Agrobacterium-mediated	–	Deletion, Insertion, substitution	Oryza sativa japonica Kitaake	Efficient coordination with environment	Nguyen et al. (2020)
Barley	*ENGase*	CRISPR/ Cas9	Production of GN1 type FNGs (Free N Glycans)	UBI promoter	Agrobacterium-mediated	78%	Indels and deletions	Golden promise	Increased abiotic tolerance	Kapusi et al. (2017)
	PDS1	CRISPR/ Cas9	Phytoene desaturate gene	CaMV 35S promoter	Agrobacterium-mediated	–	Gene editing	Carotenoid biosynthesis	Reduction in off target mutations	Raitskin et al. (2019)

genetic manipulation which are likely to be applicable to a range of fungal species (Foster et al. 2018).

3.2 Resistance Against Bacterial Diseases

Bacterial diseases such as bacterial leaf blight (BLB) and bacterial leaf streak (BLS), caused by *Xanthomonas oryzae* pv. *oryzae* (Xoo) and *Xanthomonas oryzae* pv. *oryzicola* (Xoc), respectively, are two of the most devastating diseases of rice (Verdier et al. 2012; Mehta et al. 2019b). Moreover, the advent of novel virulent pathotypes of *Xanthomonas oryzae* (Xoo) (Gonzalez et al. 2007; Mehta et al. 2019b) has rendered conventional breeding programs and resistant cultivars ineffective and further intensifying the utilization of advanced gene-editing tools to combat such diseases. The transcription activator-like effectors (TALEs) are key determinants of *Xanthomonas* pathogenicity since the activation of host target genes by TALEs is associated with susceptibility and/ or resistance in rice (Bogdanove et al. 2010; Bogdanove and Voytas 2011; Boch et al. 2014). This provides the opportunity to target several TALEs to enhance resistance towards Xoo and Xoc diseases. The sucrose-efflux transporter (SWEET) gene family in rice is the best-studied class of TALE virulence targets which include *OsSWEET11*, *OsSWEET13*, and *OsSWEET14* genes. The activation of *OsSWEET14* gene by TAL effectors *AvrXa7* or *PthXo3* of Xoo is known to facilitate the export of sugars from plant cell to pathogen which requires it for growth and virulence (Antony et al. 2010). The TALEN-based system was implemented for disrupting the gene associated with bacterial blight defense *OsSWEET14* (*Os11N3*) to confer resistance in rice lines toward *AvrXa7*- and *PthXo3*-based Xoo strains in rice lines (Li et al. 2012). Thereafter, some investigations employing TALEN and CRISPR/Cas9-targeting susceptible genes have been conducted to impart resistance toward blight disease in rice (Jiang et al. 2013; Hutin et al. 2015; Blanvillain-Baufum et al. 2017; Cai et al. 2017). In an attempt to demonstrate the CRISPR/Cas9-mediated targeted gene alterations, Jiang et al. 2013 designed CRISPR/Cas9-sgRNA constructs capable of inducing site-specific disruption in the promoter sequence of bacterial blight susceptibility genes, *OsSWEET14* and *OsSWEET11* for enhanced resistance (Jiang et al. 2013). CRISPR/Cas9 system was also deployed to construct *OsSWEET13* null mutant in *indica* rice, IR24 to prevent TAL effector gene *pthXo2*-mediated neutralization, thereby improving the resistance toward bacterial blight disease (Zhou et al. 2015). Genetic modification through TALEN of *EBEtal7* binding site in promoter sequence of *Os09g29100* gene by removal of its Tal7-binding sequence can reduce the severity of bacterial disease through *avrXa7-Xa7* defense in rice (Cai et al. 2017). Some other TAL effectors such as *AvrXa7*, *TalC*, and *Tal5* contributing to Xoo susceptibility in rice can also be exploited to target *OsSWEET14* to improve blight resistance (Blanvillain-Baufum et al. 2017). The potential of rice disease resistance genes *Xa10-Ni* or *Xa23-Ni* to impart broad-spectrum resistance to *Xanthomonas oryzae* pv. *Oryzae* has also been explored through TALEN and CRISPR/Cas9 technology (Wang et al. 2017).

Recently, a Japonica rice cultivar with an improved resistance to *Xanthomonas oryzae* pv. *oryzae* was developed by CRISPR/Cas9-based gene mutagenesis of *Os8N3/OsSWEET11*. The mutant lines were observed to possess equivalent agronomic characteristics such as plant height, leaf length/width, the number/length of panicles, and pollen development (Kim et al. 2019). Furthermore, a research group engineered a broad-spectrum resistance to bacterial blight in rice through CRISPR–Cas9 gene editing. They systematically targeted multiple sites in *SWEET* promoters to confer resistance in Kitaake, and elite varieties IR64 and Ciherang-Sub1 exhibiting normal agronomic features (Oliva et al. 2019). A multitude of such studies ascertain the prospects of advanced genome-editing strategies for engineering important cereal cultivars with reduced susceptibility to bacterial diseases. In 2019, Oliva et al. showed the role of CRISPR/Cas9 in curing bacterial blight using genes *SWEET11, 13,* and *14* in rice cultivar Kitaake. They used ZmUbi promoter and mutations in promoter regions were observed.

3.3 Resistance to Viral Diseases

Rice tungro disease (RTD) is caused by the concurrence of two different viruses, namely rice tungro spherical virus (RTSV) and rice tungro bacilliform virus (RTBV), which severely affect rice production across tropical Asia (Macovei et al. 2018; Mehta et al. 2019b). Macovei and his team attempted to engineer resistance in RTSV-susceptible IR4 rice through CRISPR/Cas9-mediated changes in the *eIF4G* gene (Macovei et al. 2018), which is known to control RTSV resistance. These resistant plants carrying mutant *eIF4G* alleles can further be exploited as a source for additional RTSV-resistant rice varieties. Kis et al. (2019) showed the role of DsRED protein for reporting purposes by indicating that the role of CRISPR/Cas9 under ZmUbi promoter via the *Agrobacterium*-mediated transfection method led to resistance against wheat dwarf virus.

4 Engineered Abiotic Stress Tolerance

Plants experience unfavorable environmental conditions very often called abiotic stress, for example, excess of sunlight, excess $CO_{2,}$ decreased availability of soil minerals, decreased availability of water or excess of water, very extreme temperatures (hyperthermia or hypothermia), presence of toxic ions in the soil, etc. (Compant et al. 2010; Hirayama and Shinozaki 2010; Lal et al. 2018). These abiotic stresses influence various attributes of the plant affecting development and output (Rejeb et al. 2014; Lal et al. 2018). Abiotic stress is responsible for up to 50% losses in crop yields (Rodziewicz et al. 2014; Sharma et al. 2020). According to IPCC (intergovernmental panel on climate change), plants experience abiotic stress due to ever-changing climatic circumstances (Mittler 2006). which result in huge loss of food security and environmental sustainability in developing countries (Andy 2016). This has attracted the attention of researchers to develop advanced adaptation strategies for plants under stress and make them adaptable under changing environmental conditions (Wheeler and Von Braun 2013). The major challenge is to identify how these plants respond to different stresses by activating different pathways and switching on/off of responsible genes (Wallace et al. 2003; Andy 2016; Anamika et al. 2019). The capability of plants to overcome or to develop resilience against all these factors solely depends upon photosynthesis in addition to various other physiological or genetic processes. A well-known feature of plants to combat abiotic stresses is the involvement of several genes, and activation and deactivation of several interlinked molecular pathways. Abruptly changing abiotic stresses such as temperature, air humidity, or light evokes multiple intracellular processes at the molecular, biochemical, cellular, and physiological levels (Vahisalu et al. 2010; Mittler et al. 2012; Vainonen and Kangasjärvi 2015; Suzuki et al. 2015; Dietz 2015; Hulsmans et al. 2016; Pommerrenig et al. 2018). CRISPR/Cas9 is used extensively for inducing site-specific mutations in many grass plant species such as rice, sorghum, wheat, and switchgrass.

4.1 Drought Resistance

Drought stress is one of the outcomes of climate change that has an adverse impact on crop growth, and yield by affecting biochemical and physiological processes (Husen et al. 2014, 2017; Getnet et al. 2015; Embiale et al. 2016; Siddiqi and Husen 2017, 2019). It is due to unavailability of water to plants which may cause shoot biomass reduction and grain yield losses. Yield losses are maximum due to water stress as compared to other stresses (Farooq et al. 2009). Water depletion in the rooting area causes increased vapor pressure deficit, which multiplies drought stress (Ahanger et al. 2014). This stress leads to increased crop yield losses when compared to other abiotic stresses. Thus, the intensity and duration of drought stress coupled with other environmental factors play a key role in determining crop yields. The reductions in yields depends on plant type, growth stage, severity, and longevity of the drought conditions. Lou et al. (2017) showed amelioration of drought stress by employing CRISPR/Cas9 approach on *SAPK* gene under *SAPK* promoter via PEG-mediated transformation. ROS detoxification was observed in the mutant plants.

4.2 Cold and Heat Resistance Stress

Every crop requires optimal temperature for its optimal growth. Below optimum temperatures result in cold stress while temperatures above optimal temperature results in heat stress. The temperature of 0–10 °C results in chilling stress which is very common in temperate and subtropical species such as cereals. Cold shocks in early reproduction stages lead to flower abortion, pollen and ovule infertility, as well as low seed sets in cereals which hamper metabolic rates and hence, grain yields (Thakur et al. 2010). The low-temperature shock causes enormous changes in membrane permeability, free proline content, and malonic dialdehyde (MDA) (Nesterova et al. 2019). Under frost conditions, photosynthesis gets hampered due to low temperature and internal injuries occur, resulting in ROS production (Sharma et al. 2020). Different physiological processes are greatly affected due to temperatures above the ambient temperature such as rate of photosynthesis and respiration, production of ROS, etc. Since flowering has low threshold value, it gets affected the most at high-temperature stress and thus, there is less seed formation and loss in grain yield (Prasad et al. 2017). *Ann3* gene was edited by CRISPR/Cas9 for curing cold response using the *Agrobacterium*-mediated approach where survival of knockout plants was observed. There was an improvement in cold stress tolerance as well as reduced electrical conductivity as observed by Shen et al. (2017).

4.3 Salinity and Submergence Stress

High salt concentration above a certain threshold concentration is considered as salt stress. Soil salinity is one of the most damaging abiotic stresses. This stress damages plant crops and yield loss has been reported in several investigations (Husen et al. 2016, 2018, 2019; Hussein et al. 2017; Siddiqi and Husen 2017, 2019). It has been reported that 7% of total cultivable land area and 20% from irrigated arable land are stressed due to excessive salt concentrations (Li et al. 2014), thus leading to decrease in crop yields via overpowering the crop performance due to non-availability of nutrients to plants. India has a 6.74 million ha area under salt stress. Submergence stress is due to waterlogging, Water-deficient conditions result in drought and excess of water results in waterlogging which further affects biological processes in crop and results in yield loss. During the early flowering, crop metabolism is very sensitive. Waterlogging gives rise to several fungal diseases, and under these conditions, requirement of metabolic energy shoots up. Production of metabolic energy decreases due to anaerobic respiration and growth of the crop is arrested. *RR22* gene was mutated using the CRISPR/Cas9 approach for salinity tolerance using the *Agrobacterium*-mediated transformation method. Similarly, the successful application of CRISPR resulted in improved agronomic traits as well as salt tolerance (Zhang et al. 2019a, b).

4.4 Adaptation Stress

Plants face different kinds of biotic or abiotic stress, and each of them has their genetic makeup to fight against these stresses and come up with a solution for adaptation in the changing environment. “Survival of the fittest” or the natural law of selection is applicable everywhere regarding the survival of the fittest. Adaptation stress is the stress faced by different crops to adjust themselves according to the evolving environmental conditions. Physiological changes, molecular changes, or biochemical changes are constitutive processes undergoing within cellular structures and switching ON/OFF of different genes allows plants to survive in the evolving environmental conditions. Zhang et al. (2020) recently published a study where CRISPR/Cas9-based base editing in maize inbred line resulted in transgene-free semi-dwarf maize, which is more efficient in withstanding environmental stress.

5 Conclusion

Cereal crops are a prime component of the human diet accounting for a significant proportion of nutrition consumed worldwide. The trends of the progressively growing population and predicted climate changes are expected to boost the global crop demand. Genome engineering techniques are powerful tools that are likely to contribute significantly to the redressal of these anticipated challenges. Advanced gene engineering techniques such as CRISPR/Cas9 have superseded the limitations of conventional genomics-based breeding approaches for crop improvement by eliminating the obstacle of genotypic limitation. Moreover, genome-editing methods surmount the imprecision associated with the use of markers by engineering innovative alternatives affecting yield and stress tolerance. Genome engineering facilitates the production of cereal crops with superior agronomical traits such as better yield, enhanced resistance to biological as well as non-biological stress, by targeting a suite of genes controlling these factors. The applications of genome-editing techniques have broadened in the field of cereal research, as it permits the biofortification of cereals in terms of favoring human health. The cereals of the future can now be developed with a specified composition and quality and offering desired nutritional performance and end-use applicability in foodstuffs. With the ability of genomic rearrangement combined with its high potential to simultaneously edit multiple genes associated with plant characteristics and the regulatory elements, the modern gene-editing tools enable crop improvement by targeting complex traits. This multiplexing approach further allows a useful combination of edits to stack multiple traits in a new variety. These techniques enable the production of transgene-free crop varieties. However, the regulation of genome-edited cereals and public acceptance puts significant constraints in the commercialization of these crops. Therefore, these issues must be addressed to accurately differentiate between transgenic and non-transgenic genome-edited crops because, unlike transgenic varieties, genetically engineered crops can be indistinguishable from crops formed by conservative breeding methods. The challenges associated with off-target alterations and changes in cleavage effectiveness remain to be overcome for establishing efficient genome-editing methods for crop improvement. The systematic analysis of target sites using efficient genomics, the upgraded delivery systems, and the availability of high throughput screening methods needs to be taken into account to modify essential cereal crops. Further, the capability of the CRISPR/Cas9 system to deploy multiple gRNAs and the availability of NGS-next-generation sequencing technologies will provide adequate data for the comparison of gene-editing systems in a diverse range of crop species. The progressive research being carried to develop and improve gene-editing methods is expected to bring a revolution by addressing the agricultural issues related to yield, quality, and biotic/abiotic stress management. Overall, the genome engineering system offers numerous opportunities to improve cereal crops by overcoming the antagonistic effects of climate change and may support global food security.

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Chapter 4
Advancement in Molecular and Fast Breeding Programs for Climate-Resilient Agriculture Practices

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Contents

Abbreviations

AI	Artificial intelligence
BBS	Biotron breeding system
CRISPR	Clustered regularly interspaced short palindromic repeats

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GBS	Genotyping by sequencing
GMCs	Genetically modified crops
ODM	Oligonucleotide-directed mutagenesis
QTL	Quantitative trait locus
SDNs	Site-directed nucleases
TALENs	Transcription activator-like effector nucleases
ZFNs	Zinc-finger nucleases

1 Introduction

Climate change is the most important issue to setting our life on earth and maintaining the coexistence of every environmental cause to run the system in an equilibrium fashion and sustainability. The concept of climate change arose as a continuous increase of average temperature from decade to decade (NAAS 2008), including simultaneous increase in CO_2, NH_4, N_2O, and GHG (Canadell et al. 2007; Spahni et al. 2005). Besides variability and unpredictability, frequent seasonal abrupt behaviors are making the game challenging. The sector that is mostly affected by climate change is agriculture and allied activities. Yield is the major target for all crop improvement basically through direct improvement or minimizing the loss by biotic and abiotic threats but all these threats are new born as direct crop improvement leaded the role since long where biotic and abiotic threats were not a major threat as an consequences, diverting global crop imrovement programmes towards sustainability isssues in the area of major cereals (Challinor et al. 2016; Stratonovitch and Semenov 2015) and other crops.To address major factors of climate changes in agriculture crop production, utilizing improved varieties invited the tolerance ability of the crop to withstand the particular stress environment. But abrupt changes of macroclimate and environmental variability need to be addressed further and that is being implemented by breeding crop variety not only for tolerance ability for a particular stress but climate resilience ability of the crop for changing environment. Testing genotypes adapted to the harsh environment need acclimatization in newer environment predicting challenges keeping a flow of newly developed variety in terms of genetic potential, and screening them under a wide area coverage of future climate through interaction and multiple levels variation of stress factors can be helpful (Atlin et al. 2017). Climate resilience research exploiting G × E interaction, dissecting genetic loci with modifying alleles for leaf phenology, senses the stress environment and makes crop suitable for stress environment and with the potentiality to sequester carbons from the open environment (Catarcione et al. 2009; Chmielewski et al. 2004). Under the environmental threat, exploiting unexplored materials can be done to achieve much improvement of valuable traits using high accuracy predictive model (Yu et al. 2016). Fast breeding is very much needed for developing worlds because of intensifying cropping pattern and risk of quick declining trends in soil fertility which can intensify the stress more (Vanlaue et al. 2015). Advances in molecular breeding approaches based on QTL detection, cloning, sequencing, and identification of candidate gene under the climate change scenario will lead the breeding program for sustainability and resilience.

Major concerns remain for the quick breeding under such conditions as predictable adaptation is not easy and implementation of individual gene effect, integrating selection criteria, advances in minor crops genomics, and integrating them in the cropping system can shape the breeding toward resilience (Kole et al. 2015). Identification of resilient responsive coral's transcript which is associated with thermal tolerance at the cellular level can be useful for better understanding of thriving organisms in changing environment (Barshis et al. 2013). New-generation breeding requires larger populations considering a large set of germplasm phenotyped through high-throughput science managing big data involving biotechnology and molecular breeding (Taranto et al. 2018). Under threat of climate change, some regions are less resilient and need more emphasis for developing resilience which include Sub-Saharan African and Latin American for maize-based cropping, wheat-based cropping in Gangetic plains, and rice in mega deltas of Asia and some potato-based cropping (Banga and Kang 2014). Conservation genomics will decipher the interaction of genes and their interaction with the environment which affect the phenotype of crops (Angeloni et al. 2012). Finer detailed study, directly linked to target traits such as ascorbate–glutathione cycle and the lipid peroxidation with drought-induced yield reduction, is the advancement of rapid breeding (Melandri et al. 2020).

2 How Weather Variable Impacting Crops

Heat wave, cold wave, untimely flood, heavy rainfall, seawater intrusion, storms, cyclone, hailstorms, and drought have been severe in the last few decades challenging crop production. Although climate change is occurring worldwide, the country with most populations depending on agriculture like India suffers a lot. As the impact of climate change is a concern, mostly medium and small-scale marginal farmers are the most vulnerable section. The variable climatic factors such as intensive rainfall by minimizing the rainy days are causing drought and heavy flood in the latter part of the twentieth century which are becoming the major climatic challenges (Auffhammer et al. 2012). Various parts of the country witnessed a wide range of drought spell and even some other parts witnessed heavy rainfall in the last decade also (Goswami et al. 2007; Venkateswarlu et al. 2011).

3 Climate Resilience

Climate resilience is the capacity of any farming part to make a holistic approach combining all the advances made recently in terms of gaining produce and minimizing the loss from wide variable challenges involving smarter crop production

(Rivington and Walthall 2012). The Intergovernmental Panel on Climate Change has predicted the rise in surface mean temperature of the earth, the concentration of CO_2 gases, and ozone gas and mentioned its predicted increase throughout the current century (Stocker 2013). Food production and its security is centered toward resilience ability in shaping the future production scenario in variable extremes of weather. The yield performance is the major key considerable fact that is affected under climatic variability and the climate resilience of the yield has the genetic basis which controls the yield, but the phenotypic interaction to the environments determines the outcome. Most of the recently developed cultivars considering a narrow genetic base can lead to less resilience in the present scenario. Single genotype and its reaction to resilience is not the ideal which invites the involvement of a larger set of genotypes with diverse response and their interaction in variable changing environment (Kahiluoto et al. 2019). The genomic region also controls the climate resilience which can be used exploiting the genomic sequence and information as reported in wheat (Juhasz et al. 2018).

4 Breeding Strategies

4.1 Trait-Based Breeding: Phenotyping to Genotyping

To make genetic gain in terms of yield under adverse climatic condition, its genetic loci and nature of inheritance need to be exploited which have been widely exploited by QTL identification to identify the adaptive nature of the traits concerned (Kole et al. 2015), adaptation in water limited environment (Tuberosa 2012), carbohydrate exporting toward reproductive organ under stress (Rebetzke et al. 2008), stay green traits (Borrell et al. 2014), and root architecture diversity for stress environment (Lynch et al. 2014; Uga et al. 2013). Major traits that confer resilience in some crops with biomass and it's partitioning which maximizes reproductive sucess must be flexible enough to harbour maximum gain under adverse threats involves partitioning to be improved with source-sink economy optimization through minimizing costitutive stress adaptation and genetic dissection of these can be done for these traits (Salem et al. 2007; Serraj et al. 2009) for resilience response. As flowering response under stress condition controls the productivity especially during heat and drought stress, so complex inheritance patterns of flowering and both the heat and drought tolerance are polygenic in nature that plays a major role (Buckler et al. 2009). By amalgamation of modified phenotype-based genotyping and integrating them in fine-tuned approaches, the gain is possible for climate-resilient agriculture (Table 4.1).

Table 4.1 Specific strategy applied for breeding in climate resilience

Recent approaches and methodology	Area and types	References
Utilization of response diversity	Exploration-based	Kahiluoto et al. (2019)
Use of adaptive traits	Trait-based Breeding	Kumar et al. (2019)
Protected agriculture	Technology-based	Henry (2020)
Plant and Soil microbes linkage	Microbial genomics	Pourkheirandish et al. (2020)
EcoTILLING	Mutational genomics	Kurowska et al. (2011)
Genetic switches	Application-based	Banga and Kang (2014)
Machine learning	Application-based	Yang et al. (2014)
High-throughput phenotyping with GWAS	Technology-based	Yang et al. (2014)
System-based plant breeding	Cumulative approach	Lammerts van Bueren et al. (2018)
Translational research	Product-based	Reynolds et al. (2019)

4.2 Speed Breeding

Conceptualizing the technology NASA used in space for growing crops in an enclosed chamber manipulating photoperiod speed-breeding has been deduced in various crops including legumes and cereals. Maintaining light intensity ranging from 400 to 700 nm, continuous light cycle with limited dark period, moderate humidity (60–70%), maximum temperature 22/17 °C, illuminating by LEDs, and halogen sources in a greenhouse or growth chambers can cut generation time drastically (Ghosh et al. 2018). In a confined greenhouse maintaining light source and other environmental factors, generation time has been reduced to 6 in the case of wheat, barley, durum wheat, pea, and 4 generations in canola in case of only 2–3 generation in normal greenhouse conditions (Watson et al. 2018). Another experiment generation time, that is, 7, 6.2, 6.0 generation per years have been achieved in chickpea in early, medium, and late-maturing genotype manipulating light, temperature, and germinating immature seeds which represents different varieties from different agro-ecologies (Samineni et al. 2019). Even crop-specific LED standardization and far-red light generate rapid flowering without the involvement of embryo rescue and other tissue culture approach (Jähne et al. 2020).

4.3 RGA

Climate-resilient plant breeding needs a quick pace for developing outcome and target variety and to reduce the long crop cycle, for which techniques have been evolving. Growing crops in winter nursery and utilizing double haploid technique for faster crop cycle reduction have been in existence since long. The rapid breeding cycle considering quick climate change happening strategies toward varietal replacement can be done by altering allelic frequencies, selecting commercial cultivars and disseminating in advance for adaptation to happen in farmer's field, and keeping these altered varieties as a parent in future breeding programs (Atlin et al. 2017). Speed breeding with single seed descent (SSD) reduces breeding cycle, increases development of favorable breeding lines, and also lowers the cost of the breeding program (Janwan et al. 2013), and this SSD technique is being used since long for isolating desirable transgressive segregants (Moon et al. 2003). Performance of a variety under climate change scenario depends on performance under varying climatic component including higher CO_2. One rapid breeding technique has been developed, that is, biotron breeding system (BBS) which uses CO_2, temperature control, day length manipulation artificially by increasing crop growth rate followed by embryo rescue for minimizing the span of the seed maturation and dormancy period, that has been conceptualized and experimented in Nipponbare rice variety where generation time is attainable to 2 months only (Tanaka et al. 2016). BBS technique has been more successful in those varieties having photoperiod-sensitive long duration cultivars.

4.4 DH and Shuttle Breeding

To reduce the time required for a variety development, CIMMYT's approach of shuttle breeding has been developed to increase the pace in variety development, increase the adaptability in multiple environment that helps the variety to adopt wide-area (Ortiz et al. 2007), and was first initiated in rice. Due to some restrictions for trans-boundary movement of materials to implement such off-season trial though, in private sectors they rely upon this technique (Lenaerts et al. 2019). Among quick breeding strategies, double haploid has been quite important since long and homozygous lines can be developed in a very short time (Mishra and Rao 2016). Numbers of varieties are being developed by using DH technique in rice and other cereal crops (Pauk et al. 2009). DH technology is a component of forward breeding and quickly screens the potentiality of a line and increase genetic gain (Chang and Coe 2009). Even DH technology can increase the effectiveness of genomic selections for low heritable traits and where there is less scope of offseason nursery as trans-boundary (Bouchez and Gallais 2000). DH technology can divert resources for evaluation lines for climate resilience instead of repeated inbreeding, and finally using in varietal development (Prasanna et al. 2013).

4.5 Reducing Crop Breeding Cycle in Perennial Crops

In the crops having a long juvenile period, flowering and reproductive transition can be optimized by the environment. Sometimes various environmental factors such as water scarcity, insufficient lights, and mineral insufficiency can lead to delayed transition; on the other ways, can also influence to cut the juvenile phase according to the extent of exposure (Zimmerman 1972). Use of various plant growth regulators (PGRs) for hastening flowering and dormancy breaking by ABA, gibberalic acids, and nitric acids, causing a reduction in crop cycle, is common in existence in agriculture practices (Nocker and Gardiner 2014). Rather than these feasible technologies, interventions in flowering pathways lead to an altered shorter breeding cycle. Flowering gene *LEAFY* has been proved to be associated with triggering effect in Arabidopsis, though these genes are highly conserved in flowering plants and flowering is interlinked with activations of series of genes by manipulating internal factors and environmental stimuli and can be exploited in these crops too (Weigel and Nilsson 1995).

4.6 Prediction-Based Early Phenotyping

Breaking the stagnant condition of genetic gain in several parts of the world in major food crops is the major challenging target under the climate change scenario (Acreche et al. 2008; Sadras and Lawson 2011). Advances in genotyping technology from simple mapping to genomic selection are based on a robust phenotyping data. Lack of robust phenotyping data due to lack of field-level recent phenotyping platform is hindering the conventional plant breeding program also as all the genomic prediction is based on a statistical model that is based on phenotyping (Desta and Ortiz 2014). Even phenotyping efficiency is the key factor for future plant breeding for genomic (Ghanem et al. 2015). Early detection of stress before symptoms develop can be implemented involving chlorophyll fluorescence, infrared spectroscopy, and spectral imaging, that is, RGB imaging that has been tested widely (Fang and Ramasamy 2015; Mutka and Bart 2015), but implementing these at canopy level is something more complex (Pauli et al. 2016). Human-driven phenotyping lacks robustness and sometimes ignored if found less amount of heritability for the traits. Development of phenotyping protocol for preferred traits that are being used by plant breeders continuously for breeding new cultivars are in utmost need. Advancement in RGB imaging technology, plant height measurement sensors such as LiDAR, and even yield estimation based on line sensor and flat-based scanner involving conveyor belt are in recent development and are used for increasing genetic gain (Friedli et al. 2016; Hämmerle and Höfle 2016; Tanger et al. 2017). These techniques are available to phenotype rigorously by increasing the number of phenotyping traits, and continuous time scale data for a long time can be analyzed for better genetic gain which is important for climate resilience (Liang et al. 2016;

Miller et al. 2017). To minimize the genotype–phenotype gap arising due to dynamic changes in the environment, plasticity of plant traits and their unpredictable changes can be addressed if the variable environment and response is studied in the same system, that is, soil plant atmospheric continuum (SPAC) as a component of high-throughput phenotyping system for analysis of plasticity of traits (Negin and Moshelion 2017). Various computational models are now in practice used in several places which predict spatiotemporal phenotyping and complex trait analysis. NIR-based phenotyping of plant physiological status correlates with wild and mutants study under climatic variations, and predicting the biochemical content in a model-based prediction phenotype is in common use (Anderssen and Edwards 2012; Osborne 2006; Wiley et al. 2009).

4.7 Advances in Selection Methodologies

Coefficient of determination and magnitude of variance were used for varietal evaluation for climate-resilient response (Mahajan et al. 2012). Trait mapping with increased resolution makes a large set of germplasms accessible for developing advanced materials for development of final crop variety involving all the measures of mapping, trait heritability, and recombination frequency (Cockram and Mackay 2018). All the traits that respond under variable environment need critical consideration and must be studied using family-based mapping and association in random population (Taranto et al. 2018). Linkage disequilibrium linkage analysis (LDLA)-based QTL mapping can be applied for crops having less divergence and quite close ancestry (Pikkuhookana and Sillanpää 2014). Climate change responsive traits are complex in nature having large genotype–environment interactions which need phenotyping platforms with manageable stress intensity causes a perfect estimation of the genetic cause of tolerance (Bolanos and Edmeades 1996; Carena 2005).

4.8 Advances in Molecular Genotyping Strategies for Faster and Higher Genetic Gain

Advancement in technologies specifically marker-based genotyping systems has been developed in such a way that higher genetic gain ultimately reduces time scale for quick delivery of product (Kumar et al. 2011) and linked markers with the genomic regions are suitable for climate change acceptable crop variety. Marker-based prediction of genomic potentiality has been utilized for genomic selection technologies which have already surpassed the conventional pedigree-based methods in several groups of crops including cereals, legumes, and forest species (Harfouche et al. 2012; Wallace et al. 2018). Problems of inability to assign some marker polymorphism to traits concerned due to nonlinear relationship, epistatic effect, and complex downstream interaction of target genes with several metabolic networks are major concern; these have been resolved by integration domains of multi-omics data including metabolomics, transcriptomics, and epigenomics involving all the regulations (Harfouche et al. 2019). Geographically, a diverse set of a large number of lines of *Arabidopsis* genome scan revealed a set of SNPs that have been attributed to various candidate genes causing environmental variation throughout the environment which shows adaptiveness for climatic variations and shows resilience (Hancock et al. 2011). Transcriptome sequencing involving within-population individual genotype-based study in various environmental regimes is widely used for candidate gene identification which shows variable expression may be associated with the trait indirectly (Urano et al. 2010). This technology improves the older version of the variety for target traits (Collard and Mackill 2008). Marker-assisted breeding reduces the time taken for delivery of a variety, and a robust system of markers for validated QTLs needs to be available for quick breeding procedure (Lenaerts et al. 2019). The advent of increasing global population and environmental problems of instability to increase the pace in the development of plant breeding with the quickest and reliable technology invited molecular plant breeding (Talukdar and Talukdar 2013). Private sector development in case of plant breeding industry with improved quality seed supply and major molecular marker-assisted breeding involving RAPD, AFLP, SSR, and SNP has been a part of routine use (Paul 2009). QTL analysis (Backes et al. 1995), association analysis (Crossa et al. 2007; González-Martínez et al. 2007) for indepth genetic analysis can be useful for climate resilience related genetic loci and associated candidate genes. For climate resilience breeding major QTL with larger phenotypic variations is needed under wide variable stress environment that must be at first need to be responsive to stress environment and then the effect on the variable environment needs to be identified. Among three major QTLs identified in pearl millet, one major QTL responses to yield more than 30% phenotypic variation under drought environment. For allele mining TILLING, sequencing-based allele mining (Kumar et al. 2010) in natural population, Eco-TILLING has been an integrated part in recent genomics technologies. GWAS has been used for a few years for QTL discovery and candidate gene identification has been done using whole-genome marker analysis. In élite lines of rice, maize (Lu et al. 2015; Wang et al. 2016a, b) GWAS has been utilized for various agronomic character and quick delivery of the product has been successful. To resolve complex traits for sustaining environmental variations, next-generation populations have been conceptualized and used in dissection traits in a large population rather than conventional mapping populations (Rockman and Kruglyak 2008). Mapping in nested association mapping population has been used widely in maize and harbors a lot of potentiality under climate change condition (Talukdar and Talukdar 2013; Tian et al. 2011). DArT allows the simultaneous isolation of a large set of polymorphism profiles without prior knowledge of sequence, and conversion to PCR-based marker system helps in improving choice for traits concerned (Fiust et al. 2015; Zhang et al. 2009).

4.9 Genomics

Evolution of genomics technologies covering structural and functional aspects is essential for predicting genomic potentiality of particular loci and utilizing this knowledge developing variety with short span of time is a boon for agriculture. Microarray, one of functional genomics, first evolved in 1995 for expression study (Schena et al. 1995). Though so many experiments for identifying genes were related to various stress, predictive cellular changes, changes in gene expression have been solved out (van't Veer et al. 2002). Recently more dependence on NGS technology, microarray has been developed irrespective of species as for nonmodel crop, where genomic information is few the use of only microarray is quite limited (Neumann and Galvez 2002). Even some study involving both NGS and microarray succeeded in developing highly annotated microarray for organisms (Marinković et al. 2012). ESTs/gene identification through gene chip assay (Baldwin et al. 1999), comparative genomics initially to predict the synteny gene from different species for finding allelic variation (Ellis et al. 1999), evolved much for gene prediction. Even transcriptomics data have been associated with phenotypic data by regulatory network development by combining eQTL. Transcriptomics plasticity has been generated in *Primula sikkimensis*, a high altitude plant species under climatic variations which can be used to explaining phenotypic plasticity (Gurung et al. 2019). Availability of genomic sequence information can answer issues such as adaptive variability, inbreeding, level of adaptation locally, and interaction with various environments (Allendorf et al. 2010). Genomics and precision breeding will be major breakthroughs for food and agriculture under changing scenarios. Genome sequencing of hundreds of crop species including unexplored segments of the population of species will cover identification of genetics of complex traits (Li et al. 2020). Even re-sequencing of a large number of crop species will increase understanding the unexplored trait for developing future variety (Ma et al. 2019). Plant response to variable climate to identify better-adapting genotype can be done using genomics technologies (Abberton et al. 2015). Genotyping by sequencing technology is gaining its wide popularity for gaining marker development and mapping. This technology is one of the promising candidates for fast breeding protocol in the perineal crops. In kiwi fruit, the GBS pipeline has been utilized for the identification of markers associated with disease resistance, which reduced the time taken as it facilitated the simultaneous isolation of a large set of markers under various environmental extreme phenotypes of the population as compared to a single marker association (Gardiner et al. 2014). Recently genomic selection technique is being used widely which is the advanced MAS strategy; in GS technology major traits genomic prediction is done based on a large set of loci, not a particular loci which reduces the time indirectly increasing genetic gain (Desta and Ortiz 2014; Heffner et al. 2010; Heslot et al. 2015). Current research is to be tuned enough which considers available crops and their accessibility for adaptive response breeding as a backyard strategy (Manners and van Etten 2018). LncRNA around 200 bp without the role of protein-coding directly has been reported to involve in stress tolerance (Golicz et al.

2018). Even the role of noncoding RNA in heat and drought tolerance has been studied widely (Hivrale et al. 2016; Zhao et al. 2016).

4.10 Generating Novel Diversity

Irradiation through various physical irradiation agents such as gamma-ray, X-ray, and fast neutron is widely used for plant mutagenesis for mutant variety development (Sikora et al. 2011). Recently, fast neutron is widely being used for saturating genomes and complete gene mutation is possible and sometimes create macro deletions (Gilchrist and Haughn 2010). More than 400 mutant varieties are registered in IAEA, having major numbers for soybean (IAEA/FAO 2017).

4.11 Epigenetics

Epigenetic changes i.e. alterations in nucleotide sequences through transgenerational response for few traits or occurrence of phenotypic plasticity in some other traits toward climate resilience is one of the major domains for concern for regulation of climate-resilient responsive traits (Baerwald et al. 2016; Burggren 2016; Kronholm and Collins 2016). In case of rice, epiallele is identified to be involved in linking DNA methylation and histone methylation manifested in dwarf stature and various floral defects (Zhang et al. 2012). Novel epiallele for climatic adaptation locally has been identified in Arabidopsis accessions where NMR19-4 allele is environmentally associated and its methylation is stable in respect of generational inheritance (He et al. 2018). To understand the climate-resilient adaptation in plants, methylation profiling, which is the most widely used technique, is being used. Among recently used techniques which evolved recently include bsRADseq (Trucchi et al. 2016), bisulfite sequencing (Cokus et al. 2008), methyl-sensitive amplified polymorphism (MASP) technique (Schulz et al. 2013), and another reduced representation epiGBS (van Gurp et al. 2016). Even epigenetic mechanisms can cause sudden hypersensitive response and chromatin restructuring which keeps a plant adapted to stress (Thiebaut et al. 2019). Plants keep adapting through changes within to address the issues such as temperature variables, moisture variations, nutrient extremities, and light intensities and to cope from these challenges plants employ epigenetic modifications along with the genetic changes through responses (Shankar and Venkateswarlu 2011). Plants memory toward previous stress imposes an adaptive mechanism for future stress response. FGT1 gene has been identified which binds to a class of heat-inducible genes and making accessible these genes for remaining active (Varotto et al. 2020). Stability and heritability of epigenetic marks are important for increasing abiotic stress tolerance as described by Gallusci et al. (2017).

4.12 Pangenomes

Direct sequencing of wild accessions yields a large set of information due to evolution in sequencing technologies helps by creating reference genome framework can be utilized in comparative genomics studies (Brozynska et al. 2016). Pangenomes in tomato uncovers some important genomic loci important for some traits that have been lost during evolution as absent in reference genome, where pan-genome identified so many loci lost due to negative selection analyzed through presence and absence variations (Gao et al. 2019). Elaborative research about wild species around several environments of gene distribution can help to breed for higher adaptability for wide environment climate resilience ability. Pan genes could find common genes across the species for biotic and abiotic stress responsive as well as further evolutionary study which can help in climate resilience research for all the respective traits (Bayer et al. 2020). Sequencing multiple individuals for identifying plant pangenome is important for gene discovery but it will expose hidden genetic variations quickly that information can be utilized in future crop improvement (Tao et al. 2019). Resequencing of 14 cultivated and 17 wild accessions of soybean revealed greater diversity in wild species (Lam et al. 2010). A study in wild rice considering 446 accessions of *Oryza rufipogon* genome sequencing revealed domestication traits linked loci (Huang et al. 2012). A comparison of 189 accession sequencing with pangenome in sunflower reveals the 10% of cultivated pangenome introgressed from wild and related with abiotic and biotic stress tolerance (Hübner et al. 2019). Even the construction of super pan-genome data using species pangenome and genus pangenome may uncover a detailed scenario of the evolution of various traits related to adaptation (Khan et al. 2020).

4.13 Evolution in Sequencing Technologies and Rapid Genomics

Comparative assessment of two sequencing platforms during *Brassica* genome assemblies considered Illumina and PacBio, where Pac Bio assembled nearly 3000 assembly specific genes and several unique TEs that are specific to new assemblies (Zhang et al. 2018). 5G technology can be applied for crop improvement integrating all the approaches to quick genetic gain and developing climate-resilient variety with higher precision utilizing the entire advance avenue evolved so far (Varshney et al. 2020). Simplicity and affordability of robust technologies of PacBio and Oxford and Nanopore technologies enabled field detection of Begomovirus in Sub-Saharan Africa in cassava (Boykin et al. 2019) and assembled a highly contagious genome of Brassica (Rajarammohan et al. 2019) which introduced quick plant genomics research for varietal development. Minimizing the gap between advanced biological research and applied breeding involving translational research for linking fundamentals and breeding in the higher temperature and limited water environment can add value to predefined research outcome (Ray et al.

2013). Translational research involving all the components viz. crop design, integration of germplasm and phenotyping, cross breeding followed by selection, evaluation of genetic gains and informatics can deliver a profitable outcome. System-based crop breeding involving trait-based breeding with corporate breeding and community approach will deliver the crop variety in an interactive and cooperative manner with more resilience.

4.14 Genome Editing

Different types of genomic editing approaches were available to create a new cultivar but the choice of approaches depends upon nature of traits, information about plant, availability of phenotypic and genotypic resources, and regulation of different countries' use of advanced generation biotechnologies, based on cisgenesis, transgenesis and genome manipulation (Rinaldo and Ayliffe 2015). When needed molecular information-based breeding methods are coupled with high-throughput molecular advanced way-out, moderate cost-based approach, and precise evaluation and prediction of quantitative trait expression which yields desirable climate-resilient varieties. Genome editing has greater potential to overcome this bottleneck and accelerate the breeding to develop novel crop varieties manipulating traits which imparts stress tolerance and nutrient enrichment and quality as well (Kamthan et al. 2016; Varshney et al. 2011) which makes sure a sustainable increase in production by adapting crops (Carpenter et al. 2001; Kahiluoto et al. 2019). Different strategies are needed for developing climate resilience in crop variety to increase genetic gain under such conditions (Varshney et al. 2011). Genome editing technologies of two categories which include oligonucleotide-directed mutagenesis (ODM) and site-directed nucleases (SDNs) and both the technology allows directive manipulation for mutagenesis, gene transfer, and remodeling expression of genes in various directive depth (Cardi et al. 2017). Transcription activator-like effector nucleases (TALENs) and zinc-finger nucleases (ZFNs)have the capacity to recognize a specific DNA sequence that linked to the nonspecific cleavage domain which includes dimerization surface that helps in DNA cleavage. The new DNA templates introduced into the genome via DNA double-strand breaks (DSB) at specific genomic location stimulate nonhomologous end joining or homology-directed repair for genetic modification (Gaj et al. 2013). ZFNs are artificial restriction enzymes generated from zinc finger transcription factors which are target specific having the capacity to recognize 3–4 nucleotide flanking sequences and bind to an extended unique 9–18 nucleotide sequence at the flanking site (Lin and Musunuru 2016). It has a limited target site for selection (Xiong et al. 2015) and poor at sequence with low guanine content and must be located within 100 nucleotides with each other. Coevolution of rapid growth of population and climate change demands novel need to think out of the old box CRISPRs is a flexible tool for targeted genome editing in basic research for improvement in crops. It speeds up the process of the development of crops which will adapt itself with the changing environment and it will make sure that agriculture will grow up with this ever-changing climate. Like TALENs and ZFNs, another most effective genome editing tool is CRISPR pronounced crisper, and specialized stretches of DNA stand for clustered regularly interspaced short palindromic repeat and the protein cas9 or CRISPR associated. It belongs to the family of the DNA sequence which originates from the archaea and bacteria act like molecular scissors. The most commonly used CRISPR is type II found in Streptococcus pyogenes, it act as hallmark bacterial defense system which edit the genome at a specific site permanently. The guide RNA is complementary to a target gene, the Cas9 nuclease creates double-strand breaks which is followed by a directed repair mechanism or non-homologous end joining (Jinek et al. 2012; Scheben and Edwards 2017; Xiong et al. 2015). It has many advantages which make it a very powerful and popular tool for genome editing as it is lower in cost, easy to use, multiple target sites can be edited within a single genome hence, in a single generation gene pyramiding can be done into a new cultivar, as directly new mutation can be introduced thus, existing diversity does not matter. Genome editing will not cause the introduction of deleterious alleles like the backcrossing method. As per Bortesi and Fischer (2015) and Osakabe et al. (2016), CRISPR has higher specificity than any other genome editing techniques according to Shen et al. (2014), Gasiunas et al. (2012), and Ran et al. (2013). Cas9 nickase may be helpful for its further improvement. But CRISPR will not be useful as same in different crops as comprehensive knowledge of the target gene(s) is required initially. As there is a negative view among the peoples about the genetic engineering crops but the use of CRISPR in rice and tomato diminishes this and accelerating the crop improvement in the first generation, it is helpful in introducing homozygous mutations in transformant, but when controlled crosses were made between the transformants, the progeny can be produced without the transgenes as transgenes are hemizygous while in the genome editing it is biallelic (Brooks et al. 2014; Zhang et al. 2014). However, through genome editing techniques no commercial varieties are available in any crop. But some examples are there in which CRISPR has been used for improvement in climate-related traits like in rice targeting *OsERF922* gene, it enhanced the resistance against blast (Wang et al. 2016a, b). Similarly, in wheat gene TaMLO has great achievement in controlling powdery mildew resistance (Appiano et al. 2015; Wang et al. 2014), in cucumber eIF4E gene disruption leads to broad virus resistance (Zhang et al. 2016), disruption of the SlDMR6-1 gene in tomato leads to resistance in broad-spectrum disease (de Toledo Thomazella et al. 2016). Hence, we are expecting different climate-resilient crops for commercial release with the help of genome editing in the next 10 years. Genetic switches technology which uses gene resource from the microbial community has been utilized in Arabidopsis which can withstand severe moisture stress (Banga and Kang 2014). Development and advances in genomic technologies and available in-depth knowledge of genes and in vitro regeneration potential make more accessible second-generation technologies based on cisgenic and genome editing potential for sustainable future food crop breeding (Osakabe et al. 2016; Rinaldo and Ayliffe 2015). Development of disease tolerant rice utilizing OsSWEET14 gene through genome editing through modifying the effector binding region is one successful approach of utilizing TALEN change. Genome editing is a quicker approach for biotechnology-based crop breeding with higher precision and can be helpful under fast breeding program (Taranto et al. 2018).

4.15 Artificial Intelligence and Climate Change

Artificial intelligence accelerates the farming through automation and increases the crop yield and quality with the help of fewer resources through precision agriculture by analyzing different parameters such as condition of soil, weather, and temperature which were collected from the prospective farm for better decision for correct and controlled farming which gives the idea about how to manage soil health, water, nutrient, monitoring the health of crop, crop rotation, optimum planting date and population, timely harvest, etc. Due to climatic uncertainty and variability, the cultivars give diverse responses to weather condition which creates thousands of datasets with respect to yield related observations. The main goal of the breeders is to predict the better progeny lines after crossing two contrasting parents and gain in yield as compared to the parents. It required advance phonemics and genomics too which allows the breeder to push the yield toward target and produces a huge amount of dataset. Many times, it is not possible to explain the missing heritability, that is, only a fraction of genetic variation such as SNP or In-Dels explains the exact phenotype. Some of the explanations are like the minor genes effects were neglected unless a large population are analyzed, there is not a linear relationship between genotypes and phenotypes, genes have to follow a complex regulatory networks but their products go some downstream modification and as in epistasis it interacts with other pathways and protein complexes. The above-discussed problems can be sorted out by increasing the number of population and the data were collected correctly so that the complete knowledge of biological, environmental, and their interaction can be obtained. For finding the best line among others in a specific environment, the combination of genomics and phenomics with big data collection is required. If the phenomics, genomics, and AI technologies will be used together, it has the capacity to accelerate the development of climate-resilient crop varieties in less time having improved yield potential and stability. Thus enhanced tolerance to the anticipated and simultaneous abiotic and biotic environmental stresses. In the modern era, for better data collection apart from molecular advance technologies, breeders must have to access the high-throughput sensors and imaging techniques to analyze situations of different traits in the field, Next-Gen AI is conceptually designed so that it will predict the breeding value for complex traits across environments and time scales. Thus, a breeder can better predict which variety or line will be going to perform better in adverse environmental condition and what kind of environment will better suit the crop like soil, moisture, humidity, temperature, etc. There is a complexity of correlation between the phenotype, genotype, and environment, and its interaction gives a more meaningful profile of plant stress response. This genotype and phenotype gap will be filled by artificial intelligence (Gosa et al. 2019).

4.16 Transgenic and Climate Change

As climate change alters the cropping pattern in time and space, it is very difficult to predict the crop yield. The crops were made adapted to the new environment either developing new crops via domestication or introducing genes of target traits into existing crops through genetic engineering. Hence, to produce the genetically modified crops (GMCs) the traits were manipulated by inserting/altering the desired genes into the Lemaux (2009), the important issue about transgenic crops is their impact on the environment. Genetically modified crops are based on monoculture farming as it required large land areas, but in India marginal and small land holding farmers are there; hence, they are not able to give the large isolation distance between GMCs and cultivated varieties. Apart from some loopholes, it has many advantages also as according to Bennet et al. (2004), as it assumes that herbicide tolerates are harmful to the environment but there is some exceptions like in sugar beet which tolerate the herbicide and it is less harmful than conventional crop as it lowers the emissions from the herbicide manufacture, its transportation and field operations. Agriculture contributes significantly to greenhouse gas (GHG) emissions mainly via rice production. Many authors also suggest that transgenic crops have the ability to reduce the release of greenhouse gas emissions due both to less pesticide applications and increasing the area grown with the help of “no-till” or “reduced-till” under conservation agriculture. Many works have already been done by many scientists in various traits improvement for adopting crops in adverse climatic conditions through genetic engineering. Ainsworth and Long (2005) worked on high CO_2 and high O_3 environments through genetic engineering to combat the changing climatic situations. The most recent research advances in genetic engineering were done by Ortiz (2008). They worked for the improvement in adaptation in different abiotic stress such as drought, salinity, or extreme temperatures in crops. Different nitrogen-containing fertilizers and manures release nitrous oxide and dioxide which are potent GHGs in the environment. Thus, our breeding strategy must be like that way only through which crop will be able to increase their nitrogen use efficiency. In barley, a candidate gene alanine aminotransferase when overexpressed increases the nitrogen use efficiency of plants at the early stage of growth. Temperature above 21–23 °C has a crucial role in climatic change as photosynthetic efficiency in C4 plants can exceed as photorespiration suppression that of C3 plants by up to 50% as these are adapted to the cool environments. Thus, through genetic engineering C4 photosynthesis into C3 plants increases biomass and grain yields per unit of water transpired (Hibberd et al. 2008). So many attempts were made to introduce transgenes into plastids and nuclear genomes for increment of photosynthetic efficiency (Maurino and Weber 2013).

5 Conclusion

Avoiding quantification of yield loss under various climatic regimes and variable responses under climate resiliency and the scenario of yield loss and reduction due to lower resilience toward climate is a major hindrance in the unavailability of pictures of climate resilience potentiality of cultivars irrespective of ecology and systems. Previous thinking on plant breeding is now at the end, which brings involvement of all the developed technologies that made revolutions in phenotyping and genotyping with reduced cost and in an effective way to make the improvement in translation mode.

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Chapter 5
Recombinant DNA Technology for Sustainable Plant Growth and Production

Saumya Pandey

Contents

1 Introduction

In recent times, the major threat to human life is malnutrition, health problems, and environmental hazards that are responsible for the loss of innumerable lives in developing countries. To achieve a healthy life, the daily intake of food must be enriched with all the essential nutrients providing basic nutrition and other health benefits (Smith and Gregory 2013). However, the population explosion resulting in loss of productive land and the occurrence of adverse environmental conditions (e.g., drought, salinity, and disease) are main hindrances in fulfilling the requirement of food per capita (Datta 2013). Thus, to accomplish the nutrient requirement of upcoming generations, the food production must be increased by 50–100% than at present despite adversely changing environmental conditions (Baulcombe 2010).

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In the mid-1960s, the introduction of Green Revolution technologies such as the use of chemical pesticides (e.g., DDT) and fertilizers, irrigation, and conventional plant breeding has led to increased crop production throughout the globe (Khush 2001). However, the mechanization and use of chemical input-based farming to increase crop productivity has caused overutilization of natural resources particularly groundwater and soil. Also, the extensive use of chemical-based inputs has resulted in a decline in its efficiency and subsequently increases in the intensity of applications (Liu 2010; Yu and Wu 2018). The long-term and excessive use of chemical-based input causes environmental damage. Today, the major focus is to adopt the technologies and practices that do not have an adverse impact on the environment, are assessable to effective for farmers, and lead to improved productivity and yield. The concept of sustainability in plant production and growth includes both resilience and persistence and has an impact on several social, economic, and environmental issues (Velten et al. 2015).

The conventional plant breeding approaches to obtain improved trait and yield have been proved insufficient to keep the pace with increasing population because the genes for desirable traits might be absent in gene pool of specific crop variety selected for hybrid production (Datta 2013). However, with the advent of several biotechnological tools, the existing gene pool of organisms can be extended by transferring the desirable genes from any sources including inter-kingdom (Kamthan et al. 2016). Recombinant DNA technology has the potential to develop genetically modified plants with desired characters such as enhanced yield and nutritional quality, increased biotic, and abiotic tolerance and thus exhibit improved adaptability for better survival (Parmar et al. 2017). Recombinant DNA technology allows faster, cheaper, and accurate insertion of specific traits from diverse sources into the plant genome compared to natural recombination or conventional breeding method.

Recombinant DNA technology is the process of combining DNA molecules from the desired organisms and transferring them into a host organism to form recombinant products that are beneficial in the field of agriculture, medicine, and industries. The prerequisite requirements for the production of sustainable and commercial transgenic plants are efficient transformation methods. Till now several methods have been developed to transfer the desired genes into the host plants. Some methods of gene transfer include vectors such as *Agrobacterium tumefaciens*, whereas other transformation methods that are vector-less such as electroporation (Arencibia et al. 1995), microinjection (De la Pena et al. 1987), particle gun bombardment (Sanford 1988), and polyethyleneglycol-mediated (PEG) transfer (Uchimiya et al. 1986) have also been developed. Among various available transformation methods, the most commonly used for the development of transgenic plants are *Agrobacterium tumefaciens*–mediated gene transfer that allows direct transfer of DNA into cell or protoplast by particle bombardment method and osmotic or electric shock. After the transformation of specific cell or protoplast, standardized tissue culture methods are used for the regeneration of transgenic plants (Nalluri and Karri 2020) (Fig. 5.1).

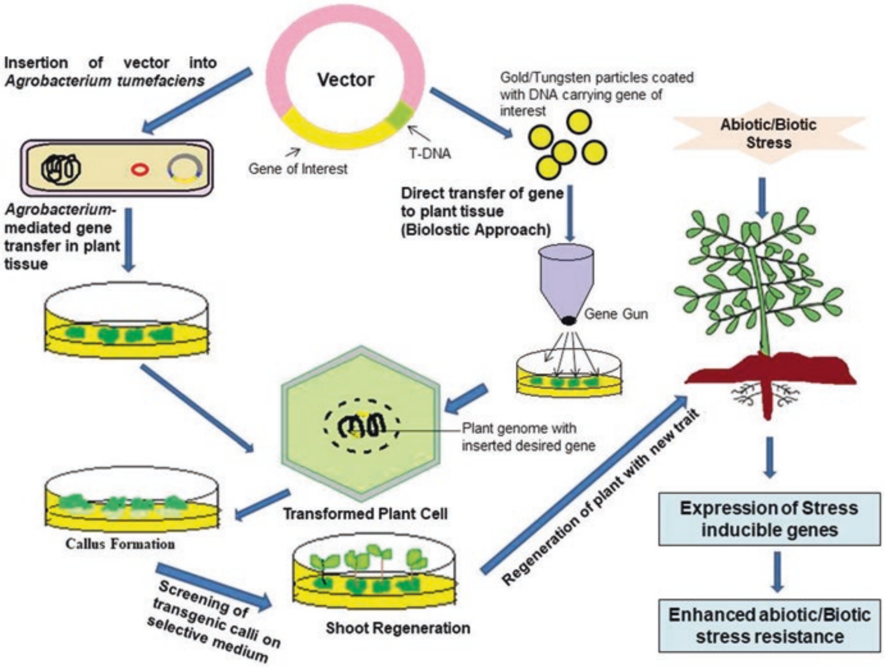
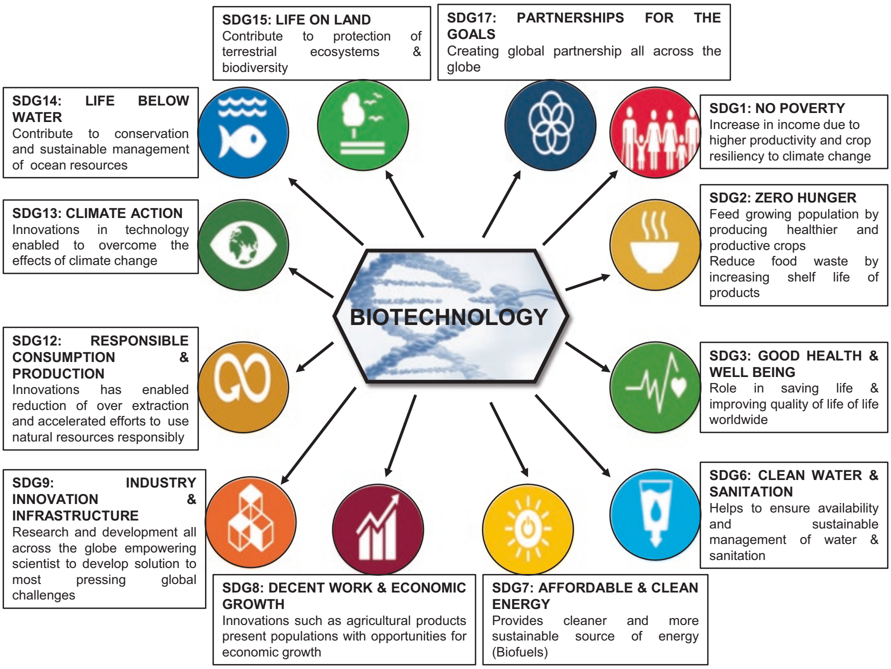


Fig. 5.1 Recombinant DNA technology approach for the genetic improvement for sustainable plant growth and productivity

2 Recombinant DNA Technology for Sustainable Development

As per the report "Our Common Future" of World Commission on Environment and Development, the idea of sustainable development is founded on the basic principle of employing the technologies with the capacity to increase the basic living standard of world's growing population, without needlessly exhausting limited natural resources and thus deteriorating the environment (Imperatives 1987).

New Sustainable Development agenda has been approved by the United Nations, which includes 17 Sustainable Development Goals (SDGs) in the year 2015. These goals aim to bring peace and prosperity globally by 2030 through ending poverty, food security, and conserving natural resources. These goals are interrelated in a way that activity plan of one field will affect the result of other and that development must balance social, economic, and environmental sustainability (Hak et al. 2016). Biotechnology paves a way for attaining sustainable development goals by improving plant health and production, providing fortified food solutions, reducing greenhouse gas emission, etc. Biotechnology plays an important role in various sustainable development goals such as SDGs1-3, SDG6-9, and SDG12-17 (ICBA 2019) (Fig. 5.2).



SDG15: LIFE ON LAND
Contribute to protection of terrestrial ecosystems & biodiversity

SDG17: PARTNERSHIPS FOR THE GOALS
Creating global partnership all across the globe

SDG14: LIFE BELOW WATER
Contribute to conservation and sustainable management of ocean resources

SDG1: NO POVERTY
Increase in income due to higher productivity and crop resiliency to climate change

SDG13: CLIMATE ACTION
Innovations in technology enabled to overcome the effects of climate change

SDG2: ZERO HUNGER
Feed growing population by producing healthier and productive crops
Reduce food waste by increasing shelf life of products

SDG12: RESPONSIBLE CONSUMPTION & PRODUCTION
Innovations has enabled reduction of over extraction and accelerated efforts to use natural resources responsibly

SDG3: GOOD HEALTH & WELL BEING
Role in saving life & improving quality of life of life worldwide

SDG9: INDUSTRY INNOVATION & INFRASTRUCTURE
Research and development all across the globe empowering scientist to develop solution to most pressing global challenges

SDG6: CLEAN WATER & SANITATION
Helps to ensure availability and sustainable management of water & sanitation

SDG8: DECENT WORK & ECONOMIC GROWTH
Innovations such as agricultural products present populations with opportunities for economic growth

SDG7: AFFORDABLE & CLEAN ENERGY
Provides cleaner and more sustainable source of energy (Biofuels)

Fig. 5.2 Graphical representation of the relationship between biotechnology and sustainable development goals (SDGS)

Recombinant DNA technology has emerged as a potential tool in the field of biotechnology that can facilitate in maintaining equilibrium between the environmental conservation and developmental needs of the world's growing population. This emerging technology has the potential to cause another green revolution and thus would eliminate the world's hunger. In recent decades, the application of recombinant DNA technology for the improvement of crop traits has resulted in a considerable increase in productivity, yield, and enhanced resistance to disease (Nasim 2003).

According to report (ISAAA 2018), genetic engineering (RDT) has become the most adopted technology in the world for crop improvement with ≈113-fold increase in crop area ever since its initial commercial production in 1996. The number of countries growing genetically engineered crops has been increased to 26 including 21 developing and 5 industrial countries. Also, an imported genetically engineered crop has been used by 43 nonplanting countries. The genetically engineered crops have an immense contribution toward global food security, sustainability, and climate change. During the year 2017, approximately 80% cotton, 77% soya bean, 32% maize, and 30% canola GM crops were cultivated in terms of global area. Canada, United States of America, and Argentina are the leading producers and exporters of genetically modified crops and their products. In developing countries, China, India, Argentina, and Brazil are among the major producers of GM crops.

The decline in the use of pesticides by 670 million kilograms has been reported after adopting genetically engineered crops. According to the 2016 study, the use of insecticide resistance variety has reduced the use of chemical insecticide sprays causing a decrease in CO_2 emissions in the environment by 27.1 billion kilograms in 1 year. From 1996 to 2016, the total profit of US$186.1 billion was estimated to be obtained by growing genetically modified crops globally (ISAAA 2018).

The developments of biotic and abiotic stress-resistant crops are the main foundation of sustainable agriculture. Recombinant DNA technology has been immensely employed in the development of plants for biotic and abiotic stress tolerance and in improving the quality and yield of plants (Anil and Deepika 2000; Parmar et al. 2017). The extensive research efforts in the area of genetic transformation have led to the insertion of genes related to several biotic and abiotic stress resistance, nutritional value, increased self-life, and modification of other traits such as yield, color, and texture of plants. A wide range of genes such as chitinase, osmotin, protease inhibitors, cystatin, defensin, glucanase, and many more have been targeted by the researcher to develop biotic stress-resistant plant varieties. Similarly, for the abiotic stress tolerance, the number of genes that have a key role in the biosynthesis of stress-protecting compounds, for example, heat shock proteins, mannitol, betaine, and glycine, has been targeted for the improvement of plants (Parmar et al. 2017) (Table 5.1).

3 Recombinant DNA Technology for Developing Abiotic Stress-Tolerant/-Resistant Plants

The adaptive potential of plants is severely affected by the rapidly changing environmental conditions which arise mainly because of anthropogenic activities (Amedie 2013; Parmesan and Hanley 2015). Thus, plants are likely to be exposed to an array of unusual environmental conditions comprising drought, heat, waterlogging, UV-radiation, salinity, nutrient imbalances, metal toxicities, freezing, high light intensity, etc., which are all together categorized as the abiotic stresses (He et al. 2018; Wani et al. 2016). Several reports have suggested abiotic stresses as major yield-limiting factors for the food crop that results in up to 70% losses in major food crop yield (Zörb et al. 2019; Mantri et al. 2012). Drought is the most important abiotic factor followed by salinity affecting 25% and 10% of arable area, respectively (Bidhan et al. 2011). Wang et al. (2003) have reported that an increase in salinity of arable land can cause a loss of nearly 50% land by the end of 2050.

Genetic engineering techniques have emerged as rapid and efficient methods, which enable direct modification of genomes of higher plants that subsequently leads to change in the metabolism of plants and thus enhancing the growth and yield in the stress conditions (Ahanger et al. 2017; Gilliham et al. 2017). To overcome the

Table 5.1 Selective reports on development of abiotic and biotic stress-tolerant plant via recombinant DNA technology

Gene engineered	Transgenic host	Trait improved	References
OsRab7 Rab family protein	*Oryza sativa*	Improved grain yield, drought and heat tolerance by modulating antioxidant, osmolytes and abiotic stress responsive genes	El-Esawi and Alayafi (2019)
HaHB4 Sunflower Homeodomain-leucine zipper I family	*Triticum aestivum*	Increased spikelet numbers per spike, tillers per plant, fertile florets, and grain number/m^2 of transgenic plant under drought stress conditions	González et al. (2019)
OsNAC14 Rice drought responsive transcription factor	*Oryza sativa*	Improved drought stress tolerance by modulating factors involved in DNA damage repair and defense response	Shim et al. (2018)
GmWRKY12 Soyabean WRKY transcription factor	*Glycine max*	Increased drought and salt tolerance Increased proline and reduced MDA (malondialdehyde) content under drought and salt treatment	Shi et al. (2018)
AtHDG11 Arabidopsis homeodomain-leucine zipper transcription factor	*Arachis hypogea*	Improved drought and salt tolerance Higher yield in transgenic plant	Banavath et al. 2018
BcZAT12 *Brassica carinata* Zinc finger transcription factor gene	*Saccharum officinarum*	Increased growth, vigor, drought and salinity tolerance	Saravanan et al. (2018)
ZmPEPC Maize phosphoenolpyruvate carboxylase	*Triticum aestivum* L	Improved grain yield and drought stress tolerance	Qin et al. (2016)
HARDY *Arabidopsis* stress-related AP2/ERF	*Trifolium alexandrinum* L.	Improved the growth of transgenic plant under drought-stressed condition	Abogadallah et al. (2011)
SbNHXLP *Sorghum bicolor* Plasma membrane Na+/H+ antiporter system	*Solanum lycopersicum*	Improved fruit yield and salt tolerance by maintaining ion homeostasis	Kumari et al. (2017)
DaCBF4 Antarctica C-repeat binding factor 4	*Oryza sativa*	Enhanced cold stress tolerance through adjusting the expression levels of stress-responsive genes	Byun et al. (2018)
IbCBF3	Sweet potato	Showed highly significant tolerance against low temperature	Jin et al. (2017)
AsDREB1 *Adonis amurensis* DREB1 transcription factor	*Oryza sativa*, *Arabidopsis*	Enhanced salt, drought, and low temperature tolerance	Zong et al. (2016)

(continued)

Table 5.1 (continued)

Gene engineered	Transgenic host	Trait improved	References
Cry1Ab *Bacillus thuringiensis* crystal insecticidal protein	Potato	Improved resistance against *Helicoverpa armigera*	Chakrabarti et al. (2000)
Cry1Ac *Bacillus thuringiensis* crystal insecticidal protein	*Elite indica* rice	Enhanced resistance to yellow stem borer (*Scirpophaga incertulas*)	Khanna and Raina (2002)
Oc-IΔD86 Modified Rice cystatin	*Lilium longiflorum*	Confer resistance to root lesion nematodes Better growth performance and increased plant mass than nontransgenic plants	Vieira et al. (2015)
Rep Replicase-associated protein	Banana	Improved resistance to banana bunchy top virus	Cheah et al. (2016)
Trichoderma-endochitinase gene	Guava	Improved resistance against Guava wilt disease	Mishra et al. (2016)

unfavorable environmental conditions, the plants can adapt to diverse range of changes at physiological, morphological, and genetical level (Ahmad and Wani 2013; Devi et al. 2017). Thus, the most efficient way to enhance the stress resistance in plants is the recognition and transfer of stress-related genes in the higher plants (Tzfira et al. 2012). On the basis of functions, abiotic stress-related genes can be categorized into three groups—(1) functional proteins: contain genes that play role in the regulation of biosynthesis and providing protection to plants such as chaperons, antioxidants protectants, late embryogenesis abundant (*LEA*) dehydrin-type genes, heat shock protein (*HSPs*) genes, *ROS* scavenging proteins, abscisic acid (*ABA*) synthesis genes; (2) signaling factors: include proteins that regulate ionic and water homeostasis and cellular stability under stress conditions such as salt stress signaling (*SOS*) genes, calcium-dependent protein kinases (*CPKs*), *MAPKs*; (3) transcriptional factors: regulate gene expression and stress signaling in plants like *NAC AREB/ABF* (basic leucine Zipper), *MYC/MYP*, *CBF/DREB*, and *ZF-HD* (zinc-finger homeodomain) (Parmar et al. 2017).

3.1 Drought Tolerance

Recently, a significant decrease in plant yield has been observed due to drought stress (Azevedo et al. 2011). Farooq et al. (2017) reported a 68% decrease in cowpea yield by drought stress. Drought stress has resulted in several physiological and biochemical alterations in plants, for example, homeostasis imbalance, increased stomatal closure and oxidative damage, decreased rate of gaseous exchange rate, and also affects the other cellular structures (Hasanuzzaman et al. 2017;

Fernández-Ocana et al. 2011). The first transgenic drought-tolerant plant (MON 87460) was developed in maize variety by Monsanto Company in the year 2009. *Bacillus subtilis*–derived cold shock protein genes expressed in maize variety has enhanced the resistance to drought stress and showed 5.5-fold increases in grain yield within a year (ISAAA 2016). Till now several drought-tolerant transgenic varieties of rice, wheat, sugarcane, canola, tomato, *Arabidopsis*, potato, and groundnut has been developed using *Agrobacterium* and particle gun methods (Deikman et al. 2012). Overexpression of *HVA1* (group 3 LEA protein) in wheat derived from *Hordeum vulgare* has shown enhanced biomass productivity and drought tolerance under stress conditions (Sivamani et al. 2000). Bahieldin et al. (2005) have stated that the transformation of immature embryos with *HVA 1* gene under the control of maize *ubi* promoter via particle bomabrdment technique results in increased yield in wheat under draught conditions. Under severe drought stress conditions, transgenic rice expressing *SNAC1* (stress-responsive NAC1) gene has shown 22–34% higher seed setting at the reproductive stage than control. A study based on DNA-chip analysis revealed that the *SNAC1* overexpression in transgenic rice variety has resulted in upregulation of a number of other stress-related genes (Hu et al. 2006).

Kim et al. (2018) have developed drought and salinity tolerance in transgenic soybean by expressing *AtBF3* gene. Various physiological changes such as increased chlorophyll content, closed stomata, and cell membrane stability, lower transpiration rate, and higher seed weight were reported in transgenic plant than nontransformed plants. Similarly, enhanced water use efficiency was observed in transgenic wheat lines under stress conditions expressing *HaHB4* gene of sunflower (González et al. 2019). Overexpression of *AnnSp2* gene in transgenic tomato has induced both drought and salinity tolerance in plants by enhancing ABA and lowering ROS content and thus improving biochemical and physiological responses in the transgenic plants (Ijaz et al. 2017). At both vegetative and reproductive stage, the high expression *AtDREB1A* gene in *Indica* rice increases drought tolerance in transgenic plants, and also the spikelet fertility and grain yield were reported to be maximum than nontransgenic plants (Ravikumar et al. 2014). Similarly, transgenic bread wheat expressing *DREB2* and *CAT1* gene has shown increased chlorophyll content, RWC (relative water content), and catalase activity under drought stress condition (Eftekhari et al. 2017).

3.2 Salinity Tolerance

Another biotic stress that has damaged the crop production by 20% of cultivated land is salinity. Globally, nearly 800 million ha (≈ 6% of total area) and in India about 6.73 million ha land is salinity striken (Turan et al. 2012). To cope with salinity, the scientist has developed several techniques for producing high-yielding transgenic varieties. Also, some plants can overcome salinity stress by inducing several metabolic changes such as the production of antioxidative enzymes, osmolytes, and upregulation of genes associated with stress response such as transcriptional factors

(TF), ion transporters, and signaling pathway elements (Rao et al. 2016). These stress-responsive genes have been utilized to produce salinity-resistance plants either by transferring from tolerant to sensitive variety or by manipulating the genes already present in the plant. Both drought and salinity stress affect crop production even under irrigated conditions. Several abiotic stress-tolerant plants such as tobacco, cotton, rice, wheat, maize, and oilseed have been developed using recombinant technology (Turan et al. 2012).

Transcription factors belonging to family bZip, WRKY, MYC, DREB, Cys2His2 Zinc finger, MYB, and AP2/ERF have been reported to play very important role in developing salt stress tolerance in plants. Overexpression of *OsDREB2A* (Mallikarjuna et al. 2011), *SNAC* (stress-responsive gene NAC 1) (Hu et al. 2006), *ONAC045* (Zheng et al. 2009), *OsbZIP23* (basic leucine zipper) (Xiang et al. 2008) genes in transgenic rice has shown enhanced salinity and drought tolerance compared to the untransformed plant. Similarly, overexpression of *GmbZIP1* in transgenic *Arabidopsis* and tobacco has shown improved tolerance against salinity, drought, and cold stresses (Gao et al. 2011). The overexpression of *MTCBF4* (*M. truncatulla*) (Li et al. 2011), *taMYB2A* (Wheat) (Mao et al. 2011), and *BrERF4* (*Brassica*) gene (Seo et al. 2010) in transgenic *Arabidopsis* have shown improved drought and salinity tolerance.

The salt-tolerant plants have also been developed by the transformation of antiporter or ion channels genes in the host plant (Rahman et al. 2017). *Arabidopsis* and rice overexpressing Na^+/H^+ antiporter gene *SOD2* (*Schizosaccharomyces pombe*) and *nhA* (*E. coli*), respectively, have shown improved salt tolerance (Gao et al. 2003; Wu et al. 2005). Similarly, the ectopic expression of *ScVP* gene encoding vacuolar H^+-pyrophosphatase, isolated from the *Suaeda corniculata* in transgenic *Arabidopsis*, has resulted in salinity tolerance. Transgenic wheat, maize tomato, and *Brassica* for gene *AtNHX1* showed higher salinity tolerance (Zhang et al. 2001; Xue et al. 2004). The ectopic expression of vacuolar H^+-ATPase subunit A, *MDVHA* gene (*Malus domestica*), in transgenic tobacco has shown improved salinity tolerance (Dong et al. 2015). Similarly, overexpression of *IrIVHA-c* gene (vacuolar-type HC-ATPase C subunit) isolated from *Iris lacteal* has shown improved salinity tolerance in transgenic tobacco (Wang et al. 2016).

The transformation of *HVA1* (LEA protein) gene from *Hordeum vulgare* into rice (Xu et al. 1996; Rohila et al. 2002) and *Morus indica* (Lal et al. 2008) has resulted into improved salinity and drought-tolerant transformed varieties. Similarly, transgenic *Arabidopsis* for helicase *MH1* (Alfalfa) exhibited improved salinity and drought tolerance (Luo et al. 2009). Several reports suggested that the overexpression of genes encoding enzymes glyoxalase I (*GlyI* gene) and glyoxalase II (*GlyII* gene) has given rise to improved salinity-tolerant transgenic plant (Yadav et al. 2005; Singla-Pareek et al. 2008).

3.3 Cold-Stress Tolerance

Low temperature has been reported to show a huge impact on crop productivity and yield and thereby causing significant crop losses (Xin and Browse 2001). The advent of recombinant DNA technology and subsequent improvement in gene transfer methods has enabled rapid and efficient transformation and development of cold stress resistance in the number of crop species (Wani et al. 2008; Gosal et al. 2009; Wani and Gosal 2011).

As most of the traits that are necessary for the adaptation of the plant to cold stress are controlled by various transcription regulatory factors, efforts have been made to identify and isolate several transcription factors associated with cold stress tolerance (Rejeb et al. 2014). Further, the genes chosen for the transformation should encode either for the enzymes involved in the biosynthesis of various osmoprotectant or for the enzymes that are necessary for modification of membrane lipid, detoxifying enzymes, and LEA proteins (Sanghera et al. 2011). The *CBF* genes which are found in most of the crop species and few vegetable species have been identified to play a very vital role in the low temperature adaptation of plants (Kumar and Bhatt 2006). Many low-temperature-inducible genes that are regulated by transcription factor, CBF/DREB1 (C-repeat binding factor/dehydration-responsive element binding), have been derived from the plants (Thomashow 1999; Houde et al. 2004). In *Arabidopsis*, *CBF3/DREB1a, CBF1/DREB1b*, and *CBF2/DREB1c* genes of AP2/DREBP family of DNA-binding proteins have been reported (Gilmour et al. 1998; Kasuga et al. 1999). Jaglo-Ottosen et al. (2001) reported that the overexpression of CBF1/DREB protein in transgenic *Arabidopsis* plant is responsible for inducing cold-stress tolerance without affecting its development and growth characteristics. However, transgenic *Solanum lycopersicum* developed by introduction of *CBF1* cDNA in plant under the control of a CaMV35S promoter has shown increased salinity, drought, and cold stress tolerance but exhibited an antagonistic effect on growth and development such as stunted growth, decrease in seed number per fruit and fruit set (Hsieh et al. 2002). Hajela et al. (1990) have studied CBF/DREB1-dependent cold response pathway in *Arabidopsis* and rice and reported that these pathways induce cold-stress tolerance in plants by the process of cold acclimation. The overexpression of *CBF1/DREB1b* and *CBF3/DREB1a* has been reported to induce *COR* gene, which can further results in several biochemical changes, for instance increase in sugar and proline content and thus improving cold tolerance of plants (Gilmour et al. 2000).

Zhang et al. (2010) have reported higher SOD (superoxide dismutase) activity and NPQ (non-photochemical quenching), and lower MDA (malondialdehyde) activity in the transgenic tomato plants expressing *CBF1 gene*. Based on the study, he suggested that during cold-stress conditions, the CBF1 protein play a chief role in the protection of Photosystem (PS) I and II.

Similarly, various structural genes also have been exploited for the development of transgenic plants. Murata et al. (1992) stated that the overexpression of *GPAT* (glycerol3-phosphate acyltransferase) gene from *Cucurbita maxica* and *A. thaliana* in transgenic tobacco has resulted in an accumulation of fatty acids in the cell wall of plants, subsequently enhancing cold-stress tolerance in plants. Kovtum et al. (2000) described that the transgenic plant expressing *NPK1* (kinase) has shown improved tolerance for cold and other abiotic stresses. Furthermore, the expression of cold shock proteins *Csp A* and *Csp B* isolated from *Escherichia coli* and *Bacillus subtilis*, respectively, in transgenic rice plants has shown enhanced stress tolerance for cold, water deficits, and heat (Castiglioni et al. 2008).

The genes encoding LEA proteins have also been widely used to produce cold-stress-tolerant plants (Sanghera et al. 2011). The over-expression of citrus gene encoding CuCOR19 (LEA protein) in tobacco plants has shown improved cold-stress tolerance (Hara et al. 2003). Similarly, the co-expression of the *RAB18* and *COR47*, and *XERO2* and *ERD10* genes (Puhakainen et al. 2004), and the ectopic expression of *COR15A* (*Arabidopsis* gene) (Artus et al. 1996), *WCS19* (wheat gene) (Gong et al. 2002) in the transgenic *Arabidopsis* has shown increased freezing tolerance. Houde et al. (2004) reported improved freezing tolerance in strawberry by the expression of *WCOR410* gene (Wheat dehydrin gene).

4 Recombinant DNA Technology for Developing Biotic Stress-Tolerant/-Resistant Plants

The plant damage occurred due to living organisms, for example, pests, bacteria, fungi, viruses, and insects, has been grouped into biotic stresses. Among all biotic stresses, the damage caused by weeds is highest (34%) followed by insects (18%) and pathogens (16%) (Oerke 2006).

4.1 Herbicide Tolerance

Several plants such as cotton, alfalfa, oilseed rape, rice, maize, canola, fodder beet, coffee, cotton, and soybean have been genetically modified using recombinant DNA technology consisting of genes that facilitate degradation of an active component of herbicide making it nontoxic (Kim et al. 2009; Green and Castle 2010; Latif et al. 2015; Tingzhang 2014). For the development of herbicide tolerance plants, the most commonly employed method for efficient genetic transformation is *Agrobacterium*-mediated and particle bombardment method (Tsaftaris 1996). These transgenic plants provide sustainable solutions to eradicate weeds by facilitating a reduction in the volume of herbicide use, the net improvement in environment, and low or no-tillage cultural practices (Brookes and Barfoot 2015), and also provide flexibility in choosing spraying time, lower inputs of labor, and fuel consumption, thus directly benefitting both carbon emissions and soil structure (James 2007). For 1966–2013, the use of herbicide tolerance cotton has shown a net reduction of about 21.3 million kilogram (7.2% reduction in usage), whereas for the herbicide tolerance the net reduction in usage of active ingredients is 2.3 million kilogram. The net environmental improvement, as depicted by the EIQ (Environmental Impact Quotient) indicator, has been improved by 14.5% and 9.5% for the HT soybean and cotton, respectively (Brookes and Barfoot 2015).

Generally, main approaches used to develop herbicide-tolerant plants are (1) transferring genes encoding enzymes that can degrade herbicides into nontoxic substances such as *gat* (glyphosate N-acetyltransferase) and *gox* (glyphosate oxidase) gene, (2) modifying plant genes such as *EPSPS* (5-enolpyruvylshikimate-3-phosphate synthase), aroA (aromatic amino acid) that encodes for biochemical targets of herbicide, (3) overexpressing unmodified target protein that facilitates normal metabolism to occur in plants (Ferry and Gatehouse 2010). Although various herbicide tolerance transgenic plants have been developed against a range of herbicides having diverse mechanism for phytotoxicity in plants, the most commonly developed and commercially grown are glyphosate-tolerant crops. The 90% land area occupied by transgenic plants contain herbicide-tolerant varieties (Owen 2008).

The *EPSP* (5-enolpyruvylshikimate 3-phosphate) synthase gene that imparts herbicide tolerance has been isolated *Agrobacterium tumefaciens* strain CP4, encodes protein product that provides tolerance against glyphosate in plants (Padgette et al. 1995). Along with *cp4* gene, glyphosate oxidoreductase (GOX) gene from *Pseudomonas sp.* strain LBr (Franz et al. 1997) has been widely used to develop several commercially available transgenic crops such as soybeans, corn, canola, and cotton.

Stalker et al. (1996) reported that the transformation of *bxn* gene encoding active nitrilase enzyme isolated from *Klebsiella ozaenae* into cotton crops produced herbicide-tolerant transgenic crops that can degrade romoxynil and ioxynil into nontoxic compounds. Similarly, expressing *tfd A* gene encoding 2,4-D oxygenase isolated from *Ralstonia eutropha* into transgenic tobacco has shown tenfold higher resistance to the herbicide as compared to nontransformed plant (Last and Llewellyn 1999). The enzyme 2, 4-D oxygenase cause degradation of 2, 4-D into the nontoxic substances (glyoxylate and 2,4-dichlorophenol). The expression of *tfdA* gene into wine grapes has shown herbicide tolerance up to 20 times higher than 2,4-D applied in corn (Mulwa 2005).

The *pat* and *bar* genes encoding phosphinothricin acetyl transferase isolated from *Streptomyces viridichromogenes* and *S. hygroscopicus,* respectively, has been reported to convert phosphinothricin- or bialaphos-based herbicides into nontoxic acetylated form (Thompson et al. 1987). These genes have been widely employed to develop glufosinate tolerance in several crops such as dry beans, cassava, cotton, corn, wheat, rice, oilseed rape and alfalfa, cotton, sugar beet, lettuce, and sugarcane (Falco et al. 2000; Aragao et al. 2002; Sarria et al. 2000). Further, the transgenic rice tolerant to herbicide oxyfluorfen has been developed by targeting the gene to chloroplast rather than the cytoplasm (Lee et al. 2000). Chloroplast transformation does not permit the transfer of foreign genes via pollen.

4.2 Insect-Pest Resistance

Globally, an insect-pest attack is the root cause of the destruction of nearly 25% of food crops per year and thus causes a threat to global food security (Arun 2017). The development of insect-pest-resistant crops via recombinant DNA technology has caused a reduction in damage of crop, and application of broad-spectrum insecticides thus provides safer, biologically sustainable solutions for insect-pest management. First, *Cry* genes encoding δ-endotoxin was used for the development of insect-resistant plants. This gene was isolated from the bacterium *Bacillus thuringiensis* causes pore formation in the gut epithelium of insects, its lysis, and subsequently leads to death (Viktorov 2019). Till now, above 700 cry gene sequences have been identified and used for the elimination of a range of pests such as *Diptera*, *Coleoptera*, *Hymenoptera*, and *Lepidoptera* in the fields (Sanchis 2011). Zhang et al. (2015) reported that yield loss in kiwifruit due to insect attack can be controlled by transforming the plant with *SbtCry1Ac* gene encoding *btCry1Ac* protein. The transgenic kiwifruit has shown inhibition rate on an average of 75.2% against fruit piercing moth *Oraesia excavate* after 10 days of infection. Similarly, resistance variety of okra against *Earias vittella* (fruit and shoot borer) has been developed by expressing *Cry Ac* genes (Narendran et al. 2013).

The increased occurrence of resistance development in pests toward Bt plants has gained focus toward other biogenic toxins which can be used to develop insect-resistant plants. Vegetative insecticidal proteins (Vip) reported in approximately 15% of *B. thuringiensis* strains shows two to three times more toxicity than δ-endotoxin protein (Lee et al. 2003). These proteins are classified into four groups based on their amino acid sequence and insect specificity, namely, Vip1, Vip2, Vip3, and Vip4. To date, insect-resistant crop has been developed only with *Vip3a* gene derived from *B. thuringiensis*, strain AB88 (Viktorov 2019). This protein has shown insecticidal activity against a wide range of insects, including *Heliothis virescens*, *Spodoptera frugiperda*, *S. exigua*, *Agrotis ipsilon*, and *Helicoverpa zea* (Estruch et al. 1996). Further, other genes such as trypsin inhibitors (Graham et al. 2002; Gessler and Patocchi 2007), lectins (Li et al. 2015), protease inhibitors (Roderick et al. 2012; Valizadeh et al. 2013), has also been used to develop insect-pest resistance in many plants.

4.3 Disease Resistance

The prevalence of a variety of pathogenic diseases in the plants caused by fungi, bacteria, and virus constraints its yield and production. However, conventional breeding methods impose various constraints on the development of resistant varieties because of the unavailability of the disease-resistant gene(s) in the gene pool of specific plants. Thus, genetic engineering has emerged as a potential tool to transfer the gene among unrelated organisms and lead to the development of various disease-resistant transgenic crops. Several genes, including chitinase, defencin, osmotin, glucanase, have been targeted to develop transgenic plants resistant against fungal and bacterial diseases (Ceasar and Ignacimuthu 2012).

Tai et al. (1999) developed transgenic tomatoes resistant against bacterial spot disease by expressing pepper-derived *Bs2* (Bacterial spot resistance gene) gene. Transgenic rice variety, named "Improved Samba Mahsuri," showing higher yield and resistance against bacterial blight diseases has been developed by expressing *Xa21*, *Xa13*, and *Xa5* (bacterial blight-resistant genes) into Samba Mahsuri rice variety (Sundaram et al. 2009). Similarly, transgenic "Improved Pisa Basmati 1" was developed by incorporating two genes Xa21 and *Xa13* (bacterial blight-resistant gene) into Pusa Basmati 1 rice variety (Rani et al. 2008).

The expression of *Pf1p* (plant ferredoxin like protein) gene controlled by CaMV35S promoter in "Sukali Ndiizi" and "Nakinyika" variety of banana has shown tolerance against Banana Xanthomonas wilt (BXW) (Namukwaya et al. 2012). Ko et al. (2016) have reported improved resistance against anthracnose in transgenic pepper when *PepEST* (carboxy esterase) gene controlled by *CaMV35S* promoter was expressed constitutively.

The transformation of MhNPR1 gene from *Malus hupehensis* into the "Fuji" cultivar of apple resulted in powdery mildew disease-resistant transgenic variety (Chen et al. 2012). The transgenic line of tomato showing increased resistance against wilt disease and early blight caused by fungus *Fusarium oxysporum* and *Alternaria solani* has been developed by transferring *samdc* (S-adenosyl methionine decarboxylase) gene into tomato cultivar "Pusa Ruby," and also expressed improved tolerance against several abiotic stresses (Hazarika and Rajam 2011).

Besides bacterial and fungal infections, viral infection in plants has also resulted in the yield loss significantly. The coat protein-mediated approach has been widely used to engineer virus-resistant transgenic plants. The transgenic chili pepper plants resistant against CMVP1 and CMVP0 pathogen were developed by the transformation of plants with *CMVP0-CP* (coat protein) gene (Lee et al. 2009). Yu et al. (2011) stated that *Agrobacterium tumefaciens*–mediated transformation of coat protein genes, that is, *ZYMV-CP* and *PRSVW-CP* into three varieties, that is, "Feeling," "China rose," and "Quality," has resulted in watermelon transgenic plant that has shown resistance to zucchini yellow mosaic virus (ZYMV) and papaya ring spot virus type W (PRSV W).

5 Conclusion

The use of recombinant DNA technology for the improvement of plant yield, growth, and enhanced resistance to biotic and abiotic stresses provides a sustainable solution to the problems arising due to population explosion by maintaining the equilibrium between the environmental conservation and developmental needs of the growing population of the world. Also, the advent of several new sequencing and transformation technologies has enabled the rapid and efficient sequencing of the genome, identification of genes governing the desired traits, and transformation into host plants.

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Chapter 6

Regulatory Role of Micro-RNAs in Plants Under Challenging Environmental Conditions with Special Focus on Drought and Salinity

Ashok Kumar, Ranjeet Kaur, and Manchikatla Venkat Rajam

Contents

Abbreviations

ABA	Abscisic acid
AGO	Argonaute
miRISC	miRNA-induced silencing complex
miRNA	Micro-RNA
ROS	Reactive oxygen species
sRNAs	Small RNAs

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1 Introduction

Plants are being sessile organisms and constantly affected by various environmental cues, both biotic and abiotic, which inflict serious damages to their growth and yield. Major crops such as rice, wheat, corn, and potato are subjected to severe yield losses each year due to the challenging environmental conditions. With the world population estimated to be reach at the 9.1 billion mark by the end of the 2050 (FAO 2009), there is an urgent need to establish food security of the nations by increasing the crop yield. Despite of the widely used farm practices and conventional breeding approaches, the global demand for food is expected to fall short of the required measures. The Food and Agriculture Organization (FAO) of United Nations has estimated that nearly one-third of all food products for human consumption is either lost or wasted annually due to the natural calamities. This amounts to nearly 1.3 billion tonnes of food and is equivalent to a loss of 750 billion US dollars each year. The advancement of the genetic engineering strategies has brought with it a promise to quench the existing shortage of supply in food, feed, and fuel to the future generations. One such revolutionizing method involves curtailing the yield penalties in the plants by designing climate-ready crops that can withstand the abiotic stresses like drought and salinity. The recent breakthroughs in the field of genome editing and small RNAs have revolutionized the way we strategize the development of tailor-made farmer-friendly crops.

Small RNAs (sRNAs) were first discovered as the double-stranded RNAs (dsRNAs) in the nematode *Caenorhabditis elegans* (Fire et al. 1998) and were later reported to be ubiquitous in all eukaryotes (Voinnet 2009; Pareek et al. 2015; Wang et al. 2019). Evolved as a part of defense system in organisms against the viral or transposon attack, small RNAs are known to modulate the action of endogenous genes at the post-transcriptional level (Borges and Martienssen 2015). This has led to the naming of the associated phenomenon of gene silencing as the post-transcriptional gene silencing (PTGS), which later gained popularity as RNA interference (RNAi). In plants, two classes of small RNAs are found, viz., micro-RNAs (miRNAs) and small interfering RNAs (siRNAs) (Voinnet 2009; Pareek et al. 2015; Wang et al. 2019; Kaur et al. 2020). These are considered to play significant roles in various key processes, especially in plants such as growth, development, reproduction, and defense responses (Mamta and Rajam 2018; Tyagi et al. 2019). Both are known to execute their actions by homology-dependent silencing of targeted genes, thereby establishing a coordinated regulation of gene function at the genetic and epigenetic levels (Chen 2005; Saurabh et al. 2014; Kaur et al. 2020; Rajam 2020). However, compared to siRNAs, miRNAs are reported to be highly specific in the down-regulation of their target genes with lesser off-target effects (Kamthan et al. 2015). Also, miRNAs can efficiently down-regulate numerous related genes to generate prominent therapeutic effect in contrast to the siRNAs, which can target simply single gene at one time (Lam et al. 2015). Overall, miRNAs are regarded as the more powerful and versatile players in targeted gene silencing and can be utilized as important tools in regulating different plant processes, including abiotic stress tolerance.

Ranging in the length of 20–24 nucleotides, the miRNAs bind to fully or nearly complementary sequence of the target mRNAs and can regulate gene expression negatively to synchronize the various related developmental processes in the plants (Pareek et al. 2015; Borges and Martienssen 2015; Kaur et al. 2020). These small RNAs have the potential to change the outlook of our current understanding on the gene function and its regulation. In this manner, plant miRNAs have been viewed as the ace regulators of gene function and are by and large extensively exploited for improving agronomic attributes in crops, especially crop yield. In this chapter, writers focused the recent works related to the biogenesis of plant miRNAs and their regulatory roles under adverse environmental conditions, with special attention to the genetic engineering studies in alleviating salinity and drought stress in plants.

2 Biogenesis and Mode of Action of Plant miRNAs

Biogenesis of plant miRNAs follows the canonical pathway and involves a complex interplay of several enzymes and intermediates as depicted in Fig. 6.1. The plant-based miRNAs are encrypted by the *MIRNA (MIR)* genes and remain localized mostly in the noncoding regions of the plant genome (intragenic or intronic) (Tyagi et al. 2019). However, studies have shown their presence within the exons of coding DNA sequences and also in antisense transcripts (intergenic) (Djami-Tchatchou et al. 2017). The *MIR* genes are mostly transcribed by DNA-dependent RNA polymerase II (Pol II) enzyme (rarely by Pol III) in the nucleus, which produces long primary transcripts (between 80 and 500 nucleotides) known as the primary miRNAs (pri-miRNAs) (Djami-Tchatchou et al. 2017). These pri-miRNAs possess the regular features of the Pol II transcripts, that is, a 5′ end cap and a 3′ end polyadenylated tail, and are sometime even get spliced (Rogers and Chen 2013).

The next step comprises of processing the long pri-miRNAs to precursor miRNAs (pre-miRNAs) by the action of DICER-Like 1 (DCL-1) protein, which is an RNase III endonuclease enzyme. Along with several other auxiliary factors such as Hyponastic Leaves1 (HYL1) and Serrate (SE), DCL-1 forms the dicing complex or the microprocessor unit, which functions under the tight control by HYL1 (reviewed in Kaur et al. 2020). For facilitating, the cleavage actions of DCL-1, the pri-miRNAs, are imperfectly folded onto the homology regions forming a hairpin-like structure. This stem-loop structure are made up of a terminal loop, an upper stem, the miRNA/miRNA* region, a lower stem, and the two arms (Kaur et al. 2020). The generated pre-miRNAs are again cleaved by DCL1 to form a highly unstable miRNA–miRNA* duplex, which then methylated at 2′-OH on the 3′ end by the HUA Enhancer 1 (HEN1), thereby preventing its further degradation by Small RNA Degrading Nuclease (SDN) (Tyagi et al. 2019). The stabilized miRNA–miRNA* duplex is transported from nucleus by exporter protein HASTY to cytoplasm, where it is sorted again into guide and passenger strands. The mature guide miRNA binds

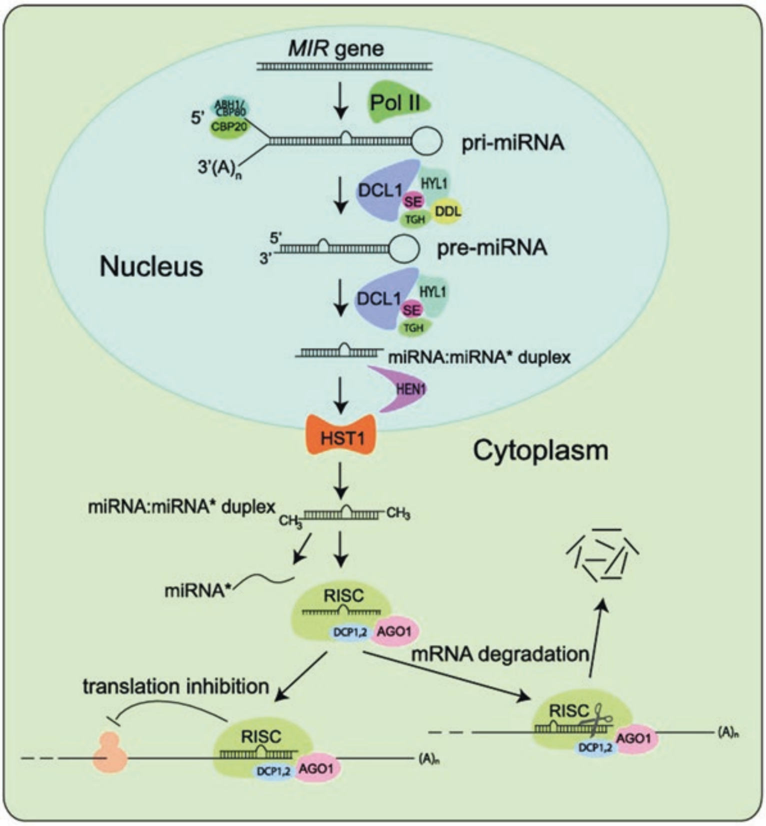

Fig. 6.1 Generalized model for biogenesis of plant miRNAs. The RNA polymerase II commonly targets to the *MIR* genes for transcription and produces the pri-miRNAs that fold back to form hairpin-like structure. Further splicing and processing occur in nucleus with the interactions of HYL1, DDL, TGH, and SE and followed by the cap-binding proteins CBP20 and CBP80. The processing protein DCL1 sequentially processes the pri-miRNAs and pre-miRNAs into one or several phased miRNA/miRNA* duplexes, which are then further methylated by HEN1 and transported them to the cytoplasm by transporter protein HST1. In the final step, the dedicated AGO1-containing RISC complex incorporates in the selected miRNA and further results into either cleavage or translation inhibition of the target mRNA transcript (From Yang and Li 2012)

to the effector Argonaute (AGO) protein via a small region (6–8 nucleotide) at its 5′end known as the seed, while the passenger strand is degraded (Tyagi et al. 2019; Kaur et al. 2020).

Together, the mature guide miRNA and the AGO proteins form the miRNA-induced silencing complex (miRISC), which then downregulates the target mRNAs based on sequence complementarity. The mode of action undertaken by miRISC depends on the complementary base pairing of the miRNA-mRNA duo. It is suggested that if miRNA binds perfectly to the target mRNA, then it results in the site-specific cleavage of the target gene, whereas if the binding of miRNA-mRNA is near-perfect and allows a few mismatches, then the silencing of desired gene occurs by translational repression (reviewed in Kaur et al. 2020). In some cases, the miRNA has been associated to be directing the methylation of the genes resulting in their loss of function (Pareek et al. 2015).

3 Diverse Functions of miRNA in Plants

The miRNAs have been involved in the functional regulation of numerous genes that are responsible for the coordination of various biological and metabolic processes in plants. These regulatory roles can be summarized under three major headings, namely, plant development, phase-transition, and response to environmental stresses (both biotic and abiotic).

3.1 miRNAs Regulating Plant Development

Plant growth and development comprise a complex network of various miRNAs and their target mRNAs that together orchestrate the controlled regulation of growth hormones and their related pathways. Several plant miRNAs have been reported and found expressed differentially during growth as well as organ/tissue differentiation. For instance, flower development is regulated by *miR172* by targeted downregulation of a key floral gene, *Apetala* 2 (*AP2*) (Aukerman and Sakai 2003; Chen 2004). *miR156* and its target gene family of *Squamosa promoter-like binding* (*SPL*) has been evidenced as the major miRNA involved in regulating the plant growth, biomass, and yield (Kaur et al. 2020). Overexpression of *miR156* reduced apical dominance and induced branching, leading to increased number of flowers, as well as seeds (Fu et al. 2012). Leaf development is mediated by *miR164*, *miR396,* and *miR319*, whereas root development is controlled by several miRNAs including *miR393*, *miR847*, *miR160*, *miR167*, and *miR390* (Li and Zhang 2016). Development of shoot apical meristems and axillary shoot meristems is governed by *miR165*/*miR166* and *miR164*, respectively (Li and Zhang 2016).

3.2 miRNAs Regulating Phase-Transition in Plants

In order to obtain reproductive maturity and produce flowers/seeds, plants make a controlled transition from vegetative phase to reproductive phase. This is an essential phenomenon of all plants and involves the key roles of several miRNAs, particularly *miR156* and *miR172* (Zhang and Unver 2018). The abundance of *miR156* is relatively high at the seedling stage, whereas the expression of *miR172* is very low. With the growth of the plant, the expression levels of *miR156* and *miR172* are gradually reversed, which significantly alters the plant architecture and effects the phase change in the plant from vegetative growth to reproductive growth (Ma et al. 2020; Zhang and Unver 2018). Apart from these, studies have shown that *miR159*, *miR166*, and *miR396* also play key roles in the regulation of developmental phase-transitions in plants (reviewed in Ma et al. 2020). Controlling the phenomenon of phase change, miRNAs have immense potential to alter the life cycle, as well as plant architecture, of the plant. This important regulatory feature of miRNAs is being currently explored to improve biomass and yield in many crops such as rice, wheat, maize, and others too.

3.3 miRNAs Regulating Response of Plants Toward Environmental Stresses

Plants encounter a large number of adverse environmental conditions during their lifetime. These can be either biotic stresses, as well as abiotic stresses. Biotic stress comprise of various plant diseases caused by several pathogenic agents such as viruses, bacteria, fungi, insects, and nematode parasites (Chauhan et al. 2017). These biotic factors adversely affect plant growth and causes huge losses in crop production. Transgenic expression of several miRNAs has been shown to highly enhance the tolerance of plants toward the various biotic stresses (reviewed in Chauhan et al. 2017). Du et al. (2011) showed the enhanced expression of several miRNAs, such as *miR160*, *miR396*, *miR166*, and *miR171*, in rice plants affected with rice stripe virus. Overexpression of *miR396* was found to provide resistance toward fungal infection in transgenic plants of *Medicago truncatula* (Bazin et al. 2013). Targeted downregulation of *miR159* provided tolerance to infection by root knot nematodes in transgenic *Arabidopsis* (Medina et al. 2017). The artificial miRNA approach was employed to target the ecdysone receptor (*EcR*) gene in cotton bollworm (*Helicoverpa armigera*) resulting in mortality and developmental defects in in vitro (Yogindran and Rajam 2016) and in vivo (Yogindran and Rajam 2015). This provided immunity to several important crops, including cotton, tomato, chickpea, and pigeon pea, and has the potential to prevent huge yield losses occurring due to its attack. Various different miRNAs are being studied for their likely roles in biotic stress control, and this knowledge can help us to engineer such crops that are tolerant to various pathogenic infections. Likewise, miRNAs are also known to be key regulators of abiotic stress responses in plants and have been elaborately exploited to develop plants that are resilient toward environmental challenges. The regulatory role of miRNAs in combating plant abiotic stress has been discussed in detail in the following section of this chapter, with special focus on drought and salinity stress management.

4 Regulatory Role of Plant miRNAs in Challenging Environmental Conditions

Many environmental factors, for example, salinity, drought, heat, cold, and flooding, cause immense challenges to the survival of a plant during its lifetime. These abiotic stresses can inflict serious damages to the growth and development of plant, thereby emanating huge yield losses. As per the recent report by the Intergovernmental Panel on Climate Change (IPCC), the average global temperatures are poised to increase by 0.2 °C per decade. This is destined to alter the world climate and impact the rainfall patterns across the nations, causing persistence of frequent droughts and flash floods in unexpected regions (Mishra and Singh 2010). It would greatly impact the crop yield, posing a huge threat to food security and sustainable agriculture. Innate defense responses of the plant put up resistance against the initial onset of the stress period, but the duration and intensity of the stress factor(s) can create irreparable damage to the plant's existence. Hence, in order to protect the plant from hostile climatic conditions, an urgent need persists to develop stress-tolerant plants. Such climate-ready crops should be able to cope up with the abiotic stresses without yield penalty to fulfil the ever-increasing food demands of the humanity. Recent investigations have shown that nontypical expressions of several miRNAs are encouraged by abiotic stresses, including drought and salinity (Xu et al. 2019; Wani et al. 2020). This further regulates the enhancement of tolerance in the plants. These stress-driven miRNAs function as negative regulatory entities by downregulating all inter-related negative regulators for stress resilience (tolerance) and vice versa for positive regulators (Basso et al. 2019; Wani et al. 2020). Here, this chapter summarizes the regulatory roles of different miRNAs in imparting resistance to plants under various abiotic stresses.

4.1 Drought Stress

Drought is considered the most damaging factor among all of the abiotic stresses. Various metabolic processes such as movement of stomata, uptake of vital nutrients, and production of photosynthetic assimilate are adversely affected in plants by drought leading to loss in crop yield (Kaur et al. 2016). Generally, two types of mechanisms are employed by plants to cope up with the drought stress, viz., drought avoidance and drought tolerance (Taiz and Zeiger 2002; Khurana et al. 2008). Drought avoidance or escape is part of the inherent morphological changes exhibited by plants in response to drought. These include mechanisms to curtail loss of moisture due to transpiration, such as diminished leaf size and reduced number of active stomata, and development of extensive root systems to replenish the water loss due to drought (Ding et al. 2013). Drought tolerance involves mechanisms at physiological and molecular levels such as adjusting to changes in cellular osmotic environment, generation of antioxidants to search the reactive oxygen species

(ROS), and modulation of various pathways to divert the cellular energy in synthesis of different stress compatible metabolites (Ding et al. 2013). Both these strategies involve several changes at the level of gene expression and enable plant in establishing drought tolerance/avoidance.

Increasing evidence has shown that miRNAs can regulate the expression of drought-responsive genes and in turn aid in enhancing plant tolerance to drought stress (Khraiwesh et al. 2012; Xu et al. 2019). Some of the earlier studies in plants employed differential gene expression assays to identify novel miRNAs as involved in drought stress response. For instance, Zhao et al. (2007) used an oligonucleotide microarray monitor the expression profile of miRNAs in rice under drought condition and suggested that *miR169* was the only member induced more prominently in the roots rather than in the shoots. Further investigation revealed the presence of two proximal dehydration-responsive elements (DREs) in the upstream of the *MIR-169g* gene, indicating that *miR-169* expression may be regulated directly by the dehydration-responsive element-binding (DREB) proteins (Zhao et al. 2007). In *Arabidopsis,* drought stress altered the expression levels of *miR156*, *miR319, miR393, miR397*, and *miR408* (reviewed in Khraiwesh et al. 2012). In bread wheat, the miRNA microarray analysis demonstrated that among 285 miRNAs (207 upregulated and 78 downregulated) and total 244 miRNAs (115 upregulated and 129 downregulated) were expressed differentially in two different specific tissues such as leaf and root, and further regulatory network analysis exhibited that *miR395* function as a regulator in responding against drought stress (Akdogan et al. 2016). Expression profiling results demonstrated the genotype-specific regulation behavior of miRNAs under drought stress and evidenced for their key role in regulating the expression of target genes in response to drought stress in barley (Ferdous et al. 2017). Recently, advanced biological techniques such as deep sequencing and degradome analysis are being employed in plants to identify and characterize the novel miRNAs regulating drought stress (Xie et al. 2015).

Typical role of abscisic acid (ABA) has been established as the plant stress hormone and primarily modulates the gene expression governing mechanisms related to drought tolerance. Reports of correlation between ABA and miRNAs were provided by the study of transgenic *Arabidopsis* plants, which were mutants for several key miRNA biosynthesis genes such as *HASTY*, *SE*, *DCL1*, and *HYL* (Zhang et al. 2008). *miR159* has been shown to be driving the ABA-mediated response in *Arabidopsis* by downregulation of key transcription factor *MYB*. In a study by Reyes and Chua (2007), ABA and drought treatments resulted in increased expression of *miR159* in germinating *Arabidopsis* seeds. Overexpression of *miR159a* produced transgenic *Arabidopsis* plants, which were hyposensitive to ABA and also demonstrated decreased transcript levels of *MYB33* and *MYB101* (Reyes and Chua 2007; Allen et al. 2010). ABA signaling during drought stress was also shown to be controlled by *miR167*, which was expressed differentially under drought conditions, including *Arabidopsis* (Liu et al. 2008), rice (Liu et al. 2009), and maize (Wei et al. 2009). It was also demonstrated that Phospholipase D (*PLD*), which was the target of *miR167d*, acts as a positive regulator of direct ABA-mediated drought stress response.

Auxin is another important phytohormone, plays a crucial role in plant stress management by altering the morphology of leaves and roots, development of vascular system, and patterning of organs (Ding et al. 2013). Plant growth is usually suppressed when it faces stressful conditions as the reserve assimilates are diverted to produce the stress-resistance molecules such as late embryogenesis abundant (LEA) proteins (Khurana et al. 2008; Kaur et al. 2018). As auxin signaling is associated with plant growth, several studies have shown that drought conditions induced suppression of auxin pathway. Overexpression of *miR393* in transgenic rice showed reduced expression of transport inhibitor response 1 (*TIR1*), which was known as positive regulator of auxin signaling, during drought stress (Zhao et al. 2007) and also reported in *Arabidopsis* (Liu et al. 2008). The downstream genes of the auxin signaling are controlled by the transcription factor family of auxin response factors (ARFs). These ARFs have been found to be under the tight regulation by the various miRNAs. For instance, the expression of *ARF6* and *ARF8* is under the control of *miR167*, while *miR160* has been shown to target the regulation of *ARF10*, *ARF16*, and *ARF17* (Teotia et al. 2008). *miR390* has been associated with the regulation of auxin pathway by controlling the expression of ARFs through the trans-acting siRNA3 (TAS3) (Xia et al. 2017). Earlier studies on cowpea showed that *miR390* targeted TAS3-ARF to mediate the drought response by managing auxin signaling and development of lateral roots (Barrera-Figueroa et al. 2011).

Changes in the expression of growth-related genes produce alterations in the morphological architecture of the plant, thereby conferring drought resistance to plants. Several studies have confirmed that the miRNAs responsible for plant growth are also involved in drought response. For instance, downregulation of *miR166* was shown to enhance drought tolerance in rice by enabling phenotypic changes, like rolling of leaves and altering the development of stem xylem (Zhang et al. 2018). Those miRNAs involved in control of growth hormones have also shown to impact drought stress in plants. For instance, *miR396* targeting the growth response factor (GRF) was found upregulated under drought conditions and also involved in modulation of the leaf development to combat stress in case of transgenic *Arabidopsis* (Liu et al. 2008), tobacco (Yang and Yu 2009), and rice (Zhou et al. 2010). Similarly, *miR166* was shown to control the root and nodule development by targeting homeodomain-leucine zipper (HD-Zip Class-III) transcription factors in *Medicago truncatula* (Trindade et al. 2010), rice (Zhou et al. 2010), and wheat (Kantar et al. 2011). A few more miRNAs such as *miR474*, *miR528*, *miR398*, and *miR397* have been found to be indirectly involved in combating drought stress-specific response in several crop plants by controlled regulation of their target genes (Ding et al. 2013).

Recent studies have shown that a single miRNA entity can have dissimilar response against to the same abiotic stress in various plant species, and more number of abiotic stresses in single plant. For example, *miR396* and *miR168* had shown aberrant expression behavior in *Nicotiana* (Frazier et al. 2011) and *Arabidopsis* (Liu et al. 2008) under drought conditions, but showed different expression in rice (Shuai et al. 2013). The *miR408* was found upregulated in *Medicago* (Shuai et al. 2013), *Arabidopsis* (Li et al. 2013), and barley (Kantar et al. 2011) but downregulated in case of crops such as rice (Shuai et al. 2013), peach (Eldem et al. 2012), and cotton (Xie et al. 2015) in response to drought conditions.

A nuclear factor-Y (*NF-Y*), member of an important transcription factor family known to be involved in drought stress response, was found downregulated by the action of *miR169* (Li et al. 2008; Ni et al. 2013). Overexpression of *miR169* resulted in repression of *NFYA5* transcripts, which were responsible for encoding one of its key subunits NF-YA, and enhanced the sensitivity against drought in both *Arabidopsis* (Li et al. 2008) and *Medicago truncatula* (Wang et al. 2011). In contrary to previous, the overexpression of *miR169* resulted in increased drought tolerance in case of rice (Zhao et al. 2007) and tomato (Zhang et al. 2011). During chickpea (*Cicer arietinum*) study, overexpression of *miR408* displayed reduced expression of marked gene plantacyanin, whereas both drought-responsive genes *Rd17* and *Rd29* along with related transcription factors were upregulated (Hajyzadeh et al. 2015). Overall, this study significantly exhibited the improvement in drought tolerance through displaying healthy growth parameters in the transgenic plants devoid of chlorosis, wilting, and drying even after 8 days of treatment with droughts, in comparison to control plants.

Thus, despite of being regarded as conserved families, miRNAs show differential behavior in different plants probably due to variations in physiological parameters such as, growth conditions, developmental stages, span, and type of the applied stress (Ding et al. 2013). Studies encompassing drought-responsive miRNAs have shown their significant response against multiple abiotic stresses and must be exploited to design multiclimate-resilient crops for the future (Xu et al. 2019). Also, the possible crosstalk between auxin, ABA, and drought should be explored from the viewpoint of miRNA regulation to reveal interesting highlights in the drought-responsive pathways in plants.

4.2 Salinity Stress

Salinity or salt stress is a major abiotic stress, which severely affects nearly 800 million hectares of global arable land that is more than 6% of the world's total land area (Munns and Tester 2008). When the soil contains high amounts of soluble salts equal to 40 mM NaCl, generating an osmotic pressure of 0.2 MPa, this soil condition is referred to as the salinity stress (Munns and Tester 2008). It usually arises due to shortage of water supply to the land, sometimes accompanying drought, and causes an accumulation of solutes in the soil (Kaur et al. 2016). Under salinity, the plant experiences two types of stress phases, viz., osmotic and ionic stress. The early occurring osmotic stress is characterized by stomatal closure and reduced development of shoots and leaves. As the salt accumulation increases over time, the ionic stress sets in, causing growth inhibition and senescence. Thus, salinity stress results in enormous loss of crop production across the entire world.

The miRNAs also play a regulatory role in the expression of multiple stress-responsive genes under salinity stress. Just like drought, salinity stress also employs the phytohormones ABA and auxin to harmonize homoeostasis in the stressed plants and overcome the challenges of salinity. Constitutive expression of *miR319* isolated from rice conferred tolerance against salinity, as well as drought stress in transgenic plants of creeping bentgrass, which displayed physiological changes such as decreased sodium uptake and increased water retention capacity (Zhou et al. 2013). Similarly, overexpression of another miRNA from rice, *miR393*, enhanced salt tolerance by regulating the ionic homeostasis in transgenic *Arabidopsis* (Gao et al. 2011). Artificially induced salinity stress of 250 mM NaCl showed the increased expression of *miRNA161* and *miRNA173* in young *Arabidopsis* plants (Dolata et al. 2016). Also, *miR161* and *miR173* were found to be engaged in the co-transcriptional control of AGO1 synthesis in the nucleus (Dolata et al. 2016). The *miR393* has been shown to target the downregulation of salt-responsive genes, such as *Auxin signaling F-box 2* (*AFB2*) and *TIR1* in *Arabidopsis*, rendering transgenic plants to susceptible toward salt stress, on the other hand overexpression of *miR393*-resistant TIR1 conferred salt tolerance (Chen et al. 2011; Iglesias et al. 2014). Similar results were obtained in case of *miR394*, which was shown to target Leaf Curling Responsiveness (LCR) in *Arabidopsis*. Overexpression of *miR394* produced plants that were hypersensitive to salinity, while transgenic expression of *miR394*-resistant LCR were tolerant toward salinity, as well as drought stress in an ABA-dependent mode (Song et al. 2013).

Recent study reported a novel microRNA, named as microRNA ovual line 5 (*miRNVL5*) targeting Cys/His-rich (*CHR*) gene in cotton. Under salt stress conditions (50–400 mM NaCl), the activity of *miRNVL5* was found to be suppressed, while its target mRNA abundantly expressed, imparting salinity tolerance by mechanisms such as reduced Na^+ accumulation and improved primary root growth. On the other hand, overexpression of *miRNVL5* in *Arabidopsis* resulted in salinity intolerance (Gao et al. 2016). In a study by Sunkar and Zhu (2004), *miR397* also showed increased accumulation in response to the multitude of abiotic stresses comprising cold, drought, as well as salinity too, in *Arabidopsis*. Constitutive overexpression of *miR417* showed enhanced expression under saline conditions and negatively regulated seed germination in transgenic *Arabidopsis* (Jung and Kang 2007). In another study, ectopic expression of *miR528* from rice resulted in increased tolerance toward salinity in creeping bentgrass (Yuan et al. 2015). The transgenic plants displayed physiological changes such as enhanced water retention, ionic balance, cell membrane integrity, chlorophyll content, and increased biomass.

Studies involving the global expression analysis of plants suffering from salt stress directed the researchers to identify and characterize various salinity-responsive miRNAs and their corresponding target mRNAs on the basis of their differential expression (Dutta et al. 2020). Salt stress upregulated a multitude of miRNAs such as *miR156*, *miR159*, *miR167-69*, *miR171*, *miR319,* and *miR396* in case of maize (Ding et al. 2009) besides *Arabidopsis* (Liu et al. 2008). Next-generation sequencing analysis has also helped to identify plenty of salinity-induced miRNAs in a multiple range of plants, including sugarcane (Bottino et al. 2013), soybean (Dong et al. 2013), radish (Sun et al. 2015) and barley (Deng et al. 2015). Recently, the benefits of high-throughput sequencing and degradome analysis were employed jointly to unearth novel miRNAs that were responsive to salt in maize (Fu et al. 2017), barley (Kuang et al. 2019), and fava beans (Alzahrani et al. 2019). Molecular and computational analyses of these salt-responsive miRNAs showed their involvement in the plant growth and development processes during the stress conditions by regulating various protective mechanisms, for example; scavenging of ROS and restoring ionic homeostasis of the cells (Sun et al. 2015; Vakilian 2020). Recent researches have involved deciphering of potential salinity-responsive miRNAs from African rice (*Oryza glaberrima*) (Mondal et al. 2018) and salt-tolerant rice varieties for instance; Pokkali and wild rice *Oryza coarctata* (Parmar et al. 2020). Given the potentiality of miRNAs in regulating salt-stress responses in plants, an in-depth characterization of these salinity-responsive miRNAs is essential for the designing salinity-tolerant crops.

4.3 Other Abiotic Stresses

Apart from drought and salinity, several other abiotic stresses also affect crop yield, and these include heat, cold, flooding, and metal toxicity stresses.

4.3.1 Heat Stress

Constantly rising global temperatures, even during the winter months, causes severe yield losses in the plants, especially those acclimatized to cooler climates. Several miRNAs have been found to regulate the heat stress response in several crops, for instance in wheat, by modulating the Ca^{2+} signaling pathway or other genes encoding various transcription factors associated with floral development and crop-yield (Kaur et al. 2019). High-throughput sequencing analysis has helped to identify several novel heat-responsive miRNAs in wheat (Xin et al. 2010; Kumar et al. 2015). Heat stress induced the upregulation of at least eight miRNAs, such as *miR156*, *miR159*, *miR160*, *miR166*, *miR168*, *miR169*, *miR827*, and *miR2005*, while *miR172* was significantly downregulated in wheat (Xin et al. 2010). Targeted downregulation of copper/zinc superoxide dismutase genes (*CSD1* and *CSD2*) by the heat-inducible expression of *miR398* imparted thermotolerance in transgenic *Arabidopsis* plants (Guan et al. 2013). Recently, Ravichandran et al. (2019) has shown that *miRNA156*, *miR159*, *miR166*, and *miR398* were extremely altered instantly exposing to heat stress for regulating thermotolerance in wheat, but their expression levels were largely returned up to the level of control through the 4-day poststress recovery time. These points indicated out to the tight regulatory control of the stress-responsive miRNAs and corresponding target genes during and after the stress period in plants.

4.3.2 Cold Stress

Cold stress includes two types of stresses, chilling (0–10 °C), and freezing (<4 °C) and causes yield losses in plants by dehydration and freezing of the cellular content (Megha et al. 2018). Sunkar and Zhu (2004) had demonstrated that expression of *miR393* was highly increased, while the expression of *miR398* was decreased under cold stress. Various genetic engineering tools, such as microarray and deep sequencing analysis, have helped to identify several cold-responsive miRNAs in different plants such as *Arabidopsis*, *Populus*, rice, and *Brachypodium* (Megha et al. 2018). Overexpression of *miR408* (Ma et al. 2015) and *miR397* (Dong and Pei 2014) had enhanced cold-stress tolerance in transgenic lines of *Arabidopsis*. Studies on *miR394* and *miR319* have also suggested their involvement in the regulation of cold-stress-induced tolerance (Megha et al. 2018). Latest study done by Sun et al. (2020) discovered that *miR535* negatively regulates cold tolerance mechanism in rice by altering the expression of C-repeat binding factor genes, namely, *OsCBF1*, *OsCBF2*, and *OsCBF3*.

4.3.3 Flooding Stress

Flooding or submergence is one more major abiotic stress that severely reduced the yield of important crops such as rice. It results in a condition known as hypoxia, characterized by the availability of very less oxygen to the plants (Bailey-Serres and Voesenek 2008). Numerous studies have identified several miRNAs, such as *miR156*, *miR159, miR528, miR166, miR167, miR171, miR172, miR319, miR395, miR397, miR408, miR474,* and *miR774*, that were differentially expressed during the early submergence and probably regulated flooding stress tolerance in different plant species (Fukao et al. 2019). Discovery of *SUB1* locus from the local landrace and its wide implementation in Asia to alleviate the problem of flooding in rice cultivation provides immense knowledge on the environmental and genetic basis of stress control in plants (Bailey-Serres et al. 2010).

4.3.4 Metal Toxicity Stress

High concentrations of metals, both essential and nonessential, can cause severe toxicity in agricultural soils and can lead to disruption of biological process in plants. Increasing evidences have pointed out the regulatory roles of several metal-responsive miRNAs, such as *miR319, miR390, miR393*, and *miR398*, in imparting tolerance against metal toxicity in plants (reviewed in Mendoza-Soto et al. 2012). *MiR319* was shown to regulate the expression of Teosinte Branched/Cycloidea/PCF (*TCP*) transcription factors, *miR393* targeted the auxin receptors *TIR1*/*AFBs*, and *miR390* controlled auxin signaling pathway via trans-acting siRNA synthesis (Mendoza-Soto et al. 2012). Apart from these, cadmium toxicity resulted in down-regulation of *miR393, miR171, miR156*, and *miR396* in *Brassica* roots (Xie et al.

2007). The expressions of *CSD* genes were regulated by *miR398* to control the induced oxidative stress after exposure of high copper or iron (Mendoza-Soto et al. 2012). In another study in rice, *miR166* was also exhibited to modulate cadmium-stress tolerance and accumulation (Ding et al. 2018).

5 Conclusion

An enormous versatility in the miRNAs for controlling and coordinating the diverse plant pathways has been ever expanding with the discovery of novel miRNAs by the revolutionizing genetic engineering techniques. The miRNAs are rightly termed as master regulators of gene expression as they are able to regulate versatile functions in plants, including growth, development, organ/tissue differentiation, phase transition, reproduction, flowering, and imparting tolerance to biotic and along with abiotic stresses. They execute their control over the target mRNA's expression by specific binding of very small homologous seed region. Also, reports have shown that single miRNA can coordinate the function of several related genes and can, thus, simultaneously participate in diverse plant regulatory pathways.

Plants respond to environmental stresses in the form of several physiological, biochemical, and epigenetic changes. Gene silencing directed by miRNAs has been regarded as the major regulating mechanism that aids in coping with the adverse effects imposed by various abiotic stresses, especially drought and salinity. Several miRNA families, including *miR156, 159, 164, 166, 319, 393, 396,* and *414*, are postulated to mediate the cross-talk between gross biomass production and abiotic stress responses. It is also possible that they might be able to confer multiple stress tolerance to plants under different field conditions. However, additional studies need to be conducted in this regard to gain confidence in the regulatory roles of plant miRNAs in imparting tolerance to multiple stresses. Also, several miRNAs usually work in tandem with a target mRNA forming a circuit with the downstream effector gene. These regulatory nodes need to be molecularly dissected to decipher the pathway undertaken by the miRNA to modulate the function of the gene and produce the desired effect at phenotypic or genotypic level.

High-throughput sequencing has emerged as one of the highly efficient methods used for rapid discovery of novel plant miRNAs. It is cost-effective and together with the bioinformatics prediction analyses, it helps to identify miRNAs under challenging environmental conditions from several plant species. Detailed characterization of these miRNAs and their target genes can help us to understand the intricate network of plant regulatory pathways in stress management. One of the popular ways of doing this involves either overexpression or downregulation of miRNAs and/or their respective mRNA targets. Furthermore, investigation of the current and new regulatory pathways upstream, as well as downstream of the miRNA target genes, would offer advanced and new insights for understanding the diverse roles of miRNAs in the regulation of stress tolerance in plants. Besides, miRNAs responsive to drought and salinity stresses have shown clear indication toward a potential cross-talk between two major plant hormones, namely, auxin and ABA. Studies on this relationship between abiotic stress and an auxin-ABA cross-talk regulated by miRNAs can unlock several associated regulatory networks governing stress-tolerance in plants.

Remarkably, the miRNAs are evolving as true potential targets in the genome editing tool, where they are employed to aim the traits improvement and stress adaptations in many plants. Several advanced biotechnological tools such as CRISPR/Cas9, TALENs, endogenous, and artificial target mimicry are currently being exploited in this regard (reviewed in Basso et al. 2019). Either single miRNA genes or miRNA gene families are being targeted by CRISPR-Cas9, which has emerged now as a very effective tool in knocking out the specific plant miRNAs for gene regulation purposes. Furthermore, a deeper understanding of the regulation and mechanism of miRNAs associated with abiotic stress tolerance in different plant species will add to the additional benefits to the genome editing tools for improving agronomic traits of important crops. Thus, miRNAs play very significant regulatory roles in the various abiotic stress-specific responses in the plants and have the potential to change the future of sustainable agriculture by developing designer high-yielding crops which are resilient to challenging environmental conditions.

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Chapter 7
Molecular Mechanisms of Heat Shock Proteins for Sustainable Plant Growth and Production

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Abbreviations

ABA	Abscissic acid
BR	Brassinosteroid
HR	Hypersensitive response
Hsf	Heat shock factor
Hsp	Heat shock protein
JA	Jasmonic acid
OE	Overexpression
SA	Salicylic acid
TF	Transcription factor

1 Introduction

Plants are continuously exposed to multiple types of stresses including heat, cold, salinity, drought, heavy metals, and to various pathogens which disturb the protein homeostasis by protein degradation and unfolding. Plants have evolved a number of mechanisms to prevent disruption of protein homeostasis by maintaining the proteins' functionality and to prevent aggregation of non-native proteins (Fig. 7.1). Hsps, also termed as chaperones and stress-induced proteins, are the major components involved in protein folding, assemblage, translocation, and breakdown under normal cellular processes and stress conditions (Park and Seo 2015). Historically, the first heat shock protein (Hsp) was identified by the Italian Scientist, Ritossa. During an experiment, when *Drosophila melanogaster* was exposed to heat, there was an identification of a gene expression on its puffing chromosome, and this led to the start of Hsps discovery. The heat stress resulted in protein synthesis which was also induced by other stresses like azide, salicylate, and so on (Ritossa 1962). This report led to the identification of the heat stress-induced protein, which was termed as heat shock protein (Hsp). The relation between the accumulation of Hsps and the heat tolerance was examined, where one report stated that when *Glycine max* seedlings were exposed to heat shock from 28 °C to 45 °C for 10 min, induction of Hsps occurred which was accompanied by depletion in other protein synthesis. Moreover, when seedlings were pretreated at 40 °C before exposure to high temperature (45 °C), seedlings behaved as tolerant due to protection by Hsps (Lin et al. 1984). Hsps are classified into Hsp100, Hsp90, Hsp70, Hsp60, Hsp40, and small heat-shock proteins (sHsps/Hsp20) on the basis of molecular weight ranging from 10 to 200 kDa (Shinozaki and Yamaguchi 2000). Heat shock domain, which is a carboxylic terminal, is present in all Hsps. Apart from their role under thermal stress, Hsps are also involved in various other stresses such as salinity stress, where variable Hsps were differentially upregulated in *Populus trichocarpa* after salt treatment (Yer et al. 2018). The role of sHsp (ThHsp18.3) from *Tamarix hispida* was demonstrated in yeast *Saccharomyces cerevisiae* transformed with *ThHsp18.3,*

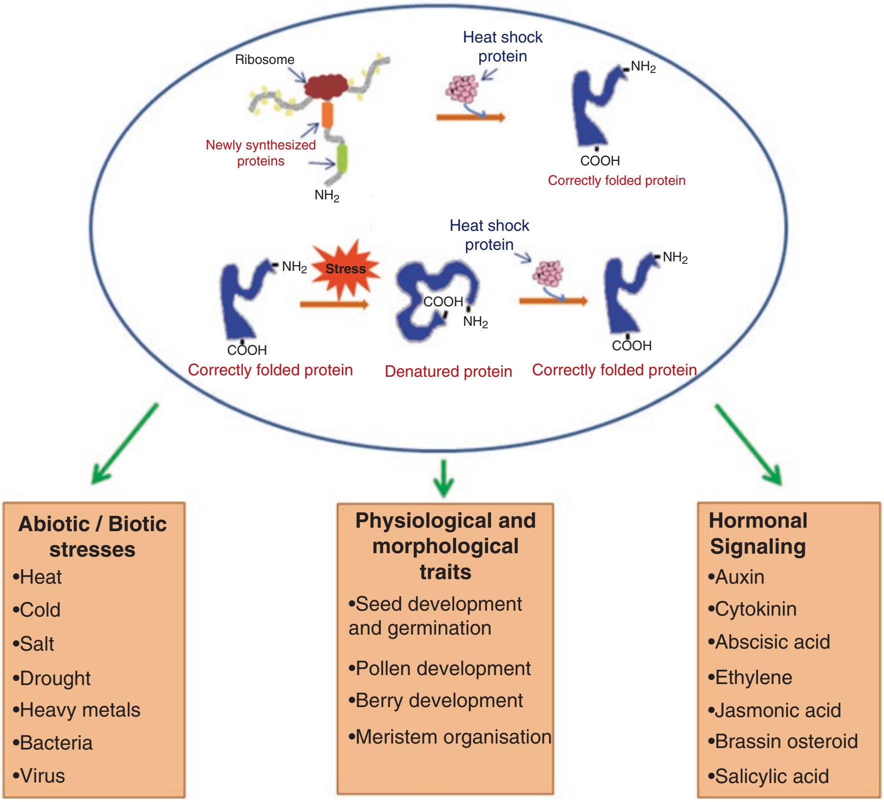

Fig. 7.1 Functions of Hsps: Within cell for correct folding of newly synthesized protein and in assisting protein in its functional form after stress (Above). And its role in plants including morphological, physiological traits, stress tolerance, and hormonal signaling

which showed to bestow enhanced tolerance against abiotic stress such as salt, heavy metals, drought, and low and high temperatures (Gao et al. 2012).

Hsps are also involved in various cellular developmental processes in plants such as pollen development (Marrs et al. 1993), growth of plant root and inflorescence (Bekh-Ochir et al. 2013), chloroplast biogenesis and development (Latijnhouwers et al. 2010; Oh et al. 2014), seed germination and maturation (Chang et al. 2018; Chauhan et al. 2012; Wu et al. 2015), and in other developmental phenotypic characteristics such as leaves' shape, stem thickness, and siliques size (Leng et al. 2017). Hsps are important proteins in plant developmental and defense responses in various ways; for example, they respond to different stress hormones, involved in hormones biosynthesis as well as through their interaction with different proteins and transcription factors for providing tolerance under stress conditions (di Donato and Geisler 2019; Jacob et al. 2017; Sable and Agarwal 2018).

In this chapter, we aim to focus on the importance of Hsps in plant growth and development by reviewing recent findings on plant Hsps in physiological and morphological events and how they respond to various environmental stresses including biotic and abiotic. Hsps' interaction and response to different transcription factors which are involved in stress signaling and plant development had been an important area of study to uncover its role in plants. Their role as chaperones has been reported in many ways such as their interaction with various proteins involved in defense and in hormone biosynthesis to proceed with the process of defense signaling, as well as in the biosynthesis of hormones. Research through transgenic and mutant approaches to functionally characterize Hsps; their hormonal crosstalk and transcriptional regulation have been discussed in this chapter.

2 Heat Shock Proteins as Molecular Chaperones

Belonging to a multigene family, Hsps acts as molecular chaperones under normal and in multiple stress conditions. Their name signifies them as a heat shock protein, but they are not restricted to respond to only heat stress. They are also induced under other abiotic and biotic stresses. Hsp100 family comprises proteins of molecular weight 100–104 kDa. Under heat stress conditions, they maintain the cellular proteostasis by sustaining the function of important polypeptides, where aggregates of the non-functional proteins are resolubilized and damaged polypeptides are degraded (Gupta et al. 2010). Disaggregation of protein is performed by Hsp proteins belonging to Hsp100, the caseinolytic protease (Clp) family. Hsp100 is pervasive and present in yeast, bacteria, and multicellular plants. Their expression was induced after heat stress and developmental signal. One and two forms of Hsp100 proteins are present in yeast and bacteria, respectively. Whereas multiple forms of Hsp100 proteins are present in plants that are localized to various compartments of the cell such as chloroplast, mitochondria, cytoplasm, or nucleus (Mishra and Grover 2016).

Hsp90 is the most abundant and highly conserved Hsp present in the cytosol of prokaryotic and eukaryotic cells and get induced under multiple stress conditions. Under normal conditions, Hsp90 binds to variable intracellular proteins like actin, calmodulin, receptor proteins, and kinases (Gupta et al. 2010; Matsumiya et al. 2009; Te et al. 2007). Hsp90 regulates its role by binding, inhibiting, or triggering its target protein activity. Many protein complexes that bind with co-chaperones like tetratricopeptide repeat (TPR)-type have Hsp90 as one of their major components (Takahashi et al. 2003).

Family of Hsp70 is an extremely conserved classes of Hsps in plants and plays a role as chaperone for proper folding of protein during their translocation to their target destination and to prevent the formation of clumps of newly synthesized proteins. ATP driven in nature, C-terminal peptide-binding domain, and N-terminal ATPase domain are present in Hsp70 proteins (Mayer and Bukau 2005). Another Hsp, that is, Hsp60, also known as chaperonins, is present in bacteria (GroEL), mitochondria, and chloroplasts (Wang et al. 2004) and contributes in folding of proteins that are transported to mitochondria and chloroplasts (Lubben et al. 1989).

In chloroplast, functional conformation of newly imported proteins is attained by limited plant chaperonins (Jackson et al. 2001). Hsp40/DnaJ consists of 70-amino acid J-domain which binds to nucleotide-binding domain (NBD) of Hsp70 and tends to increase the affinity of Hsp70 for their clients. Thus, Hsp40 acts as a co-chaperone of Hsp70 (Kampinga and Craig 2010).

The ubiquitous and evolutionarily conserved class of Hsp family is the family of small Hsps (sHsps) having a molecular weight of 12–42 kDa. They are found in archaea, bacteria, and eukaryotes. They prevent unwanted protein–protein interactions and assist in denatured protein refolding, also known as “holdase” (Zhang et al. 2015b). They are also named as Hsp20 because most of the sHsps are of molecular weight ranging from 15 to 22 kDa. They differ from other Hsps due to the presence of an intensely conserved α-crystalline C-terminal domain consisting of a long chain of 80–100 amino acid. They perform their role in an ATP-dependent manner. The protein complex formed by co-operative binding of sHsp with a substrate of non-native protein, later interacts with chaperones such as Hsp70/Hsp40 and ClpB to rejuvenate denatured proteins (Gupta et al. 2010; Muthusamy et al. 2017). With respect to cellular localization, functions, and sequence similarity, sHsps are diverse Hsp family and according to one of the earlier reports, nuclear genomes encode all sHsps (Waters et al. 1996). Reportedly, they are divided into five subfamilies based on their subcellular localization: mitochondria subfamilies, cytosol subfamilies (cytoplasm and nucleus), chloroplast, peroxisomes, and ER subfamilies (van Montfort et al. 2001). Interestingly, in animals, fungi, and green algae, none of the plant organelles Hsp20 homologs are present (Waters et al. 2008).

Till date, sHsps are found in various organisms such as 10 sHsps in human (Kappé et al. 2003), *Saccharomyces cerevisiae* have two sHsps (Bentley et al. 1992), 27 in wheat (Pandey et al. 2015), 23 in rice (Sarkar et al. 2009), 35 in pepper (Guo et al. 2015), 19 sHsps in *Arabidopsis thaliana* (Scharf et al. 2001), 8 in *VvHsp20* genes in grape (Ji et al. 2019), and 37 in *Populus trichocarpa* (Zhang et al. 2015a). Denatured proteins are maintained in their folding-competent state by Hsp20 and through the Hsp70/90 chaperone system, Hsp20 allows their subsequent ATP-dependent disaggregation (Kotak et al. 2007). Hsp20 also forms 200–800 kDa oligomeric hetero-complexes and thus acts as ubiquitin. They work in an ATP-independent manner and prevent the formation of denatured protein aggregates and avoid inappropriate folding (Fu 2015).

3 Role of Hsps in Regulating Plant Physiological and Morphological Traits

Heat shock proteins are expressed in plants growing under optimal natural environmental conditions. Initially, a report stated the accumulation and expression of Hsps in seeds, seed pods, and flowers during a normal growing season in *Medicago sativa*. They observed frequent expressions of Hsps in reproductive structures, pointing toward the importance of Hsps in reproductive success (Hernandez and Vierling 1993). Hsp101 is regulated by various developmental processes in plants such as in maize, and expression of Hsp101 is controlled in an organ-specific manner. Abundancy of Hsp101 had been reported in embryo, developing tassel, ear, silks, and endosperm of maize, whereas in the floral and vegetative meristematic regions, it was found to be less, along with its low level in roots, leaves, mature pollen, anthers, and tassel (Young et al. 2001). There are certain Hsp genes that are activated or expressed at definite stages of embryogenesis and gametogenesis, and during seed germination and maturation, indicating their importance in developmental functions (Coca et al. 1994; Mascarenhas and Crone 1996). In maize, Hsp81, a member of Hsp90 gene family is strongly expressed during pollen development at pre-meiotic and meiotic prophase stages (Marrs et al. 1993). In tomato, Hsp70 is expressed in developing microspores throughout its development. Hsp70 is synthesized during the initial stage of pollen development and accumulates in mature and pollinating pollen (Duck and Folk 1994). Higher expression of Hsp70 genes was observed in the pollen development bicellular stage in comparison to its other stages in maize (Gagliardi et al. 1995). The role of a subclass of Hsp70s was analyzed through a transgenic/mutant approach. After overexpression/knockdown/knockout, no visible phenotype was observed, but Hsp70-1 Hsp70-4 double and Hsp70-2 Hsp70-4 Hsp70-5 triple mutant plants exhibited different developmental phenotypes like round and curly leaves, short siliques, and the mutants were also hypersensitive to salt, osmotic, high glucose, heat, and cold stresses. This study concludes that individual Hsp70 can perform specific and redundant functions with other subclasses of cytosolic/nuclear Hsp70 (Leng et al. 2017). Su and Li (2008) reported the importance of stroma-localized Hsp70s in plant development in *Arabidopsis thaliana* ΔcpHsc70-1 and ΔcpHsc70-2 mutants, and observed no change in phenotype in ΔcpHsc70-2 mutant, whereas Δcphsc70-1 mutants exhibited phenotypic deformities which were observed in cotyledons, leaves, root growth, and also in growth retardation (Su and Li 2008). Silencing of Hsp70 in tomato leads to mortality and severe growth retardation under normal and drought stress conditions (Aghaie and Tafreshi 2020).

Heat shock protein (SlHsp17.7) from tomato plays a role in regulation of sugar metabolism pathway. This had been proved in *SlHsp17.7*-RNA interference (RNAi) tomato lines which contain low sucrose and fructose contents with decreased expression of sugar metabolism genes (Zhang et al. 2018b). High accumulation of Hsp17.9 and Hsp17.6 had been reported in sunflower seeds during seed maturation and germination indicating its role toward desiccation tolerance of seeds. During seed germination, Hsp17.6 and 9 were also involved in the mobilization of reserved lipids and structural proteins between the cytoplasm and membrane-bound organelles (Coca et al. 1994). Constitutive expression of wheat Hsp26 in certain developmental growth stages had been reported by Chauhan et al. (2012). They overexpressed the above said protein in *Arabidopsis thaliana* and observed that the transgenic plants produced seed with increased germination potential under high temperature. Promoter study in transgenic rice and *Arabidopsis thaliana* confirmed the role of chloroplastic sHsp26 during seed maturation and germination (Chauhan et al.

2012). The role of NnHsp17.5 in seed germination vigor was reported by overexpression in *Arabidopsis thaliana* (Zhou et al. 2012); similarly, in another report, rice OsHsp18.2 played a role in improving seed vigor, longevity, desiccation tolerance, and seedling establishment. Through proteomic analysis, *OsHsp18.2* overexpressed *Arabidopsis thaliana* lines, showed its presence as abundant in dry seeds and a high expression at the late maturation stage but a significant reduction after germination. OsHsp18.2 protects and stabilizes the cellular proteins from impairment during seed development such as during seed maturation, storage, and drying by impeding ROS build-up (Kaur et al. 2015). In Pea, a mitochondrial Hsp22, shows strong accumulation during seed development, and under heat stress, it acts as a holdase to prevent protein aggregations of some protein and co-precipitates with other for their refolding by client proteins (Avelange-Macherel et al. 2020). Similarly, in *Triticum aestivum L, TaHsps* showed high expression during seed development and also in heat stress, signifying their role in different stages of seed development (Kumar et al. 2020).

Recently, a reduction in seed length and delay in seed germination were shown in CI-sHsp-silenced rice transgenics (Sarkar et al. 2020). Silencing of Hsp90 leads to plant phenotypic variations such as flowering time, stunted plant growth, and other morphological traits (Kadota and Shirasu 2012; Queitsch et al. 2002). Hsp90 is reported to participate in the process of seed embryo formation and seed germination. A dramatic increment in the number of *AtHsp90-1* transcript was seen in developing embryo, whereas a slow increase of *AtHsp90-3* was observed during pod elongation and a slight decrease in nearly mature embryos. Hsp90 also affects the elongation of the hypocotyl (Xu et al. 2012). Inhibition of Hsp90 in *Nicotiana benthamiana* resulted in meristem death and severely stunted growth with chlorotic leaves (Park and Seo 2015). Their silencing in *Arabidopsis thaliana* resulted in abnormalities in plant phenotypes such as epinastic cotyledon, disc or radial symmetry of cotyledons, and growth of abnormal root hairs (Queitsch et al. 2002). Hsp90-RNAi lines of *Arabidopsis thaliana* showed increased purple pigment accumulation in the cotyledons with the development of narrower leaves. The developing plants showed an absence of apical dominance, and produced numerous primary inflorescences with anomalous stem and expanding number of rosette leaves with delayed flowering (Sangster et al. 2007). Hsp40 is a key target of farnesylation which controls meristem organization, ABA hypersensitivity, and drought tolerance (Barghetti et al. 2017).

An essential ATPase, cpHsc70, was reported to interact with the VIPP1 (vesicle-inducing protein in plastids 1) for thylakoid upkeep and biogenesis. Functions of two Hsp70 homologs viz. cpHsc70-1 and 70-2 were examined in *Arabidopsis thaliana* through artificial microRNA (amiRNA) and co-suppression study, and their role in normal plastid structure development and function was reported. The mutant plants showed a white phenotype with impaired normal growth having abnormal chloroplast with near non-appearance of thylakoid membranes (Latijnhouwers et al. 2010). Oh et al. (2014) reported the role of chloroplast localized Hsp90.5 in plant growth and development, and chloroplast thylakoid formation by forming Hsp90.5 co-suppression transgenic lines in *Arabidopsis thaliana* (Oh et al. 2014).

In strawberry, class-I low-molecular-weight (LMW) Hsps are significant in fruit ripening (Medina et al. 1998) and *VvHsp20* genes from grape were reported to be involved in grape berry development (Ji et al. 2019). In tomato (*Lycopersicon esculentum*), under normal growth conditions, chloroplast-localized Hsp21 promotes fruit maturation and ripening. Hsp21 accumulates carotenoid in the developing fruit which results in fruit reddening and ripening (Neta-Sharir et al. 2005). During floral development in *Arabidopsis thaliana*, Hsp18.2 is needed for maintaining the structural integrity of flower by proper flower bud differentiation. Under normal growth conditions, transgenic *Arabidopsis thaliana* carrying a construct of GUS fused *Hsp18.2* gene, showed constitutive expression of *Hsp18.2* in styles, sepals, and filaments which indicates organ specificity of Hsp18.2 (Tsukaya et al. 1993). BOBBER1 (BOB1), a NudC domain-containing sHsp, is reported to express throughout growth, embryogenesis, and a range of post-embryonic developmental processes in *Arabidopsis thaliana*. During embryogenesis, BOB1 is essential for auxin gradient formation and the normal partitioning and patterning in the apical domain of the embryo. Perez et al. (2009) formed partial loss of function BOL1 mutants (bob1-3) in *Arabidopsis thaliana* and observed the bob1-3 phenotypes showing pleiotropic development defects throughout different developmental phages such as a reduction in shoot and root growth rate, pattern deformities in leaves, flowers, and inflorescence meristem which included pronounced serrated leaves, aberrant number of floral organs, change in floral identity, and pin-formed inflorescences (Perez et al. 2009). Study conducted on Hsf and Hsp gene families in *Populus* showed high expression levels of most *Hsp60* and *Hsp70* genes in the upper stem, implying their presumed function in the initial stem growth. The *Pt18.3I-sHsp* expression was also found to be higher in the stem, suggesting its promising role in stem development (Zhang et al. 2015a).

Recently, the role of Hsp70 was suggested in programmed cell death (PCD) at a threshold during leaf development in *Aponogeton madagascariensis*. PCD forms perforation during leaf development. During early stage of leaf development, when PCD is active, Hsp70 influences PCD pathways by protein refolding and regulating anthocyanin level and caspase-like protease (CLP) activity (Rowarth et al. 2020). Earlier, in *Pisum sativum,* the expression profiles of three cytoplasmic *Hsp70* genes entitled as *PsHsp71.2, PsHsc71.0 and PsHsp70b* were investigated. Constitutive expression of *PsHsc71.0* and *PsHsp70b* was observed in leaves. *PsHsc71.0* and *PsHsp70b* were also found to be expressed in maternal and zygotic organs all through the seed developmental period, whereas *PsHsp71.2* was found to be expressed only in zygotic organs (DeRocher and Vierling 1995). Stomata-localized Hsp70 in *Arabidopsis thaliana* proved to be an important in germinating seeds for heat tolerance and differentiation (Su and Li 2008). In rice, they are important for normal chloroplasts differentiation from the pro-plastids and under high temperature (Bionda et al. 2016).

4 Hsps Bestow Biotic and Abiotic Stress Tolerance in Plants

4.1 Hsp100

In plants, the role of Hsp100 proteins in heat tolerance has been widely studied (Hong and Vierling 2001; Lin et al. 2014). One of the important roles of Hsp100 is the re-solubilization of protein aggregates by interactions with the chaperone system comprising of sHsp (Bösl et al. 2006). Effects of heat acclimation in rice seedlings are due to positive interaction between Hsp100 and HSA32 (heat stress-associated 32-KDa protein) (Lin et al. 2014). Increase in thermotolerance was observed in rice overexpressing *AtHsp101* (Katiyar et al. 2003). Mutants of Hsp100 proteins in rice, *Arabidopsis thaliana,* and maize showed sensitivity toward heat stress (Mishra and Grover 2016). According to reports, Hsp101 and Hsa32 (heat stress-associated 32-KDa protein) form a complex and were involved in long-term acquired thermotolerance (LAT) in rice. On comparing between japonica Nipponbare and Indica N22, japonica showed a better LAT phenotype than Indica N22 (Lin et al. 2014). *Hsp100* overexpressed in tobacco cells increased the survival rates of cells after *Clavibacter michiganensis* ssp. *sepedonicus* infection (Shafikova et al. 2013).

4.2 Hsp90

Hsp90 plays a crucial role in biotic and abiotic tolerance in plants. Under normal conditions, Hsp90 dimers are combined with Hsf monomers. However, these Hsf monomers convert to trimers under stress conditions and initiate transcription by binding to HSE on the promoter of Hsp genes. Various genome-wide analyses on different plants have shown an induced expression of Hsp90; for example, the expression analysis of *NtHsp90* genes in tobacco showed upregulation on treatment with salt, cold, heat, and ABA stresses (Song et al. 2019); barley HvHsp70 and HvHsp100, HvHsp90 were manifested with induced gene expression under heat stress during reproductive stage and responded to heavy metal, drought, and salt stress in a tissue-specific manner (Chaudhary et al. 2019), and in *Brachypodium distachyon* (L.) *P. Beauv.,* some of the *Hsp90* genes showed an upregulation under salt and drought stress (Zhang et al. 2017).

Involvement of Hsp90 in signal transduction pathways was reported to regulate biotic and abiotic stresses, where their main substrates are kinases and transcription factors that positively/negatively regulate the expression of defense-related genes and interact with other signaling pathways in plants (Xu et al. 2011). For abiotic stress tolerance/response, Hsp90 localized at different cellular compartments responds differently to different stresses. The Hsp90 homeostasis is very important because they play the above role via a mechanism which involves Ca^{2+} or ABA dependent pathways. Such as in *Arabidopsis thaliana,* AtHsp90 isoforms localized at different cellular compartment, that is, AtHsp90.2 (cytosol), AtHsp90.5 (chloroplast), and *AtHsp90.7* (ER, i.e., endoplasmic reticulum) overexpressed in *Arabidopsis thaliana*, and showed reduced salt and drought stress tolerance, and in germination rates, but enhanced tolerance to high Ca^{2+} stress. However, their mechanism varies as the transgenic overexpressing cytosolic Hsp90 delayed the ABA-responsive genes expression, whereas in chloroplast and ER-localized Hsp90 transgenics under stress conditions, no effect on these gene expressions was observed (Song et al. 2009). Hsp50.2, a member of Hsp90 family, overexpressed in rice exhibits an enhanced drought tolerance in transgenic (Xiang et al. 2018) and rice *Hsp90,* overexpressed in yeast and tobacco, provided salt tolerance in both the systems (Liu et al. 2006). Recently, MeHsp90 in cassava showed drought resistance by recruiting MeWRKY20 and MeCatalase1, where one is involved in ABA biosynthesis and the other in H_2O_2 detoxification, respectively (Wei et al. 2020).

Hsp90 mediates tolerance against microbial pathogens by the activation of cytosolic R proteins which have leucine-rich repeat and contain nucleotide-binding domain; in addition, RAR1 and SGT1, the co-chaperones of Hsp90, and their combination regulate RPMI and RPS4 (cytosolic R proteins) (Hubert et al. 2003; 2009). Hsp90's role in rice blast fungus and innate immunity in rice has been well documented in rice, where Hsp90 and its co-chaperone Hop/Sti1 complex engaged in anti-fungal immunity and chitin response (Chen et al. 2010). Single multi-chaperone machinery was said to be composed of Hsp90 together with Hsp70/Hsc70 (Young et al. 2004). In one of the studies, the mechanism of chlorosis by RNA silencing of Hsp90C in tobacco had been reported (Bhor et al. 2017).

4.3 Hsp70

The functionality of Hsp70 family genes was analyzed in the *Capsicum annuum* genome database, where the transcript expression and promoter analysis of *CaHsp70* revealed their involvement in growth, development, and in heat stress tolerance of pepper. *CaHsp70-2* from *Capsicum annuum L.* was overexpressed in *Arabidopsis thaliana*, and manifested with enhanced thermotolerance (Guo et al. 2016). Hsp70 induction was also reported in heavy metal stress (Cd, Cr, Cu, Fe, Ni, Pb, and Zn) in aquatic moss *Leptodictyum riparium* (Esposito et al. 2012; 2018). Recently, transgenic tobacco harboring *RcHsp70* from heat-tolerant variety of Chinese rose exhibited enhanced heat and cold tolerance with better photosynthetic performance and proline content (Jiang et al. 2020). Also, heterologous overexpression of *HmHsp70* from *Hypsizygus marmoreus* in tobacco enhanced their thermotolerance capacity (Xu et al. 2020).

Transgenic sugarcane harboring *Erianthus arundinaceus EaHsp70* demonstrated an elevation in drought and salinity stress tolerance due to improved germination ability and enhanced chlorophyll retention, when compared to non-transgenic (Augustine et al. 2015). Sustained expression of Hsp70 also plays an important role in rice plant memory due to pre-exposure to stress (Goswami et al. 2010), which may be due to epigenetic changes and cellular signaling networks. Drought tolerance was manifested in *Arabidopsis thaliana* heterologously overexpressing Chrysanthemum *Hsp70* (Song et al. 2014). Under flood stress, accumulation of Hsp70 increases, with the higher ratio in the cotyledon than in the root (Komatsu et al. 2013), poplar (Guzmán et al. 2014), winter wheat (Kosová et al. 2011), and pea subjected to cold stress (Taylor et al. 2005).

One of the most highly conserved classes of Hsps is Hsp70 family, playing an important role in biotic stress resistance. Hsp70 promotes viral infection by regulating viral reproduction and movement (Park and Seo 2015). Cytoplasmic Hsp70 functions in hypersensitive response (HR) by *Phytophthora infestans*-mediated infection and non-host resistance in *N. benthamiana* to *Pseudomonas cichorii* (Kanzaki et al. 2003). Significant accumulation of CaHsp70 in pepper leaves induces the HR to *Xanthomonas campestris* (*Xcv*) infection. In pepper, silenced *CaHsp70* plants showed susceptibility to *Xcv* infection and altered cell death response (Kim and Hwang 2015). In *Nicotiana benthamiana,* infection by Cucumber necrosis virus (CNV) triggers Hsp70 protein and transcript level. Although Hsp70 plays an immense role in plant biotic stress tolerance, it is also found that in susceptible *Solanum lycopersicum* species, a fungal infection resulted in the accumulation of Hsp70 but not in the resistant species. Therefore, depending on the nature of the infectious agent and host itself, the role of Hsp70 varies from supportive to deleterious (Kubienova et al. 2013).

4.4 Hsp60

Along with other Hsps, Hsp60 has been identified to enhance their transcript expression level under salinity stress in *Populus tremula L.* (Yer et al. 2018). Sarkar et al. (2014) developed the co-expression network from the heat stress transcriptomic data, which showed induced expression of Hsp60 at 42 °C after 2 h and at recovery time up to 4 h at 27 °C (Sarkar et al. 2014). Recently, in pepper, CaHsp60 was reported as a positive regulator in mitigating heat and other abiotic stresses. They had higher gene expression under these stresses and the knockdown of CaHsp60 showed sensitivity toward heat stress (ul Haq et al. 2019). Similarly, the expression of *UpHsp60* along with *UpHsp90* from a sterile *Ulva pertusa* is positively regulated by temperature changes and also by heavy metal stress (Tominaga et al. 2012). Singh et al. (2016) performed the genome-wide analysis of Hsps in foxtail millet and identified several Hsps to be induced under abiotic stress, in which Hsp60 was observed to be highly induced under drought stress (Singh et al. 2016). Interestingly, one of the recent reports analyzed the expression of chloroplast localized Hsp60 in *Thalassia hemprichii*, a marine seagrass during the diel cycle which comprised of temperature and light shifts. From the observation, it was concluded that Hsp60 showed an increase in expression with an increase in light and temperature and act as an agent in imparting tolerance against oxidative stress and photoinhibition (Rotini et al. 2020).

4.5 Hsp40/DnaJ

The presence of highly conserved J-domain (70 amino acids sequence) in Hsp40s makes them function as molecular co-chaperones to regulate Hsp70 proteins activity (Rug and Maier 2011). In *Lycopersicon esculentum,* their role was investigated by the generation of Hsp40/DnaJ (LeCDJ1) transgenic plants. After exposure to stresses like NaCl, PEG, heat, and H_2O_2, the expression of LeCDJ1 was induced. The transgenics showed better growth, chlorophyll content, lesser accumulation of malondialdehyde, and low relative electrical conductivity (Kong et al. 2014).

Various studies of virus-plant interactions had reported Hsp40's role in viral pathogenesis. Reportedly, Hsp40 had been shown to play a role in plant immunity, where its overexpression caused a HR-like cell death. Silenced lines of Hsp40 in soybean increases susceptibility of the plant to *Soybean mosaic virus* (Kampinga and Craig 2010). Both Hsp70 and Hsp40 interactions provide plant immunity in microbial pathogenesis (Park and Seo 2015). In another report, *CsHsp45.9* from cucumber, which was especially expressed in flowers, was strongly induced by *Pseudoperonospora cubens*is and showed upregulation when treated with other stresses like JA, ABA, SA, mechanical wounding, heat, cold, and salinity. This showed that CsHsp45.9 was responsive to biotic and abiotic stress (Li et al. 2012). Hsp40 functions in plant immunity, such as in soya bean, and overexpressed Hsp40 causes HR-like cell death in transgenics, and Hsp40 silenced lines showed *Soybean mosaic virus* susceptibility (Liu and Whitham 2013).

4.6 Small Hsp(sHsp)

There are various reports which highlight the role of sHsps in heavy metals stress. In genome-wide analysis of Indica rice species, a total of 11 Hsps were detected to be induced under arsenic (As) stress, out of which seven were sHsps (Chakrabarty et al. 2009). Various transcriptomic analyses under AsV stress observed an induction of sHsp, which showed its involvement in As response (Norton et al. 2008; Rai et al. 2011; 2015). *Tamarix hispida, ThHsp18.3* transformed yeast cells showed higher tolerance than non-transformed yeast cells under different heavy metal stresses (Gao et al. 2012). Proteomic and physiological analysis of poplar showed induction of *sHsp20, 22,* and *23* under cadmium (Cd) stress at an early time period compared to the late time period. Induction and accumulation of sHsps indicate their involvement in the stability of proteins and the maintenance of cellular homeostasis (Yang et al. 2015).

Overexpression of sHsps has shown to bestow tolerance to plants, such as in pepper, *CaHsp16.4* provided tolerance against drought and heat stress (Huang et al. 2019), and reduction in ROS accumulation was manifested in *CaHsp25.9* transgenics, whereas *CaHsp25.9*-silenced plants showed sensitivity to heat, salt, and drought stresses. Similarly, *AtHsp26* in *Arabidopsis thaliana* showed tolerance to heat stress

(Xue et al. 2010). *PmHsp17.9* from *Prunus mume* provided tolerance against heat stress in *Arabidopsis thaliana* (Wan et al. 2016). *Primula forrestii PfHsp17.2,* overexpressed in *Arabidopsis thaliana,* displayed higher salt tolerance and increased thermotolerance (Zhang et al. 2018a) and *TaHsp23.9* from wheat enhanced the tolerance of *TaHsp23.9 Arabidopsis thaliana* transgenics to heat and salt stress (Wang et al. 2020). Recently, overexpression of *SlHsp17.7* showed tolerance in tomato fruits against cold stress injury by mitigating ROS injury (Zhang et al. 2020). *LimHsp16.45* from David lily was reported to be involved in enhancing the ROS scavenging enzyme activity as well as cell viability under high salt and temperature stresses by its ectopic overexpression in *Arabidopsis thaliana* (Mu et al. 2013). Similarly, *CsHsp* genes from *Camellia sinensis* were heterologously expressed in *Arabidopsis thaliana* and conferred tolerance to heat and cold stresses (Wang et al. 2017). Thermomemory in *Arabidopsis thaliana* has been regulated jointly by Hsp21 and metalloprotease FtsH6 protein, in which lack of FtsH6 causes accumulation of Hsp21 in thermomemory later stages and enhances the thermomemory capacity (Sedaghatmehr et al. 2016). Reportedly, Ca^{2+} concentration inside the cell under heat stress was directly related to the activation Hsp20 in plants (Swindell et al. 2007).

A number of sHsps are associated with biotic stress such as viral infection (Verchot 2012). NtsHsp in *Nicotiana tabacum* exhibited *Ralstonia solanacearum* disease resistance because the *NtsHsp*-silenced plants showed disease symptoms (Maimbo et al. 2007). Previously, in *Glycine max*, strong induction of *GmHsp22.4* was observed against *Meloidogyne javanica* nematode infection in the resistant genotypes compared to susceptible one (Lopes et al. 2013). Recently, *GmHsp22.4* was functionally characterized in *Arabidopsis thaliana* by overexpression and knockout of its ortholog in *Arabidopsis thaliana*. Overexpressed transgenics showed resistance to the infection, whereas the mutants were susceptible toward the same (Hishinuma-Silva et al. 2019). According to reports, *AtHsp20*s from *Arabidopsis thaliana* gets induced by virus infection like *cucumber mosaic cucumovirus* (CMV) and *potato virus X potexvirus* (PVX) (Whitham et al. 2003). Li et al. (2015) found that expression of Hsp20 was significantly affected by RSV (Rice stripe virus) infection (Li et al. 2015). This shows that small Hsps are immensely active in coping with various environmental stresses (Hu et al. 2015).

5 Crosstalk Between Heat Shock Proteins and Hormones

5.1 Auxin

Auxin plays an indispensable role in regulating plant growth and in multiple developmental and stimulus-responsive processes in almost all phases of the plant life cycle. Upon perception of temperature, the transcription factor PIF4 (phytochrome interacting factor 4) regulates the genes involved in auxin biosynthesis. However, at increasing temperature, Hsp90 and the co-chaperone SGT1b were shown to regulate auxin signaling by stabilizing TIR1/AFB. The inhibition of Hsp90 leads to proteosomal degradation of TIR1, thereby interfering with the auxin-related processes at both lower and higher temperatures. So, the stabilization of the auxin receptor by Hsp90 might be involved in root and hypocotyl elongation, as they are temperature-dependent. This suggests the involvement of Hsp90 and SGT1 in integrating temperature and auxin signaling for regulating plant growth and development. Hsp90 can reduce the auxin-responsive phenotypes in plants with point-mutated TIR1 gene. Further, in vitro and in vivo studies showed interaction of Hsp90 with TWD1 (TPR-immunophilin FKBP42) of *Arabidopsis thaliana,* which is the interacting partner of auxin transporting ABCB isoforms and is responsible for their effective functioning. So, mutating *twd1* results in abnormal auxin transport (di Donato and Geisler 2019). Auxin is responsible for modulating Aux/IAA protein stability, thereby repressing ARFs (auxin response factors). However, recent studies in immature sunflower embryos show that HaIAA27 (Aux/IAA protein) suppresses activation by HaHsfA9 (heat shock factor, i.e., Hsf). So, overexpressing HaIAA27 in tobacco seeds resulted in downregulation of the HsfA9 gene. Thus, auxin modulates the accumulation of the HaIAA27 protein and also induces its TIR1-dependent proteasomal degradation (Carranco et al. 2010) (Fig. 7.2).

5.2 *Abscisic Acid*

Abscisic acid (ABA) responds to number of biotic and abiotic stresses and is commonly referred as a stress hormone. Hsfs can be induced either in an ABA-dependent or ABA-independent pathway. The ABA-independent pathway is indicated by Dehydration Response Element Binding (DREB) TFs. Several stresses such as heat, cold, drought, salt, and wounding causes induction of HsfA3, which acts as a target of DREB2A thereby resulting in Hsp production thereby providing stress tolerance (Fig. 7.2). ABA-dependent signaling depends upon the constitutive inhibition of SnRK2 protein kinases by PP2C phosphatases. Binding of proteins pyrabactin resistance/pyrabactin resistance 1-like/regulatory component of ABA receptors (PYR/PYL/RCAR) to PP2Cs occurs in the presence of ABA, thus releasing the inhibition on SnRK2. Activated SnRKs phosphorylates ABA-responsive transcription factors, that is, ABA response factors 1 and 3(ABF1, ABF3) and ABA responsive element-binding proteins 1 and 2 (AREB1 and AREB2), mediating ABA response (Jacob et al. 2017). In *Arabidopsis thaliana* snrk2d/e/i triple mutant, no expression of seed-specific HsfA7b and HsfA9 was observed (Nakashima et al. 2009). However, HsfA2, HsfA9, HsfA7a, HsfA7b, HsfB2a, and HfB2b were transiently induced during seed imbibition (Chiu et al. 2012). So, heat stress activates these Hsfs which were partially mediated by ABA.

Further studies suggested that Hsc70 overexpression and a dominant-negative mutation of Hsp90 interfere with ABA-mediated stomatal closure. To further study the effect of ABA on Hsc70, Hsp90, SGT1, and RAR1, quantitative RT-PCR was performed which showed an increase in Hsc70-4 and decrease in SGT1a mRNA. This

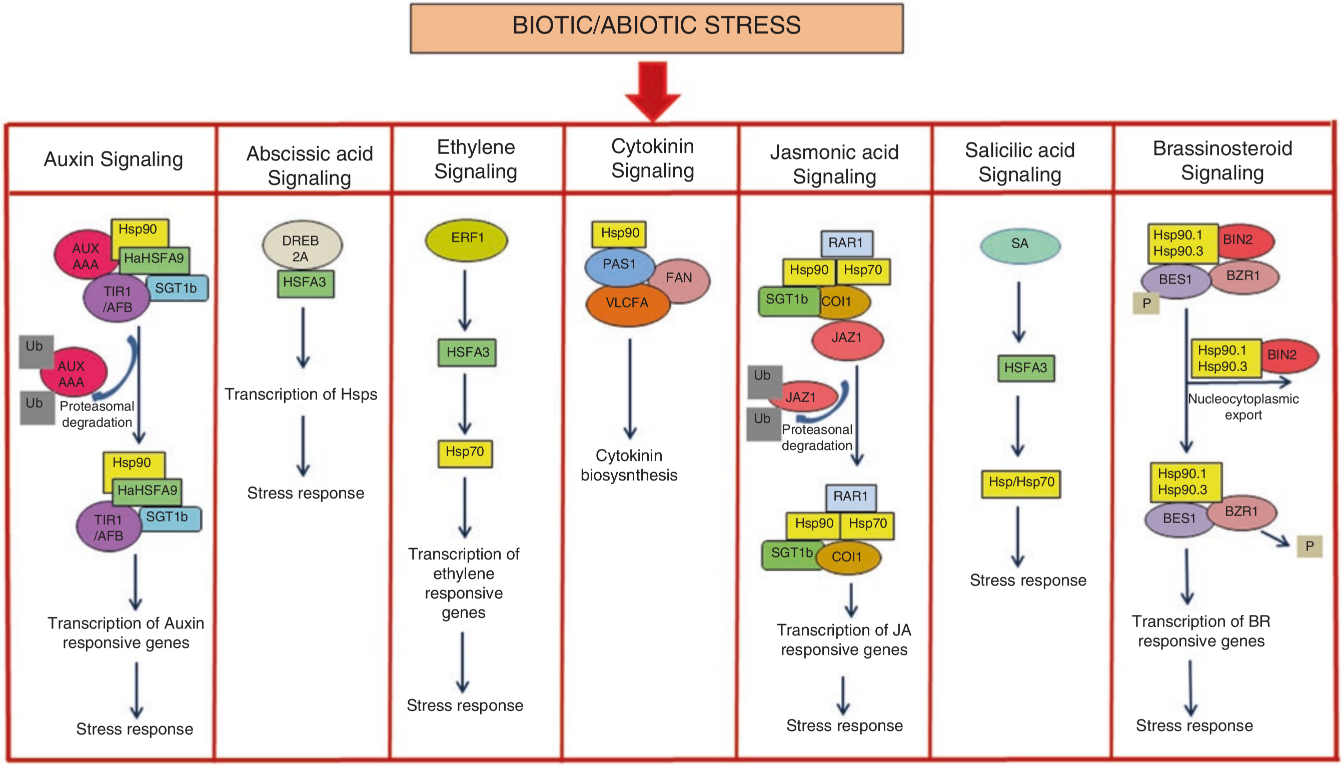

Fig. 7.2 Role of Hsps in hormonal signaling in plants

shHsc70-4 is involved in alleviating ABA signals, whereas Hsc70-1 and Hsc70-4 regulate ABA signaling. In the seed germination assay, Hsc70 overexpressing and Hsp90 dominant-negative mutant plant shows hypersensitivity to ABA. Hsc70/Hsp90 mediates the stomatal closure and regulates responses to ABA (Clément et al. 2011). During heat stress, DREB2A induces the transcription factor AtHsfA3, thereby regulating the expression of Hsps. *Arabidopsis thaliana* overexpressing AtDREB2A induces genes related to drought, salt, and heat stress. Therefore, the plants overexpressing DREB2A exhibited a significant enhancement in thermotolerance as compared to the knockout plants in which it was decreased (Sakuma et al. 2006).

Two genotypes of Japonica rice variety (Nipponbare), with flat leaves in wild type (WT) and semi-rolled leaves in mutant *hts* (high-temperature susceptibility), were exposed to heat stress. The *hts* plants suffered more damage as compared to the WT and had a higher level of ABA and $H_2O_{2.}$ Thus, it was inferred that ABA acts as a negative regulator in *hts* plants under heat stress. This was further validated by the exogenous application of ABA in WT and *hts* plants. The WT plants showed increased dry weight, ATP, and NAD(H) content as well as increased expression of *Hsp71.1* and *Hsp24.1*, whereas these decreased in *hts* plants, thus confirming the role of ABA as a negative regulator by modulating *hts* plants against heat stress (Li et al. 2020). Small Hsp22 plays an important role in the crosstalk between auxin and ABA. sHsp22 negatively regulates the ABA signaling. ABA signaling negative regulator, ABI1, is required for auxin-induced expression of sHsp22, since it induces auxin-induced hypocotyl elongation and also increases trafficking of PIN proteins. Thus, the ABI1-sHsp22 modulates the crosstalk between ABA and auxin (di Donato and Geisler 2019).

5.3 Ethylene

Ethylene (ET) is involved in various processes of plant development and acts as a mediator to stress responses. The ET signaling involves ethylene response factors (ERFs) which bind to the sequences containing AGCCGCC motifs and regulates biotic stress responses by binding to dehydration-responsive elements (DRE) (Müller and Munné-Bosch 2015). Wu and Yang (2019) treated rice seedlings with heat and in combination with ET precursor. They observed a lesser reduction in seedling's fresh weight and elevated expression of ET-related genes and of HsfA1, HsfA2a, c, d, e, and f in treated combination compared to heat stress alone, therefore suggesting the involvement of Hsf and ET signaling-related genes in the regulating mechanism under heat stress, thus providing thermotolerance to rice seedlings (Wu and Yang 2019). ERF-1 *Arabidopsis thaliana* transgenic plants resulted in higher heat tolerance as compared to the non-transgenic. Later, microarray analysis of heat shock-treated ERF1 transgenics showed an upregulation in the HsfA3 and Hsp70 transcript levels. Thus, confirming that ERF1 enhances thermotolerance in

Arabidopsis thaliana by recognizing the GCC box element containing AGCCGCC motifs on the promoter of HsfA3 and Hsp70 (Cheng et al. 2013) (Fig. 7.2).

Small Hsps genes, that is, *SlHsp17.6, SlHsp20.0,* and *SlHsp20.1,* were reported to be regulated by ET during the process from mature green fruit to ripening stage in two different tomato cultivars and in their ripening mutants viz. *nor*/*nor*, *Nr*/*Nr, rin/rin* mutant, and ACS2 antisense. Ethylene treatment resulted in suppression of the *SlHsp* genes in all mutants except the *rin*/*rin* mutant. In the *rin*/*rin* mutant, *MADS-RIN* gene is mutated which is a transcription factor. Further using chromatin immunoprecipitation and in silico studies, they showed binding of MADS-RIN at the multiple CArG motifs present in the promoter of *SlHsp17.6*, *SlHsp20.0,* and *SlHsp20.1*.These findings suggest that ET acts as a regulator of *SlHsp* genes in the transition from mature green to the ripening stage of tomatoes (Shukla et al. 2017). In tomato, *SlHsp17.7A* and *B* genes expression were reported to be downregulated in vegetative tissues by exogenous ET application, whereas their upregulated expressions were observed in silenced lines of ET biosynthetic gene, *SlACS2,* which produced 50% ethylene in vivo. And in the overexpression lines of ripening regulator, SlMADS-RIN, *SlHsp17.7A* expression was found to be downregulated. This concludes, that the expressions of SlHsp17.7A and B were modulated by ET and ripening inhibitor, during tomato fruit ripening (Upadhyay et al. 2020).

5.4 Cytokinin

Cytokinin is involved in regulating cell division and also in plant growth and development. Cytokinin perception and signaling are mediated by a two-component signaling system. It has been hypothesized that Hsp90 interacts with TPR-containing FKBP-type immunophilin known as pasticcino1 (PAS1). Studies on *pas1* mutants revealed its role in regulating cell division and differentiation. Earlier reports suggest that PAS1 regulates the shuttling of FAN, a FKBP-associated NAC transcription factor and also functions as a scaffold of VLCFA (very long fatty acid) biosynthesis complex which resides in the ER (di Donato and Geisler 2019) (Fig. 7.2). In *Populus* leaves*,* an increase in temperature resulted in enhance emission of isoprene level, which was correlated with an increased level of isoprene precursor, dimethylallyl diphosphate (DMADP) (Rasulov et al. 2010). An increase in DMADP ultimately results in increased cytokinin biosynthesis, as it acts as the substrate for isopentenyl transferase, the main enzyme involved in cytokinin biosynthesis. Thus, according to the hypothesis, heat shock increased the cytokinin levels, thereby triggering the expression of cytokinin responsive proteins (Černy et al. 2014).

5.5 Jasmonic Acid

Jasmonates include jasmonic acid (JA) and its conjugate form, JA-Ile, plays a key role in regulating various stress conditions and in plant growth and development (Balfagón et al. 2019). SKP1 protein, Cullin protein, and the F-box protein (COI1) together form the SCF-type E3 ubiquitin ligase, commonly referred as SCF^{COI1} complex. Jasmonate receptor comprises JAZs (jasmonate-ZIM domain proteins) and COI1 co-receptors, which initiate proteasomal degradation of JAZ proteins upon binding of JA-Ile, thereby, activating JA responses by releasing MYC2 and other transcription factors. In a study, *hsm1* mutant of *Arabidopsis thaliana* was used in which *SGT1b* gene was mutated. So, knocking out *SGT1b* resulted in reduced COI1 levels, suggesting its role in regulating the level of COI1, and therefore playing a role in JA signaling (Zhang et al. 2015c). It was shown that COI1 interacts with SGT1b–Hsp70–Hsp90 complexes and this complex is involved in hormonal signaling. In addition, there is an interaction of SGT1 with Hsp90-RAR1 (required for Mla12 resistance), suggesting their role in stabilizing plant disease resistance (R) proteins. In Hsp90 RNAi lines, treatment with coronatine (analog of JA) showed differential regulation of JA-responsive genes. These results were further reproduced by treatment of seedlings with GDA or Ver155008-inhibitor of Hsp70, suggesting the role of SGT1b, Hsp70, and Hsp90 in the JA response (di Donato and Geisler 2019) (Fig. 7.2).

The role of JA and heat shock in the sesquiterpene biosynthesis and accumulation was investigated in *Aquilaria sinensis*. For this, *A. sinensis* cell suspension cultures were given heat shocks. Following heat shock, induced expression of genes involved in JA biosynthesis pathway and in the sesquiterpene accumulation was observed. In addition, exogenous application of methyl jasmonate also increased the sesquiterpene biosynthesis. These results suggested a significant role of JA in the signaling cascade induced by heat shock (Xu et al. 2016).

5.6 Salicylic Acid

Salicylic acids (SA) participate in defending plants against biotrophic pathogens, and are necessary for HR and systemic acquired resistance (SAR). Salicylic acid is involved in the accumulation of heat-induced Hsp/Hsc70 and thus provides thermotolerance in plants. Reportedly, SA and heat shock treatment were given individually and in combination with tomato seedlings, which resulted in elevated levels of Hsp/Hsc70 in comparison to the seedlings treated with heat shock only, suggesting SA-mediated increase in Hsp70 by inducing Hsfs (Fig. 7.2). However, constitutive expression of the HsfA1gene was observed in the presence and absence of SA (Snyman and Cronjé 2008). In rice*, OsHsp18.0* overexpression lines showed an increase in SA level upon infection by any *Xoo (Xanthomonas oryzae* pv. *oryzae)* strains but decreased in the knockdown lines, suggesting activation of SA signaling in *OsHsp18.0* overexpression lines for *Xoo* resistance. Additionally, overexpressing

OsHsp18.0 also enhances heat tolerance, while *OsHsp18.0* silencing reduces it, confirming that OsHsp18.0 plays a key role in regulating both biotic and abiotic stresses (Kuang et al. 2017).

5.7 Brassinosteroid

The steroidal plant hormone, brassinosteroid (BR), has a major role in the regulation of stress responses as well as in numerous developmental processes. The BR co-receptor comprises of brassinosteroid insensitive1 (BRI1) and BRI1-associated receptor kinase1 (BAK1). BR signaling requires the downstream inactivation of BIN2, that is, brassinosteroid insensitive2, as it phosphorylates brassinazole resistant1 (BZR1) and BRI1-EMS suppressor 1 (BES1), thereby inhibiting activation of BR-inducible genes. Hsp90 interacts directly with BIN2, BZR1, and BES1, and its inhibition affects the BIN2 level and Hsp90.1/Hsp90.3 nuclear localization. The dephosphorylated state of BES1 is maintained by Hsp90.3, whereas Hsp90.1 and Hsp90.3 are involved in the export of BIN2. So, in the presence of BR, Hsp90.1/Hsp90.3-BIN2 complex is transferred to cytoplasm, thereby inhibiting the activity of BIN2 and dephosphorylating BES1 and BZR1 (Fig. 7.2). In recent findings, in vivo as well as in vitro study showed that TWD1, that is, TPR-immunophilin FKBP42 twisted dwarf 1 from *Arabidopsis thaliana* interacts with Hsp90. On BR perception, TWD1 causes autophosphorylation of BRI1 and BAK1. Thus, it was suggested that in BR signaling, TWD1 acts as a positive regulator upstream of BIN2 and it also plays a significant role in maintaining the conformational state of BR co-receptor complex (di Donato and Geisler 2019).

6 Conclusion

Plant Hsps are diverse group of essential proteins that are inevitable for physiological, morphological, and stress tolerance processes in plants. Over the past years, plant Hsps act as an initial line of defense which accumulates in response to different environmental stresses, and behaves as a buffer system for cellular homeostasis. Exposure of plants to heat stress induces the heat shock response; however, they are also elevated by other abiotic and biotic stresses. They are involved in various processes such as molecular chaperones for protein folding, proteins import and for translocating unstable proteins for proteasomal/lysosomal degradation. Genome-wide analysis and their expression profiling have demonstrated their involvement in plant growth, development, and stress processes. Transcriptional regulation and hormonal crosstalk have enlightened the relation between Hsps with transcription factors and phytohormones. Considerably this has improved our understanding of Hsps in plants and has led to their importance for further functional characterization in plants. To date, many Hsps have been functionally characterized which has generated improved crops in terms of growth and stress tolerance (Table 7.1).

Table 7.1 List of functionally characterized plant Hsps and their functions in plants

References	Hsp gene name	Origin of the gene	Model plant for characterization	Transgenic approach/ Mutants	Function/Stress tolerance
Katiyar et al. (2003)	*AtHsp101*	*Arabidopsis thaliana*	*Oryza sativa*	Overexpression	Heat
Gao et al. (2012)	*ThHsp18.3*	*Tamarix hispida*	*Saccharomyces cerevisiae*	Overexpression	Temperature, drought, salinity, and heavy metals
Su and Li (2008)	*ΔcpHsc70-1*	*Arabidopsis thaliana*	*Arabidopsis thaliana*	Knockout mutants	Developmental deformities in cotyledon, leaves, roots, and growth
Zhang et al. (2018b)	*SlHsp17.7*	*Solanum lycopersicum*	*Solanum lycopersicum*	RNAi	Sugar metabolism
Zhou et al. (2012)	*NnHsp17.5*	*Nelumbo nucifera*	*Arabidopsis thaliana*	Overexpression	Seed germination vigor
Kaur et al. (2015)	*OsHsp18.2*	*Oryza sativa*	*Arabidopsis thaliana*	Overexpression	Seed development
Katiyar et al. (2003)	*AtHsp101*	*Arabidopsis thaliana*	*Oryza sativa*	Overexpression	Thermotolerance
Xiang et al. (2018)	*Hsp50.2*	*Oryza sativa*	*Oryza sativa*	Overexpression	Drought
Guo et al. (2016)	*CaHsp70-2*	*Capsicum annuum*	*Arabidopsis thaliana*	Overexpression	Thermotolerance
Xu et al. (2020)	*HmHsp70*	*Hypsizygus marmoreus*	*Nicotiana tabacum*	Overexpression	Thermotolerance
Augustine et al. (2015)	*EaHsp70*	*Erianthus arundinaceus*	*Saccharum officinarum*	Overexpression	Drought and salinity
Song et al. (2014)	*CgHsp70*	*Chrysanthemum* sp.	*Arabidopsis thaliana*	Overexpression	Drought
Jiang et al. (2020)	*RcHsp70*	*Rosa chinensis*	*Nicotiana tabacum*	Overexpression	Heat and cold
Tominaga et al. (2012)	*UpHsp60*	*Ulva pertusa*	*Ulva pertusa*	Expression analysis	Temperature and heavy metal
Tominaga et al. (2012)	*UpHsp90*	*Ulva pertusa*	*Ulva pertusa*	Expression analysis	Temperature and heavy metal
Kong et al. (2014)	*Hsp40/DnaJ (LeCDJ1)*	*Lycopersicon esculentum*	*Lycopersicon esculentum*	Overexpression	NaCl, PEG, heat and H_2O_2
Li et al. (2012)	*CsHsp45.9*	*Cucumis sativus*	*Cucumis sativus*	Overexpression	Jasmonic acid, abscisic acid, salicylic acid, mechanical wounding, heat, cold and salinity
Gao et al. (2012)	*ThHsp18.3*	*Tamarix hispida*	*Saccharomyces cerevisiae*	Overexpression	Heavy metal stresses

(continued)

Table 7.1 (continued)

References	Hsp gene name	Origin of the gene	Model plant for characterization	Transgenic approach/ Mutants	Function/Stress tolerance
Huang et al. (2019)	*CaHsp16.4*	*Capsicim annum*	*Capsicim annum*	Overexpression	Drought and heat stress
Huang et al. (2019)	*CaHsp25.9*	*Capsicim annum*	*Capsicim annum*	Overexpression	Heat, salt, and drought stress
Xue et al. (2010)	*Hsp26*	*Saccharomyces cerevisiae*	*Arabidopsis thaliana*	Overexpression	Heat
Wan et al. (2016)	*PmHsp17.9*	*Prunus mume*	*Arabidopsis thaliana*	Overexpression	Heat
Zhang et al. (2018a)	*PfHsp17.2*	*Primula forrestii*	*Arabidopsis thaliana*	Overexpression	Salt tolerance and increased thermotolerance
Wang et al. (2020)	*TaHsp23.9*	*Triticum aestivum*	*Arabidopsis thaliana*	Overexpression	Heat and salt stress
Zhang et al. (2020)	*SlHsp17.7*	*Solanum lycopersicum*	*Solanum lycopersicum*	Overexpression	Cold stress
Mu et al. (2013)	*LimHsp 16.45*	*Lilium davidii*	*Arabidopsis thaliana*	Overexpression	Salt and temperature stresses
Wang et al. (2017)	*CsHsp17.7*	*Camellia sinensis*	*Arabidopsis thaliana, Pichia pastoris*	Overexpression	Heat and cold
Wang et al. (2017)	*CsHsp21.8*	*Camellia sinensis*	*Arabidopsis thaliana, Pichia pastoris*	Overexpression	Heat and cold
Wang et al. (2017)	*CsHsp18.1*	*Camellia sinensis*	*Arabidopsis thaliana, Pichia pastoris*	Overexpression	Heat and cold
Hishinuma et al. (2019)	*GmHsp22.4*	*Glycine max*	*Arabidopsis thaliana*	Overexpression	*Meloidogyne javanica* nematode infection
Upadhyay et al. (2020)	*SlHsp17.7A, B*	*Solanum lycopersicum*	*Solanum lycopersicum*	Expression analysis	Ethylene and ripening
Kuang et al. (2017)	*OsHsp18.0*	*Oryza sativa*	*Oryza sativa*	Overexpression	*Xanthomonas oryzae* pv. *Oryzae* infection, heat, Salicylic acid

Still, there is insufficient information on their mechanism such as how Hsps recognize their substrate and regulate them, how they receive the signals to activate the transcription of other downstream genes such as heat shock-responsive genes. In the future, efforts should be made to unravel the mechanism of Hsps on how they interact with other types of proteins, transcription factors, or co-chaperones to give better plant growth, for example, plant height, biomass, seed size, and production, and also on how they provide tolerance against stresses. Exploring these areas of research will provide better strategies for crop improvement.

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Chapter 8
Physiological and Molecular Responses to Heavy Metal Stresses in Plants

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1 Introduction

Modernization and extensive industrialization have worsened the deposition of heavy metals in soil, which imparts harmful effects on soil and crop productivity (Hassan et al. 2017). It damages soil texture by altering its pH, affecting the presence of different elements and plants' molecular or physiological growth activities by accumulating heavy metals directly or indirectly (Panuccio et al. 2009). Plants encountered with heavy metal toxicity show symptoms such as chlorosis, root browning, stunted growth, delayed growth or even death. In addition, heavy metals such as copper (Cu), cobalt (Co), molybdenum (Mo), zinc (Zn), manganese (Mn) and nickel (Ni) have been considered as essential elements for the development of plants as well as for their biological process pathways (Pierart et al. 2015). However, some heavy metals such as mercury (Hg), lead (Pb), aluminium (Al), chromium (Cr), arsenic (As), cadmium (Cd) and beryllium (Be) are considered toxic, and once the concentration of these heavy metals reaches above the supra-optimal levels, it causes high reduction in crop productivity (Xiong et al. 2014). Moreover, these elements have been reported to cause various abnormalities such as morphological and metabolic disorders via interference of the redox homeostasis of cells through developing reactive oxygen species (ROS) such as superoxide anion radical (O^{2-}), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH-) (Gill and Tuteja 2010; Pourrut et al. 2011).

A huge number of findings have highlighted the negative influence of heavy metal accumulation on food crops, leading to various human health effects (Nabulo et al. 2011; Shahid et al. 2015). Moreover, in order to survive against the stress of heavy metals, several defence mechanisms have been developed by plants, such as binding to phytochelatins/metallothioneins, sequestration of metal into vacuoles, decrease in uptake of heavy metals and antioxidants activation (Shahid et al. 2015). The first step taken by plants for defence is reducing the metal uptake when stimulated with heavy metal toxicity that is achieved through the help of root as well as cellular exudates. Exudation restricts metal entry in to the cell through increasing efflux/cell wall biosorption, which is classified as an avoidance mechanism. Amino acids, phytochelatins, peroxide, glutathione, metallothioneins and superoxide dismutase-like enzymes get involved in such defence mechanisms (Hossain et al. 2012). Moreover, a continuous extreme stress on plant cell leads to exhaustion of its defence system and creating a thrive condition, in which plant triggers different specialized mechanisms for metal detoxification. Plants also progress for symbiotic relations with various organisms (e.g. mycorrhizal fungi) during the stressed conditions. Various signalling pathways involving several genes have been found to develop in plant as its defence mechanisms. Among the various pathways of plant defence mechanisms, MAPK (mitogen-activated protein kinase) cascade is considered important during abiotic stress. In eukaryotic organisms, a major defence mechanism has been seen through MAPK pathway with the help of cell division, stress-related genes expression, cell differentiation, as well as inhibiting the actions of other (Ghori et al. 2019).

Presently, transcriptomics, proteomics and metabolomics are being normally used to decipher the heavy metal tolerance response in plants and its regulatory pathways (Singh et al. 2016). In addition, these omics approaches along with several other genomic approaches have been found to be very useful for the development of improved varieties of plant with boosted abiotic stress tolerance (Mosa et al. 2017). QTLs (Quantitative trait loci) and other candidate genes have been identified in some of the plant species that possess iron, cadmium and zinc tolerance with the help of marker-assisted selection or QTL pyramiding, and these genetically improved plant species can be exploited for further improvement of crops (Courbot et al. 2007; Meyer et al. 2016). In addition, various findings using genetic engineering have also been reported for the improvement of crop, affected by heavy metal stress tolerance (Farinati et al. 2010; Verma et al. 2017). However, these techniques such as genetic engineering and plant breeding require intensive research work and are time consuming. Therefore, alternative strategies or techniques are the need of hour for the improvement of crop production and their productivity under heavy metal stresses. Of note, sustainable agricultural production could be improved using newer strategy such as plant-associated microbes. Various fungi and bacteria have been reported for promoting the plant growth even under heavy metal stress. They impart constructive effects on plants by some of the direct/indirect mechanisms such as formation of biofilms, phytohormones, production of exopolysaccharide and siderophores (Tiwari et al. 2016, 2017). The link between microbial remediation and heavy metal tolerance in plants has drawn the attention of scientific communities in recent years. Subsequently, these plant–microbe–metal association could prove advantageous over heavy metal tolerance in plant and improve the biomass production (Glick 2003; Taj and Rajkumar 2016; Hansda and Kumar 2017). In this regard, the current chapter describes the heavy metal stress and their detrimental effects on plants, signalling responses, functions and detoxification capabilities of phytochelatins, metallothioneins, amino acids, organic acids, chaperones and function of plant-associated microorganisms in stress tolerance to heavy metals.

2 Effect of Heavy Metals on Plants

Fast expansion of industries, urbanization and extreme agricultural amendments have increased the release of pollutants in the environment over the past few decades (Fig. 8.1). Based on the physiological properties of bioactive metals, they are classified into two categories such as redox-active metals (Cu, Cr, Mn and Fe) and non-redox-active metals (Hg, Zn, Al, Cd and Ni) (Valko et al. 2005; Jozefczak et al. 2012). Subsequently, these redox metals were reported to cause oxidative injury through Haber Weiss and Fenton reactions, leading to the production of oxygen free radical species or ROS in plants. This results in protein or cell membrane defragmentation, DNA strand breakage, disruption of cell homeostasis and photosynthetic pigment damage, which may lead to the death of plant cell (Fig. 8.2) (Schutzendubel and Polle 2002; Flora 2009). On the other hand, oxidative stress indirectly gets

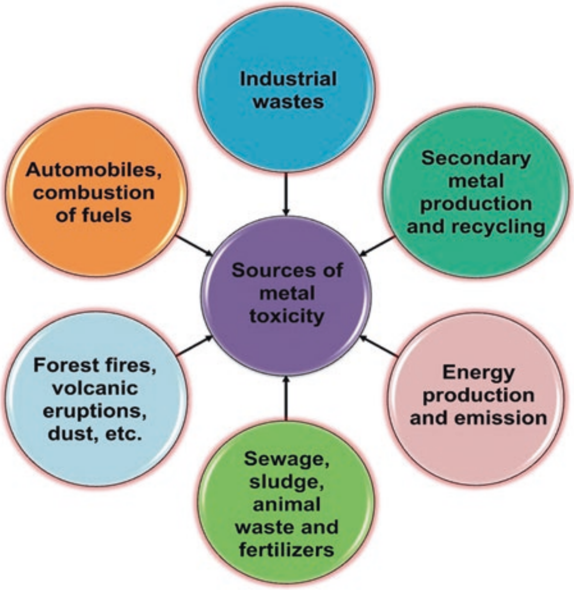
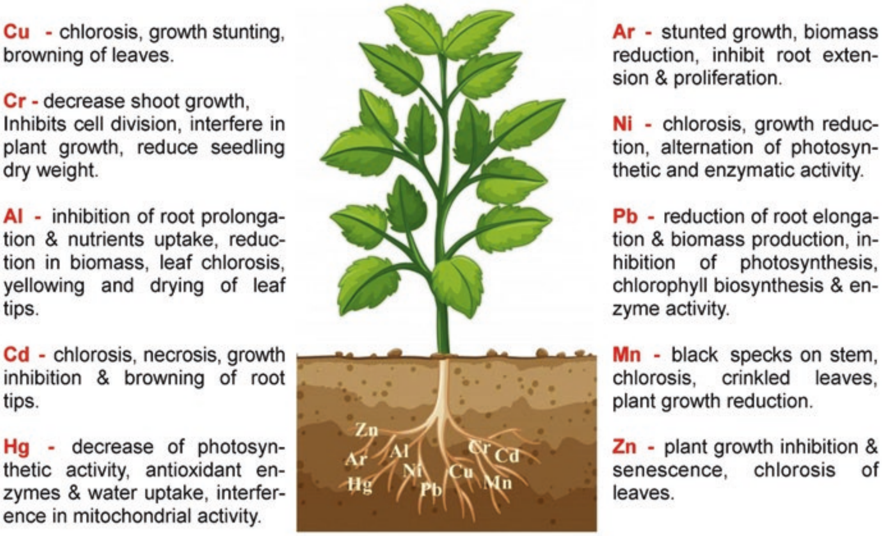


Fig. 8.1 Accumulation of various heavy metals in soil and water ecosystems from varieties of sources



Cu - chlorosis, growth stunting, browning of leaves.

Cr - decrease shoot growth, Inhibits cell division, interfere in plant growth, reduce seedling dry weight.

Al - inhibition of root prolongation & nutrients uptake, reduction in biomass, leaf chlorosis, yellowing and drying of leaf tips.

Cd - chlorosis, necrosis, growth inhibition & browning of root tips.

Hg - decrease of photosynthetic activity, antioxidant enzymes & water uptake, interference in mitochondrial activity.

Ar - stunted growth, biomass reduction, inhibit root extension & proliferation.

Ni - chlorosis, growth reduction, alternation of photosynthetic and enzymatic activity.

Pb - reduction of root elongation & biomass production, inhibition of photosynthesis, chlorophyll biosynthesis & enzyme activity.

Mn - black specks on stem, chlorosis, crinkled leaves, plant growth reduction.

Zn - plant growth inhibition & senescence, chlorosis of leaves.

Fig. 8.2 Symptoms of excessive heavy metal toxicity in plants induced in non-redox active metals through several mechanisms such as glutathione depletion, binding to sulphydryl group of proteins, inhibiting anti-oxidative enzymes or instigating ROS-producing enzymes like NADPH oxidases (Valko et al. 2005; Bielen et al. 2013). In the present chapter, heavy metals are described based upon their mechanism of action in plant biological system, whether they are redox active or inactive metals in plant cells. Heavy metals such as Mn, Cr and Cu can participate in redox reaction in plant and three metals which can participate in non-redox reaction, namely, Al, Zn and Ni are described to showcase their impact on plants, regardless of possessing different redox states.

2.1 Copper (Cu)

Copper is an important element for the plant growth and survival. It is considered an important micronutrient, which performs various essential physiological functions in plants, such as catalysis of redox reaction in chloroplasts, mitochondria and cytoplasm (Fargasova 2004) and as an electron carrier in the course of plant respiration (Yruela 2009). It is also considered an essential component of plastocyanins and cytochrome oxidase and plays a vital role in carbon assimilation as well as in ATP synthesis of plant cell. However, if the concentration of Cu increases above its optimal range, it turns toxic for plants (Lombardi and Sebastiani 2005). Cu generally exists in different states in soil, but plant utilizes only Cu^{2+} (Maksymiec 1997). Copper availability greatly depends on soil pH and its phyto-availability increases with the declining pH (Azooz et al. 2012). Moreover, Cu concentration in soil is usually found in the range of 2–250 $\mu g \cdot g^{-1}$ and it has been reported that a healthy plant can absorb around 20–30 $\mu g \cdot g^{-1}$ DW (Sheldon and Menzies 2005). Toxicity and uptake of Cu by plant are subjected to plant nourishing conditions, concentration of Cu^{2+} in soil, length of exposure and species genotype. Cu overload causes oxidative stress in plants, which further steers to massive damage to macromolecules and membranes on different biochemical pathways and DNA (Ghori et al. 2019) with some noticeable symptoms, that is, inhibited growth and retarded root growth (Bouazizi et al. 2010).

2.2 Chromium (Cr)

Tons of metals get deposited in the water and soil due to industrial discharge and sewage disposal. Cr is one of that metals causing severe contamination or pollution in soil and groundwater (Shanker et al. 2003). It has been reported as a toxic agent for suppressing the development and growth of plants. Plants never absorb Cr directly; instead, Cr transfers and accumulation takes place through the carrier ions such as sulphate or iron. Under reducing conditions, Cr^{6+} gets convert into Cr^{3+}, which is more toxic form of Cr. It can indirectly alter the soil pH and directly affect the sorption of nutrients. Roots of the plants hold the highest concentration of Cr than any other part. It is observed that Cr manipulates some of the mechanisms taking place inside the cell and it can also induce metabolic disorders during seed germination (Emamverdian et al. 2015). Cr depresses the amylase activity and consequently helps in transportation of sugar to embryo axes. It has been reported to cause harmful effects on plant basic metabolism like physiological (water and mineral) and photosynthetic processes. In addition, Cr has also been reported to affect enzyme activities, thus producing ROS. Usually it has been observed that Cr causes toxicity in plants in three different ways: (1) changes in essential plant pigments as well as alteration in anthocyanin synthesis and photosynthesis, (2) increases glutathione and ascorbic acid production that negatively influence plants, (3) induces alternate metabolites production to contribute stress tolerance like phytochelatins and histidine (Ghori et al. 2019).

2.3 Zinc (Zn)

Zn is one of the indispensable elements required for the development and growth of plants. It is considered an essential constituent of several special proteins such as Zn fingers that bind to RNA and DNA and help in maintaining their stabilization and regulation. Zn has been reported to play a significant part in the metabolism of auxin, carbohydrate and proteins, and participate as a co-factor in the enzymatic reaction, as well as it is involved in different enzyme-catalyzed reactions occurring in the plant cells. It is also involved in the formation of pollen and provides resistance against pathogens. Its deficiency causes severe yield loss in crops, whereas its excess amount leads to Zn toxicity along with dire consequences (Ghori et al. 2019). Divalent state of Zn (Zn^{2+}) is the most prevalent form present in soil, which is utilized by plants (Broadley et al. 2007). Its bioavailability/phytoavailability relies on different variables, such as the total Zn concentration in soil, type of clay, presence of other heavy metals, soil's pH, lime content, organic matter of soil and salt amount (Bucher and Schenk 2000; Aref 2011).

Zn concentration in soil in the range of 150–300 $\mu g \cdot g^{-1}$ is considered highly toxic (Yadav 2010). Excess amount of Zn^{2+} in plant cells produces ROS, which negatively affects the integration and permeability of membrane (Mishra and Prakash 2010; Hosseini and Poorakbar 2013). Excess amount of Zn carries out genotoxic effects in plants, which results in genetic-related disorders in plants. Zn toxicity modifies enzyme reactions required for the cells, which leads to plant growth retardation and senescence. Zn toxicities have been reported to cause chlorosis, which spreads from younger leaves to the older leaves with prolonged toxicity. Toxicity of Zn is also seen to cause accumulation of other heavy metals such as Mn and Cu in shoot and root of plants (Nagajyoti et al. 2010), and it also causes phosphorous deficiency that can be noticed by the leaves colour change from green to purplish red (Ghori et al. 2019). It is reported that Zn toxicity inhibits photosystems I and II by effecting photosynthesis and leads to negative effects on overall ATP synthesis, though these effects are reversible.

2.4 Cadmium (Cd)

Usually, Cd is used in pesticides to counter pathogens, leading to the deposition over the surface of soil. Moreover, the limits of Cd use for agricultural soil is around 100 ppm (parts per million). Plants experiencing Cd toxicity shows chlorotic leaves, growth retardation, brown root tips, as well as decline in root growth. Excessive Cd concentration could cause inhibition of Fe (III) reductase, leading to deficiency of Fe (II), ultimately affecting photosynthesis. Subsequently, reduction in chlorophyll synthesis, as well as enzyme inhibition concerning CO_2 fixation, could also affect photosynthesis. Various important metals' (Ca, Mg, K and P) water and physiological pathways uptake reduces the absorptions and translocation of nitrate through deterring nitrate reductase. It is recorded that Cd disturbs the water balance and causing imbalance in the integrity of plasma membrane throughout the course of lipid peroxidation (Nagajyoti et al. 2010). Excessive level of Cd can cause injury to nucleolus and induces irregularity and fragmentation of chromosomes. Applications of Cd in plant cells are to attach sulphur-containing groups (sulphydryl) of several structural proteins to their protein misfolding, which furthermore restricts redox reaction in electron transport chain. High level of Cd leads to calcium displacement with Cd in calmodulin causing inhibition of calmodulin-dependent phosphodiesterase activity (Rivetta et al. 1997). Synthesis and accumulation of proline amino acid get induced by high level of Cd. A study described that plant growth can be accelerated with the lower metal concentration, photosynthetic pigment and biomass, while higher metal concentration leads to decline in these aspects (Tauqeer et al. 2016). During an experiment, treatment of fenugreek plants with Cd displays substantial inhibitory effects (Alaraidh et al. 2018). In addition, root uptake of Cd ions was reduced by biochar along with its bioavailability in rice plants (Rizwan et al. 2018).

2.5 Mercury (Hg)

Hg is the metal which brings no beneficial effect for plants at all; instead, it produces toxicity to plants (Hameed et al. 2017). Hg is found in the soil in many predominant forms such as HgS, methyl-Hg and Hg^{2+} ionic and make it a unique element. Hg can stay longer in the soil, as it is absorbed into the clay, organic matter and sulphides. It can be chelated and precipitated as hydrogen, sulphide, carbonate and phosphate. With the help of anaerobic bacteria, it can be converted into methylated form (Tangahu et al. 2011) and give phytotoxic effects via absorption into plants. Toxicity of Hg can be visibly observed depending upon the area affected. It can bind with proteins of water channels and can block the flow of water to the plant cell. According to the reports, Hg could affect chloroplast and mitochondrial activity by obstructing electron transport chain and cause oxidative stress along with biomolecules oxidation and membrane degradation (Nagajyoti et al. 2010). Further, a study revealed that, when plants are treated with Hg, their genomic template stability gets highly affected due to interference in cellular functions as well as obstruction in plant growth and development led by mercury (Malar et al. 2015).

2.6 *Arsenic (As)*

Since long time, As is believed to be doubtful for living beings; yet, scientific communities are writing so much for its role concerning its effects. In recent years, Ar has been explored for its nutritional benefits, it being used as growth enhancing or promoter, organic arsenic additives for animal feeds. It has been reported that toxicity of other toxic metal such as selenium could be reduced by As (Meharg and Macnair 1992). Moreover, As is considered an analogue to phosphate and competes for same carriers present in plasmalemma of plants. Several plants can tolerate the toxicity of As, as in the grass, generating suppression of K and As carriers, leading to detoxification, and consequently resulting in reduction of As influx (Meharg 1994). As is found in three forms based on its reaction with other components such as organic, inorganic arsenicals and gas, and among the three forms, inorganic As compounds are considered as most toxic.

2.7 *Nickel (Ni)*

Ni is one of the metals of transition element, whose emission has been increased in the ecosystem with the progression of industrialization. Ni and its derivatives have various commercial and industrial uses, as well as it is also a key component in the structures of many important enzymes viz., methyl-CoM reductase, ureases, peptide deformylases, glyoxalases, superoxide dismutases and some hydrogenases. Ni is involved in various biochemical pathways such as acidogenesis, methane biogenesis, ureolysis and hydrogen metabolism. In addition, it helps to maintain stress tolerance or defence, cellular redox state, and increases the efficiency of nitrogen use (Vatansever et al. 2017). Both lower and higher plants require small quantity of Ni for various biochemical reactions (Lin and Kao 2005). Ni divalent ion (Ni^{2+}) is considered the most stable ion used in seed germination and iron uptake, as well as it is reported to be very stable in the biological system and in the environment (Poonkothai and Vijayavathi 2012). The toxicity of Ni in plant could depend on cultivars as well as the plant species, which may range from 25 to 246 $\mu g \cdot g^{-1}$ DW (Iyaka 2011). In addition, the toxicity of Ni occurs through the excess use of fertilizers, sewage disposal, mining, burning of fuel and smelting (Aziz et al. 2015). Plant surviving Ni toxicity displays some physical symptoms such as deficiency of nutrients, chlorosis, disrupted functioning of cell membrane and necrosis. Ni use to mitotic and enzymatic activities impedes with the uptake of other metals, inhibits the nitrogen metabolism and induces oxidative stress.

2.8 Lead (Pb)

Pb is one of the heavy metals causing contamination of soil by mining, smelting and natural weather processes (Ashraf et al. 2015). Contamination of Pb leads to chlorosis, reduction in root length and stunted growth in plants. As soon as Pb enters the cell, it alters the permeability of cell membrane, inhibits sulphydryl-containing enzymes, creating imbalance in mineral distribution and reduces the water content. Pb toxicity inhibits the germination and retards seedlings growth. As Pb dislocates chloroplast ultrastructure and inhibits the production of essential pigments including carotenoids, chlorophyll and plastoquinone, plants' photosynthetic pathways get negatively affected. Additionally, Pb toxicity causes electron transport chain and Calvin cycle blockage, closing of stomatal pores due to scarcity of carbon dioxide (Sharma and Dubey 2005). Studies have reported that growth of plant is notably reduced due to increased Pb levels and it accumulates mainly in roots, followed by petiole and leaf tissues. In plants, Pb stress increases the concentration of anti-oxidative enzymes, and it is concluded that water hyacinths consist proficient mechanisms to stand with Pb toxicity (Malar et al. 2014).

2.9 Aluminium (Al)

Al is known for its inhibitory effect causing retardation of plant growth, especially in acidic soils (pH: 5 or 5.5), as most of the phytotoxic form of aluminium (Al^{3+}) is ubiquitous (Liu et al. 2014). Low concentration of Al in the soil can boost the plant growth (Kidd and Proctor 2000) but aluminium concentration of around 2–3 $\mu g \cdot g^{-1}$ in soils with less than 5.5 pH can prove to be hazardous for majority of the plants (Pahlsson 1990). Al toxicity affects the root maximum, as accumulation of Al takes place there and inhibits root growth in minutes or hours. It also changes the colour of root and thickness of lateral root (Ma et al. 2001). Al toxicity causes enzymatic irregulation of sugar phosphorylation (Rout et al. 2001), and addition of Al with carboxylic functional groups of pectins in root cells (Lidon and Barreiro 2002), or causes difficulty in cell division, which results in the improved structural firmness of cell wall and double helix in DNA (Foy 1992). Due to Al toxicity, plants also face nutritional deficiency that induces stress in shoots just like phosphorus deficiency causing discoloration of leaves, leaf veins and stems, followed by stunting of leaves, yellowing and dead leaf tips, curling and rolling of young leaves and petioles death (Mossor-Pietraszewska 2001; Wang et al. 2006; Bian et al. 2013). One more indication of Al toxicity on plant could be chlorosis over margins and central part of matured leaves and necrotic spots on the border of young leaves (Steiner et al. 2012).

2.10 Manganese (Mn)

Mn is one of the essential micronutrients that participate in various biochemical pathways and growth processes in plants such as respiration, photosynthesis, synthesis of many important enzymes like nitrate reductase, malic enzyme and isocitrate dehydrogenase (Todorovic et al. 2009). Mn acts as an important cofactor for Mn-dependent superoxide dismutase (MnSOD) (Millaleo et al. 2010), involved in nitrogen and carbohydrate metabolism, synthesis of acyl lipids, carotenoid and fatty acid and activation of hormones (Millaleo et al. 2010; Gajalakshmi et al. 2012). Mn contributes to the photosystem II by splitting water molecules into oxygen (Arya and Roy 2011) and its main function is to provide protection from photo damage in photosystem II (Hou and Hou 2013). The most soluble and stable form of Mn is Mn^{2+} in the soil environment. However, soil with less organic matter, low pH and reduced redox potential would boost the Mn^{2+} toxicity and availability to plants (Hue and Mai 2002). Mn can easily translocate from root to shoot, making a visible symptom on its aerial parts due to fast Mn stress reflex as compared to other metal toxicity. Symptoms include darkened leaf veins on older foliage, crinkled leaves, brown spots on aged leaves (Reddy 2006), black specks on the stems (Maksimovic et al. 2012) and chlorosis. Furthermore, manganese toxicity influence leads to the production of 270% and 130% more ascorbate peroxidase (APX) in leaves to counter toxicity of Mn (Gonzalez et al. 1998).

2.11 Heavy Metals and Genotoxicity

Promutagenic damages such as inter and intra-molecular cross-linkage of proteins and DNA, rearrangements, modifications of DNA base, depurination and breakage of DNA strand occur when heavy metals bind with nucleus due to the generation of oxidative species by metal toxicity. It generates promutagenic adduct 8-oxoG (7,8-dihydro- 8-oxoguanine), which in the absence of DNA repair, misses pairs with adenine and leads to transversion of C to T (Kasprzak 1995; Cunningham 1997). In the roots of maize, it is observed that accumulation of Ni in plant cells decreases mitotic activity of meristem. Moreover, when *Helianthus annuus* is exposed with concentration and time-dependent Cd, Cu and Ni, it shows clastogenic effects (Chakravarty and Srivastava 1992).

3 Defence Mechanisms Employed by Plants Against Heavy Metal Stress

To get protection or to tolerate the toxicity of heavy metals, the primary way utilized by the plants is the synthesis of diverse cellular biomolecules. This comprises the synthesis of lower molecular weight protein metallochaperones, mugineic acids, chelators (phytochelatins, putrescine, glutathione, nicotianamine, putrescine, organic acids, spermine), cellular exudates (phenolics and flavonoids), metallothioneins, heat shock proteins (HSPs), hormones (jasmonic acid, salicylic acid and ethylene) and amino acids (proline and histidine) (Sharma and Dietz 2006; Dalvi and Bhalerao 2013; Viehweger 2014). When the synthesized biomolecules are not capable of getting protection from the metal stress, it leads to increase in induction of ROS (Mourato et al. 2012). Protection from heavy metal stress and free radicals, plant self-defence mechanism develops several antioxidant components comprising enzymes such as glutathione reductase, superoxide dismutase, catalase and guaiacol peroxidase, and non-enzymatic antioxidants include alkaloids, carotenoids, phenolic compounds (flavonoids, tannins and lignin), glutathione (GSH), ascorbate (AsA), tocopherols and proline, which act as free radical scavengers (Sharma et al. 2012; Shafeeq et al. 2012). Moreover, in stress-related protein synthesis, as well as various signalling pathways, transduction gets activated, once they sense the heavy metal stress. Furthermore, these pathways lead to stimulation of transcription factors, which can initiate transcription for various stress response genes. In response to various metal stresses, different signalling pathways get activated and induce MAPK cascade, ROS signalling pathway, hormonal signalling and Ca–Calmodulin pathway (Fig. 8.3).

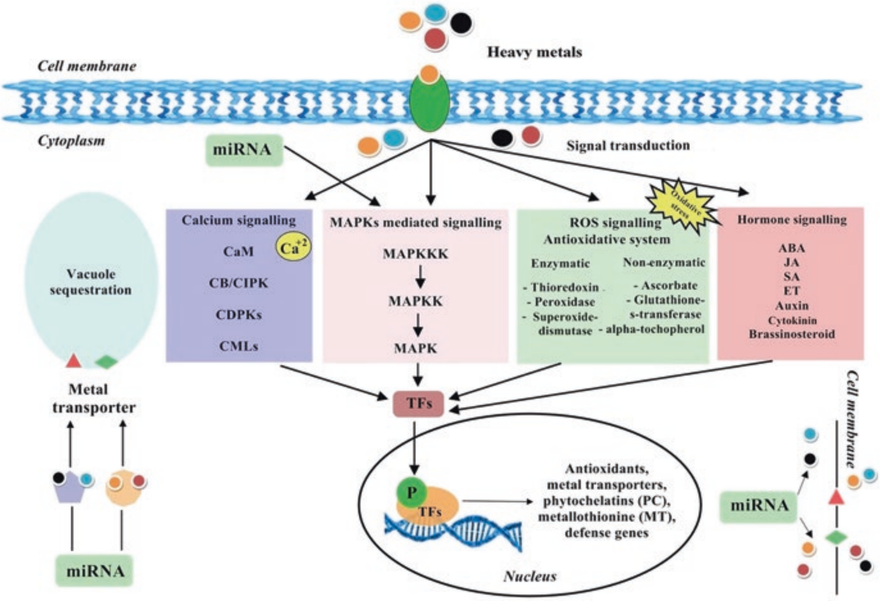


Fig. 8.3 Schematic representation of plants response against heavy metal stress and crosstalk of signalling pathways including MAPKs, calcium, ROS and hormone signalling molecules, which triggers signal transduction to enhance the expression of metal responsive transcription factors (TFs). TFs carried out the regulation of the expression of stress or metal responsive genes (metal transporters, antioxidant genes, metallothionine, phytochelatins and MIR genes (miRNA), which eventually help plant in counteracting the stressed condition

3.1 Primary Defence by Plants

First-line defence of plants acts by proving physical barriers against the metals stress. This changes the outer layer of plant or its morphology such as thick cuticle, biologically active tissues like cell walls and trichrome, when plant encounters with heavy metal stress. In addition, symbiosis of mycorrhiza also creates barriers against the metal stress (Hall 2002; Wong et al. 2004; Harada et al. 2010). Generally, there is more than one mechanism in plants to resist stresses depending upon the site of injury or stress. Therefore, different mechanisms of action target different metal ions and exclude them into different compartments to prevent its exposure to other cellular organelles. As the plant encounters the metals stress, adaptive mechanisms get activated. Citric acid has shown strong binding affinity against heavy metals such as Fe and relatively less affinity for other metals such as Co, Ni, Cd and Zn. Additionally, nitric oxide (NO) and histidine are reported for their capability to chelate heavy metals in plant xylem and cells. NO, an effective signalling molecule, has been reported to monitor the concentrations of hormones, as well as reactive oxygen species, through initiating transcriptional changes in the cell. NO gives both negative and positive types of effects, depending upon absorption and site of NO in the plant cells (Saxena and Shekhawat 2013; Hakeem et al. 2017). It helps in the transformation of oxygen radicals to H_2O_2 and O_2, thereby decreasing the oxidative stress. NO also helps to improve enzyme activity through binding and scavenging hydrogen peroxide. NO activates glutathione synthesis and is also known as antioxidant and can detoxify the free radicals in plant cell (Karplus et al. 1999; Lamattina et al. 2003; Shi et al. 2007; Zheng et al. 2009; Siddiqui et al. 2011).

Plants cell wall is composed of various abundant compounds such as carbohydrates, proteins, amino acids and phenolics, possessing different functional groups such as –SH, –COOH and –OH. These functional groups are attached to trivalent and divalent metal ions. As soon as metal ions enter the plant, it gets surrounded into a separate cubicle and it is removed from the cytosol. These cubicles are usually plant's central vacuole, which is the main metal storage site inside the cell. Vacuolar proton-ATPase (V-ATPase) and vacuolar proton pyrophosphatase (V-Ppase) are the two proton pumps involved in pumping these metal ions into the vacuoles. The vacuoles contain different types of molecules, which are attached to the metal ions to detoxify and sequester them. When a metal enters into the cytosol, they get chelated by metal-binding ligands. Two types of metal-binding ligands can be produced by plants, namely metallothioneins and phytochelatins. The phytochelatin proteins are Cys-polypeptide-rich and are described in reference to Cd toxicity. It was first revealed in yeast undergoing fission stage and was recognized as Cd-binding cadystins A and B. Lately, it has been observed in fungi, plants and cyanobacteria (Gupta et al. 2013). Many metals induce the phytochelatins synthesis, and among them, Cd is highly effective. Phytochelatins bind with Cd with the help of its thiol group in the Cys residue, and the relation among synthesis of phytochelatins and accumulation of metal ions was also reported (Fujita 1985).

Mostly, entry of metal ions in plant cells is restricted by plant root or turned into sequester form and kept inside the cell compartments to detoxify them. However, several special plants known as hyperaccumulators are used to transfer toxic metals via xylem from root to shoot. This plant group tends to show comparatively greater tolerance to heavy metals. The presence of heavy metal transporters, nicotianamine and organic chelators in their shoot cell membrane, leads to heavy metal transport via xylem (Hossain et al. 2012). Some enzymes present in the plants are capable of modifying heavy metals into varying oxidative states or organic compounds. Additionally, these varieties of enzymes along with proteins help in detoxification, transportation, as well as chemical modification of metals, through activation of metal-responsive transcriptional factor 1. These transcription factors are associated with various families like WRKY, basic leucine zipper, ethylene-responsive factor and myeloblastosis protein and play a vital role in gene regulation involving stress of Cd (Yang et al. 2005). Ligand-binding proteins, also known as HSPs, are reported to be involved in countering the oxidative stress. HSP70 and HSP25 are believed to be engaged in the safety of proteins against permanent denaturation, which could occur due to proteolytic degradation and oxidative stress (Zhen et al. 2007; Hossain et al. 2012).

3.2 Phytochelatins (PCs)

Plants have adapted many mechanisms, and out of them, short-chain thiol-rich repetitions of peptides are produced from sulphur-rich glutathione (GSH) with the help of phytochelatin synthase (PCS) enzyme. This enzyme has the basic structure of (γ-glutamyl-cysteinyl) n-glycine ($n = 2$ to 11), which allows it to attach with heavy metals when their concentration reaches toxicity levels (Lee et al. 2003; Chen et al. 2008; Wang et al. 2009; Shukla et al. 2013). PCs manufactured in the cytosols are actively transported to the vacuoles in the form of metal–phytochelatin complexes (Rauser 1995; Manara 2012). It is believed that its transport is interceded by Mg ATP-binding cassette (ABC) transporter or ATP-dependent carrier (Sytar et al. 2013; Gupta et al. 2013; Song et al. 2014). In plants, PCs not only provide defensive mechanism against heavy metals, but it also offers protection against other stressor such as heat, UV-B, herbicide and salt (Zagorchev et al. 2013). In addition, early detection of heavy metal-stressed plants can be done with the help PCs as biomarker (Saba et al. 2013). Production and accumulation of PCs are in the aerial organs and roots, but majority of studies suggest their synthesis and storage in roots only (Yurekli and Kucukbay 2003). Many metals induce the synthesis of PCs, and among them, Cd is highly effective. PCs bind with Cd with the help of its thiol group in the Cys residue, and then synthesized complex is placed with the help of ABC transporters in the vacuoles. The relation between production and accumulation of PCs for metal ions was checked (Fujita 1985). Length of PCs chain varies among and within plant species and also with heavy metal types (Brunetti et al. 2011). PCs in plant under heavy metal stress make synergistic defensive system along with antioxidative enzyme (Chen et al. 2008). A great effort has been made to recognize and clone genes of PCs responsible for its synthesis (Cobbett 2000) and various PCs genes have been identified in distinct plant species such as rice and *Brassica juncea* (Heiss et al. 2003; Shen et al. 2010).

3.3 Metallothioneins (MTs)

MTs are polypeptides or metal-binding proteins in cytoplasm with low molecular weight and are composed of small cysteine. First, they were extracted from equine kidney and later observed in variety of eukaryotes including mammals, plants, invertebrates, fungi, as well as in some prokaryotes (Du et al. 2012). Production of MTs occurs due to translation of mRNA (Macovei et al. 2010). PCs in plants mainly deal with Cd toxicity, whereas these MTs show affinity to deal with Zn, Cu, As and Cd (Yang and Chu 2011). In addition, it exhibits several features and functionality in different organisms according to its occurrence. It is believed that MTs in plant cells are extremely different in terms of their molecular and structural properties (Leszczyszyn et al. 2013), and they are assumed to have more and diverse functions as compared to other living organisms. These ligands present in plant cells help in nullifying the toxicity of heavy metals through intracellular metal ions homeostasis, metal translocation and its adjustment and cellular sequestration (Memon et al. 2001; Gou et al. 2013). MTs are also involved in cellular-related events such as maintenance of the redox level (Macovei et al. 2010), repair of plasma membrane (Mishra and Dubey 2006), cell proliferation, ROS scavenger (Wang et al. 2004) and its maintenance and growth of damaged DNA (Grennan 2011). There are some other endogenous and exogenous factors involved in the production of MTs, such as osmotic stress, release of various hormones, drought, extreme temperatures, nutrient deficiency, natural and dark-induced tissue senescence, viral infections and injuries (Yang and Chu 2011; Manara 2012; Du et al. 2012). MTs have been classified into four subcategories based on residue arrangements of Cys (Huang and Wang 2009). As they exhibit patterns of organ and developmental phase specificity, type 1 MTs are primarily expressed in roots, whereas type 2 MTs' expression typically takes place in shoots, type 3 MTs initiate into leaves, and in the course of fruit ripening, type 4 MTs are observed in plentiful amount in the developing seeds (Kohler et al. 2004; Yang and Chu 2011). Of note, during the extreme sequence diversity of plant MT, each of MT subcategories is further divided (MT1 to MT4) into its respective isoforms (Freisinger 2011). Sugarcane MT2 and Arabidopsis MT4 are subdivided into five subclasses, namely, MT2-1, MT2-2, MT2-3 (Guo et al. 2013) and MT4a, MT4b (Memon et al. 2001). Moreover, all kinds of MTs and their isoforms have been found capable of attaching with heavy metals and to work as metal chelators or storehouse in plants. However, their function in MTs plant, their binding capacity, characteristics for metal affinity and localization of tissue could be varied depending upon the plant species.

3.4 Proline (Pro)

Proline is α-amino acid having five proteinogenic carbons. It can act as a free radical scavenger, metabolic osmolyte, antioxidant, a constituent of cell wall and stabilizer for macromolecules (Seregin et al. 2003; Pavlikova et al. 2007). Pro also gets involved in promoting seed evolvement, extending stem length, and leads the plant growth toward reproductive stage (Zarei et al. 2012). In higher plants, synthesis of Pro occurs non-enzymatically in response to stress, initiated by abiotic and biotic stressors, such as drought, oxidative stress, excessive salinity, heavy metals and increased solar ultraviolet (UV) radiation (Szadados and Savoure 2010). Pro plays various roles during the stressed conditions of the plant, such as recovery, adaptation and signalling (Fidalgo et al. 2013).

There are a number of mechanisms identified through which plants induce Pro. Heavy metals have been reported to induce the accumulation of Pro concentration in plants, leading to water imbalance disorder (Clemens 2006). ROS scavenging stimulated by heavy metal stress through Pro is predominantly conducted via quenching singlet oxygen and detoxifying hydroxyl radicals (Tripathi and Gaur 2004; Mourato et al. 2012). Increase in antioxidant enzyme activities, their protection, cellular redox homeostasis maintenance (Murato et al. 2012), Chl reconstruction, as well as maintenance of intracellular pH (Rastgoo et al. 2011), are linked with Pro activity in the course of exposure to heavy metals. Moreover, Pro has been stated to act as stabilizer for protein and metal chelator (Mishra and Dubey 2006). Proline induction in the plant as response to metal stress is greatly dependent on its concentration, metal specific and organ. Some literature shows that Pro tends to accumulate additionally in shoots of stress bearing plants as compared to their roots (Sharma and Dietz 2006; Zengin and Kirbag 2007). During one experiment performed on cauliflower seedlings, it was observed that initiation of Pro was highest with Hg in comparison with Cd and Zn (Theriappan et al. 2011). When proline was sprayed on the foliar parts of plant growing under heavy metal stress conditions, it showed to be an effective way to reduce toxic effect of metals and boost protective mechanisms against stressors by sharply increasing content of endogenously produced Pro and sustaining to cope under stressed conditions. It was also observed that exogenous Pro can form complex with different metals such as Zn, Cd, Cu, and so, it can reverse inhibition of nitrate reductase activated by metal toxicity (Hayat et al. 2013).

3.5 Arbuscular Mycorrhiza (AM)

AM is a symbiotic mycorrhizal fungus, which is attached to the roots of mostly vascular plants under diverse climatic settings, where it gets photosynthetic assimilations from plants. By virtue of this, AM increases nutrition of mineral status and improves their pollution and stress tolerance capacity (Johansson et al. 2004; Leung et al. 2007; Upadhyaya et al. 2010; Garg and Chandel 2010; Aloui et al. 2011). Various reports showing mycorrhizal symbiosis with plant roots under heavy metal stress call for bioremediation approaches. However, its several as well as essential applications toward plants make it unavoidable to analyse this relationship from defensive aspects, especially against external stressors like heavy metals. Mycorrhizal fungi's principal mechanism acts as a barrier by placing metals within cortical cells (Turnau 1998), producing glutathione and HSPs (Hildebrandt et al. 2007), metal binding to mycelium or cell wall with sequestering them in their organelles or vacuole (Hall 2002). In addition, it participates or chelates metals in the soil through production of glycoprotein or by producing phosphate metal complexes within the hyphae (Andrade and Silveira 2008), and thereafter, it reduces metal strength by heightened root and shoot growth (Mohammadi et al. 2011) to nullify the heavy metals' impact on plant. The different strategies used by AM as soon as facing the heavy metals toxicity put forward that various mycorrhizal fungi species could embrace the remedial application or act in a specific manner that suits the established condition in plant/rhizosphere. One of the studies has shown that when AM is in symbiotic relation with ryegrass (*Lolium perenne* L.), it reduces the transfer of several heavy metals such as Zn, Cd and Ni from soil matrix to various parts of the plant and, as a consequence, causes heavy metal immobilization in soil (Takacs et al. 2001). It is seen that lettuce plants (*Lactuca sativa* L.), along with zinc sulphate stress and with AM fungus (*Glomus etunicatum*), possess higher concentration of cellular protein and increase the content of antioxidant enzymes as compared with the independently surviving ones, due to the presence of sequestered Zn in AM's hyphae, though sugar and chlorophyll content declined in both plants (Farshian et al. 2007).

3.6 Role of Transport Protein in Heavy Metal Stress

Transport proteins has a noteworthy role in the metal homeostasis. With the help of biochemical and molecular techniques, mechanistic characteristics and their physiological roles can be recognized. Heavy metal toxicity and its tolerance can be attained through detoxification and efflux of metal consequent to their respective uptake or by inhibiting the uptake of metal in the roots. Nowadays, uptake of metal via phytoremediation is a hot topic for researchers. Some major transport proteins which are involved in heavy metal transport include (CPx-type) ATPases, which perform a major role in heavy metal transport in higher plants (Williams et al. 2000). In addition, these transportations belong to ZIP gene family, which is responsible for different cations movement like Fe, Cd, Mn and Zn (Guerinot 2000). ZIP family has been seen in several other species besides plants and concerned with the heavy metal homeostasis and is also involved in divalent cations transport. Few ZIP proteins are also found to activate against the response generated from Zn and Fe present in the roots of *Arabidopsis*. Typically, a ZIP protein is composed of eight transmembrane categories with C and N terminal and both exposed to apoplast.

Moreover, first, ZIP transporters were recognized in *Arabidopsis;* it is reported that several ZIP family members transfer metal ions such as Fe, Cd, Mg and Zn. ZIP1 and ZIP3 are chiefly present in roots and get activated predominantly during zinc stress. They are concerned with divalent cations transport and help to activate a particular type of ZIP protein just like *Arabidopsis* in response to Zn and Fe accumulation in the roots. ATZIP4 is present in *Arabidopsis* shoots and roots and the concentration gets increased upon the restriction of Zn and is assumed to play an important role in Zn nutrition (Manara 2012).

Natural resistance-associated macrophage protein (NRAMP), a transporter for metal, is known to be present in various organisms such as plants, bacteria, fungi and animals which help to transfer several metal ions (Nevo and Nelson 2006). In particular, these transporters are expressed in tonoplast membrane and plasma membrane of plant shoots and root. According to Thomine et al. (2000), there is a homology between plant metal transporter family in *Arabidopsis* meant for Cd and Fe and transport to NRAMP genes. NRAMP genes code metal transporters as well as AtNramp are found responsible for the rearrangement of both the metal Cd (toxic) and Fe (nutrient). Curie et al. (2000) described that over-expression of AtNramp1 in transgenic *A. thaliana* plants leads to improved resistance against iron toxicity.

Moreover, movements of Cu throughout the plant take place with the help of Cu transporters (CTR), and according to current reports, Cu transporters are situated on the plasma membrane of various organisms (Puig and Thiele 2002). In *Arabidopsis*, it has been noted for their pollen development and growth as well as it helps to transport of Cu ions. When metals' uptake occurs in root, it moves to shoots through phloem and xylem with the help of chelate complex form with organic components such as malate and citrate. In addition, various categories of transporters get engaged into metal movement within the plant transport, and among them, P type ATPase are mainly utilized for exergonic ATP hydrolysis reactions, which are intended to deal with the heavy metal cations. The CPx-type ATPases or heavy metal ATPases (HMAs) get involved in the soft metal cations transport and are considered the efflux pumps due to their ability to remove metal ions from cells. It helps to accumulate Zn and Cd ions in xylem obtained from around the tissues. A member of HMA family found in *Arabidopsis* is AtHMA4, and if it is overexpressed, it increases Zn and Cd resistance in plants and thereby causes rise in transfer from root to shoot (Mills et al. 2003; Verret et al. 2004). Multidrug and toxic compound extrusion proteins (MATE) is a member of membrane-localized efflux proteins family (Schaaf et al. 2004; DiDonato et al. 2004; Schaaf et al. 2005). Plants usually tend to compartmentalize metals and transport them to vacuole to detoxify metal ions. A highly specific transporter moves various elements present in the tonoplast. Meanwhile, ABC transporter family is subdivided into two groups known as PDR and MRP, and is engaged in sequestering and chelation of metal ions and also transports them to the vacuole. PC and Cd complex is a very common transport method in the vacuole that proficiently is transported by ABC transporters. In the plants, the first identified vacuolar ABC transporter was HMT1 with the ability to transfer its formed complexes in an Mg- ATP-dependent manner in vacuole (Ortiz et al. 1995).

Cation diffusion facilitator (CDF) or metal transfer proteins (MTP) transport family tends to transport metals into vacuoles and apoplast or endoplasmic reticulum from cytosol. Its members consist of six transmembrane domains, histidine-rich region between transmembrane, where C terminal is engaged in efflux of cation (Mäser et al. 2001). In *Arabidopsis*, ZAT1 transporter is expressed and function in sequestration of Zn. Overexpression of ZAT1 transporter provides Zn toxicity resistance and stored up in the roots (Kawachi et al. 2008). CaCA transporter family known as the ubiquitous family usually utilizes Ca ions involved in efflux of Ca^{2+} across membrane with the use of counter ions such as Na^+, H^+ or K^+ (Emery et al. 2012).

3.7 Signal Transduction Pathways Under Heavy Metal Stress in Plants

3.7.1 The Calcium–Calmodulin Pathway

When plants get exposed to heavy metal stress, it negatively affects the Ca channels activity and enhances flux of Ca into the plant cell. Ca acts as the secondary messenger and activates protein calmodulin that monitors the uptake, metabolism and transport of heavy metal. Moreover, Ca–calmodulin pathway was studied under various stress condition of Pb, Ni and Cd, which revealed the importance of calmodulin as an important cellular target. Subsequently, Pb has been found to attach with entire Ca binding sites of calmodulin and increases its activity by 90% (Ouyang and Vogel 1998). In the same way, Mg, Na, Zn and K ions get attached to Ca binding sites of calmodulin with low affinity and other auxiliary sites have been known for other functions of calmodulin. Most of the metals behave like Ca analogues, which activate calmodulin for signal transduction (Snedden and Fromm 2001). Increase in Ca concentration is linked with NO, leading to increase in cytosolic concentration of Ca^{2+} as a response to heavy metal or other abiotic stress (Khan et al. 2014).

3.7.2 Oxidative Stress and Reactive Oxygen Species (ROS)

The maximum studied plant response toward heavy metal stress is production of ROS (Jalmi et al. 2018). Plants' molecular oxygen level gets highly reduced when it encounters with heavy metal stress, which gives rise to highly sensitive intermediate products such as superoxide radicals, hydroxyl radicals and other known species as ROS (Lopez-Millan et al. 2005). It has been noted that ROS free radicals affect cellular membranes by virtue of DNA damage through the processes of chain reaction of lipid and proteins decomposition. Meanwhile, ROS acts as an important plant defence mechanism and it also works as biomarker for different development stages of plant. Production of ROS occurs by cells in normal conditions and is considered a key regulator for certain physiological processes such as senescence, germination and stomatal closure (Yuan et al. 2013). ROS can also regulate gene expressions and act as signalling molecules. Currently, it is revealed that responses generated because of stress in plants are a consequence of a temporal–spatial coordination, which occurs due to ROS and other signals generated via stress-dependent chemicals, compounds and hormones (Baxter et al. 2014). Moreover, there are various antioxidants such astocopherol, glutathione, ascorbic acid and enzymes including peroxidase, catalase, glutathione reductase, superoxide dismutase and ascorbate peroxidase by which plant keeps this versatility bearing species under strict regulation (Sytar et al. 2013). Furthermore, H_2O_2 is the only chemical component which can cross plasma membrane out of all the ROS and this is the only reason for its direct involvement in cell-to-cell signalling (Mittler et al. 2004; Pitzschke et al. 2006). H_2O_2 is also involved in acclamatory signalling, regulation of senescence, stomatal aperture control, inducing tolerance to various stresses, growth and development, and in programmed cell death in plants. H_2O_2 is also reported to be involved in cascades downstream signalling that operate with the help of Ca-binding proteins such as G proteins, calmodulin and instigation of phospholipid signalling. H_2O_2 is observed to control and regulate the MAPK pathway at different stages, as well as it reacts with and transcriptional, kinases, phosphatases, factors (Opdenakker et al. 2013). Moreover, various cells of plants use ROS to produce lignin, which gives protection in cell wall against water loss and pathogen invasion.

3.7.3 The MAPK Cascade

In signal transduction, MAPKs play very important role for being a signalling module. MAPKKK, MAPKK and MAPK are the three modules that cascade usually consists. Moreover, serine/threonine residues get activated with the help of phosphorylation. MAPKKKs are the one of the most varying kinases and they may instigate in a same MAPK cascade all of which eventually unite to one MAPK. Hence, such conditions also reveal the interaction and coordination of varied plant pathways (Jonak et al. 2002; Ichimura et al. 2002). Moreover, phosphatidylinositol and Ca^{2+}dependent protein kinase (CDPK) are essential for the MAPK activation and this was observed during the stress of Cu and Cd (Thapa et al. 2012). Subsequently, MAPK effect is primarily based on its activation time as phosphatases regulate the MAPKs through dephosphorylation. Three types of phosphatase, such as dual specificity (Ser/Thr and Tyr) phosphatases (DSPs), protein tyrosine phosphatases (PTPs) and protein serine–threonine phosphatases (PSTPs), have been identified up till now (Bartels et al. 2010). Plasma membrane-associated phospholipase enzymes synthesize phosphatidic acid, phosphatidylglycerol, phosphatidylcholine and phosphatidylethanolamine, which also activates the MAPK. As a secondary messenger, phosphatidic acid is very important and it is involved in ROS synthesis as well (Bargmann and Munnik 2006).

MAPK cascade and its known mechanism and information in plants toward the metal stress response is still not very clear, but a study described that activation of MAPK on exposure to metals is short term, varying from 5 min to 1 h. Moreover, various MPK (MPK3 and MPK6) inductions have been studied in *Arabidopsis* through H_2O_2 experimental models (Kovtun et al. 2000; Rentel et al. 2004). It is assumed that each abiotic stress trigger deals with the stress in more than one pathway. Several transcriptional factors such as MYB, MYC and bZIP are believed to be involved in downstream response and trigger MAPK signalling due to exposure of heavy metal stress (Roelofs et al. 2008). MAPK controls the expression of genes through transcription factors activation/repression like WRKY and TGA. The WRKY family is classified on the basis of the number of different areas and is divided into three groups and its transcription factors have been noticed involving in various abiotic and biotic stresses. It has been noticed that transcription factors WRKY and Zn finger are involved in plant heavy metal stress. The expression of ZAT12, WRKY25 and WRKY33 was down-regulated through MPK4 during oxidative stress, which suggests the production of ROS, controlled by these transcription factors (Pitzschke et al. 2009). In addition to MPK4, antioxidant enzymes such as Cu/Zn superoxide dismutase and catalase expression in knockout plants also get altered.

3.8 *Involvement of Phenolics and Plant Hormones in Heavy Metal Stress*

Phytohormones such as ethylene and jasmonic acid are known to play an important role in the stress exposure. Their production and regulation are linked with MAPK cascade. These stress hormones are primarily concerned with various abiotic stresses such as salinity and heat stress. During the stress conditions, salicylic acid concentration increases as it plays a vital role to control the abiotic and biotic stress. Moreover, the main functions of this plant hormone are to regulate the concentration of ROS and antioxidants along with its activation in various gene expressions (Hossain et al. 2012). Auxin, salicylic acid and abscisic acid are involved in protection against the stress of heavy metal, which was studied via cis-DNA regulatory element of promoters. In Cd treated plants of *Brassica juncea*, auxin-responsive mRNA was detected (Minglin et al. 2005). Furthermore, nitrilase protein and SAMT gene activation enhance the expression of abscisic and salicylic acids and are detected from mercury-treated *Arabisopsis* and Pea plants, respectively, via proteomics analysis.

Cd has been reported for producing abscisic acid, as well as ethylene, in the plant and these hormones initiate a set of sequence responses in the cell. Apart from plant hormones, amino acids also play a very important role in maintaining the plants' normal health. Accumulation of proline occurs in plants, when it is highly stressed of heavy metal. In addition, free radicals produced due to heavy metals stress can be neutralized with proline. One of the studies on mung bean revealed that exogenously induced proline tolerance against stress of Cd encourages the production of glutathione-metabolizing enzymes and glutathione (Hossain et al. 2010). Polyamines are found in all organisms and in plants; the commonest polyamines are putrescine spermine and spermidine. They play a vital role in the growth and developmental process by scavenging ROS produced by abiotic and biotic stress. Polyamine and proline are considered as a "general adaptation syndrome" response for the plant against metal or other biotic stress and nutrient deficiency (Hossain et al. 2012). Plants also produce large numbers of metabolites and one of them is phenolics and these compounds are synthesized from cinnamic acid. Their synthesis and accumulation get enhanced when plants come across any heavy metal stress (Diáz et al. 2001). In wheat, phenolic contents are greatly increased in response of Ni stress; similarly, soluble and insoluble phenolics are also increased when *Phaseolus vulgaris* is exposed to Cd stress. Phenolic content has been known for its metal chelating properties because it acts as antioxidant. Phenolic compounds containing hydroxyl ion bind with metals, especially Fe and Cu. They also prevent peroxidation of lipid through tricking of lipid alkoxyl radicals which are synthesized under stress condition. A group of phenols such as flavonoids have been reported for their protein-binding capacity which helps to protect phospholipids through hydrogen bonding. Additionally, phenolic compounds act as an antioxidant which scavenges free radical species like superoxide ion and H_2O_2 through giving hydrogen atoms or electrons. Moreover, three structural properties of phenol make them act as antioxidants, and among them, the 3-OH group in C ring and the 5-OH group in the A ring are the most effective in giving electrons (Michalak 2006).

Glutathione is the most common tripeptide thiol present in almost every plant and has an important role to play in providing defence against ROS and sequestering heavy metals by regulating the concentrations of H_2O_2 and various other cellular processes (Cobbett and Goldsbroughn 2002; Freeman et al. 2004; Foyer and Noctor 2005; Mullineaux and Rausch 2005). It is a main site of reduced sulphur storage and transport. It has been present in almost every organelle such as chloroplast, cytosol, vacuole, mitochondria, endoplasmic reticulum, etc., where it maintains intracellular environment, as it is considered as the main redox buffer. Glutathione primarily fights with heavy metal stress via controlling ROS and H_2O_2. It is oxidized upon the degradation of H_2O_2 and the ratio of oxidized as well as reduced form of glutathione is normally used as an indicator of ROS generation and redox balance within the cell. During oxidative stress, its reduced form is directly involved in diminishing the free radicals (Foyer and Noctor 2005). It also prevents cells from impending contact with reactive metals and in detoxification effect of heavy metals via conjugating with dangerous components and transferring them to cell vacuole for detoxification. During the stress conditions, glutathione concentration within the cytosol greatly decreases, which suddenly affects the redox potential of glutathione. Such conditions help plant cell to generate redox signal on exposure of metal stress (Nocito et al. 2006). Apart from all of these functions, glutathione is also engaged in the transcriptional control of different genes. According to Queval and Foyer (2012), approximately 1450 genes are regulated by low glutathione level in *Arabidopsis* mutant lines.

3.9 *Methylglyoxal (MG) Production in Response to Stress in Higher Plants*

MG, a reactive αβ-dicarbonyl aldehyde, is synthesized in various higher plants due to different metal stress responses. MG is instinctively generated through non-enzymatic pathway with the help of inevitable pathways (glycolysis), when a plant is under stress. Moreover, MG can be produced with the help of enzymes using photosynthesis intermediates, known as dihydroxyacetone phosphate (DHAP) and glyceraldehyde-3-phosphate (G3P) (Espartero et al. 1995; Yadav et al. 2005a, b). The rate of glycolysis is high when the plants are facing stress conditions. Similarly, the level of MG is also found higher in plants during the metal stress. In tobacco, the level of MG was observed to increase 1.7-fold, and 1.5-fold in pumpkin during high temperature, salinity, heavy metal stress and drought. Therefore, it has been found that higher amount of MG in plants could be due to higher stress level and its signalling response.

MG is a mutagen and a genotoxic which can cause antioxidant system inactivation, inhibition of cell proliferation, as well as degradation of proteins at a high level in cells (Ray et al. 1994; Wu and Juurlink 2002; Hoque et al. 2010; Hossain et al. 2011). High level of MG can cause breakage in DNA strands and sister chromatic exchange, enhanced point mutations and endoreduplication (Chaplen 1998). According to Saito et al. (2011), synthesis of MG in chloroplast must be detoxified quickly, as it acts as an intrinsic mediator for photo-reduction of O_2 at photosynthesis I, which paves the way for the release of oxygen radicals. Therefore, the main objective of stress tolerance in plants is to swiftly detoxify MG as rapidly as it is produced. In mitochondria, glyoxalase system regulates the cellular metabolism of MG. Two enzymes, glyoxalase I and II, are involved in the two-step reaction for the conversion of MG. Both enzymes work together to translate MG and other 2-oxoaldehydes to their 2-hydroxyacids utilizing glutathione as a cofactor.

4 Conclusion

Plants are the primary source of food and nutrition for all kinds of living organisms. Due to this key reason, heavy metal toxicity in plants is a matter of concern. Not only it is emerging as a main health hazard to humans and plants, it is also posing a serious threat to food safety. Heavy metal toxicity is carried out via targeting important processes and molecules of the plant cell, such as nuclear DNA and proteins, leading to excessive expression of ROS. This imposes dangerous physiological, metabolic and morphological abnormalities in plants. In response, plants activate a series of systems to defend against heavy metal toxicity. Out of all, major processes are metal chelation by forming metallothioneins metal complex or phytochelatins, vacuole sequestration, maintenance of metal intake via transporters and intensification of antioxidative mechanisms. Plants' response against heavy metal toxicity is the result of intricate signalling network, working inside the cell to transmit the intracellular or extracellular response. The most important signalling components involved are hormone signalling, calcium signalling and MAPK signalling, which are discussed in this chapter. Moreover, aside from signalling components, other regulators such as proline, transcription factors, microRNAs and symbiotic association with AM fungi also have a significant contribution in regulation of heavy metal stress. Despite a number of findings to date on activation of various signalling components, decrypting the complete regulatory network of plants' response to heavy metal stresses is still unknown, and still needs further investigation. Moreover, latest reports on the activation of MAPKs by metals and metal transporters and their regulation by MAPKs in yeast and animals also urges the presence of this mechanism in plants. Nevertheless, unsystematic study keeps this field uncanny in plants. Therefore, investigation of regulators of such metal transporters will provide remarkable processes of metal stress tolerance in plants.

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Chapter 9
Morpho-anatomical, Physiological, Biochemical and Molecular Responses of Plants to Air Pollution

Azamal Husen

Contents

1 Introduction

In the recent past, air pollution has become a growing concern. Globally, the number of air pollution incidents is increasing in many cities. The World Health Organization (WHO) has pointed out that climate change is one of the serious health threats of the twenty-first century, and air pollution is considered as the single largest environmental health risk (WHO 2016a). Further, according to a report published by WHO (2016b), indoor and outdoor air pollution is accountable for about seven million deaths every year. It has been estimated that around 800 people per hour, or 13 people per minute, die due to dirty air quality. Almost, four million of these deaths are noticed in the Asia-Pacific region. Commonly associated diseases related to air pollution are stroke and heart disease, respiratory illness and cancers. At the same time, these air pollutants also damage the climatic condition; for instance, fine particles of black carbon from fossil fuel combustion and increase in

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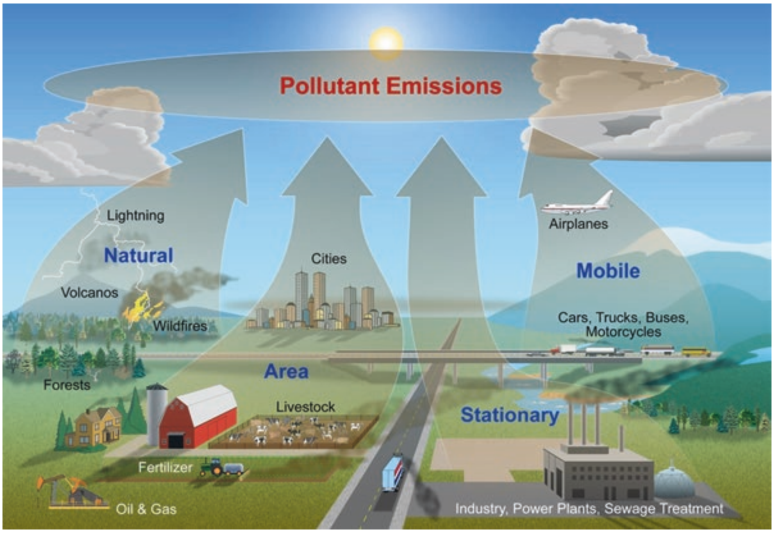

Fig. 9.1 Sources of air pollution. (Adapted from NPA 2018)

the ground level of ozone concentration have shown various adverse impacts at the global level. Several sources of air pollution have been illustrated in Fig. 9.1.

Very recently, in Wuhan (China) due to the outbreak of a new coronavirus (COVID-19), the National Aeronautics and Space Administration (NASA) and European Space Agency (ESA) pollution monitoring satellites have noticed a remarkable decrease in nitrogen dioxide over China. Figure 9.2 represents nitrogen dioxide concentrations, across China from January 1–20, 2020 (before the quarantine) and February 10–25 (during the quarantine). According to NASA, the levels of nitrogen dioxide (a pollutant mainly released by burning fossil fuels) were down as much as 30% (NASA 2020). Similarly, to combat with COVID-19 in India, a 'Janta Curfew' on March 22, and thereafter for 21 days, the world's largest lockdown (with around 130 billion people) imposed from March 24, 2020, to April 14, 2020, resulted in a significant improvement in the air quality of the country as monitored by the Central Pollution Control Board (CPCB). According to the data from CPCB, out of the 103 Indian cities where air quality was recorded, 23 registered 'good' air quality whereas 65 others recorded satisfactory air quality (CPCB 2020). At the same time, new data showing pollution levels over Europe showed a marked decline in pollutants, particularly nitrogen dioxide, over northern Italy (ESA 2020). Thus, certainly, this situation will decrease health-related problems associated with our planet. However, until the genesis of this book chapter, no vaccine has been invented to cure pandemic COVID-19; and the world is facing an unprecedented challenge with communities.

Plants are sessile in nature, and fixed permanently at the site of germination, thus often handle changing and challenging environmental conditions (both abiotic and biotic stresses). Air pollutants (mainly carbon monoxide, lead, nitrogen

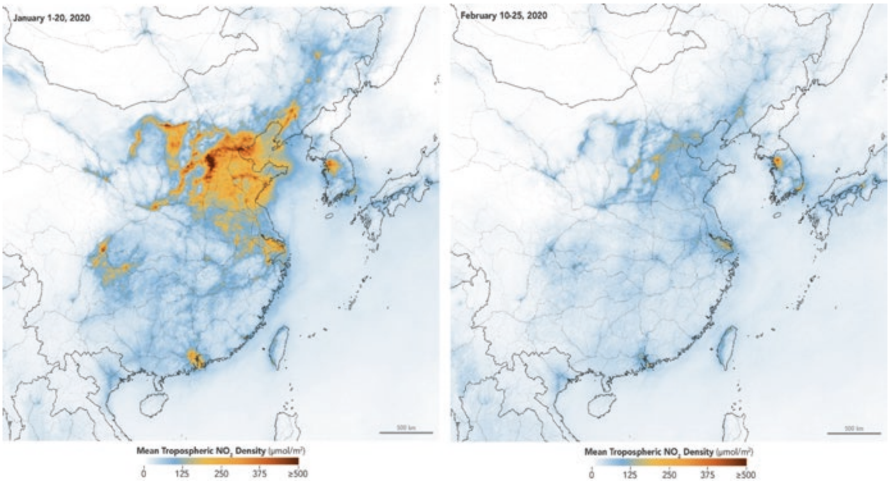

Fig. 9.2 February satellite readings in the troposphere (the lower atmosphere) of nitrogen dioxide, a pollutant primarily released from burning fossil fuels, show a dramatic decline compared to early January when power plants were operating at normal levels. (Adapted from NASA observatory 2020)

oxides, sulphur oxides, ground level of ozone and particulate matters) and/or poor air quality influenced plant health and developed an adverse impact. To escape from such kinds of challenges, plants develop different types of strategies, physical barriers as well as inducible defence mechanisms. Several investigation have been carried out to examine the impact of air pollution on the various aspects of plants such as growth and development, foliar morphology, biochemical changes and various enzymatic activities (Gupta and Ghouse 1987; Husen et al. 1999; Husen and Iqbal 2004; Joshi et al. 2009; Iqbal et al. 2010a, b; Adrees et al. 2016; Yadav et al. 2019; Mukherjee et al. 2019; Ainsworth et al. 2020). Additionally, it has also been noticed that many plant species released some kinds of fine particles such as pollen, spores and other fine particles which have shown to produce allergic response in humans.

Some reports have shown both so-called immediate (acute) and long (chronic) impacts of air pollution on plant growth and developmental processes (Shaibu-Imodagbe 1991; Husen 1997; Jean-Pierre 2020), which may depend on the types of plant species, exposure time, concentration and types of pollutants. Anthropogenic (industrial emission, coal-based power plant emission, vehicular emission, etc.) or naturally produced air pollutants, often transported from one place to another, create haze, get deposited on the various plant species which create changes/harmful impacts on plants' biological activities (Fig. 9.3). Further, their impact may vary according to the source of pollution, types of pollutant, season, wind direction and velocity, exposure duration, plant species and so on.

Coal-based power stations emit many pollutants such as sulphur dioxide, nitrogen oxides, mercury, lead, particulates and various other heavy metals and damage plant growth and production (Husen et al. 1999; Nighat et al. 1999, 2008; Husen

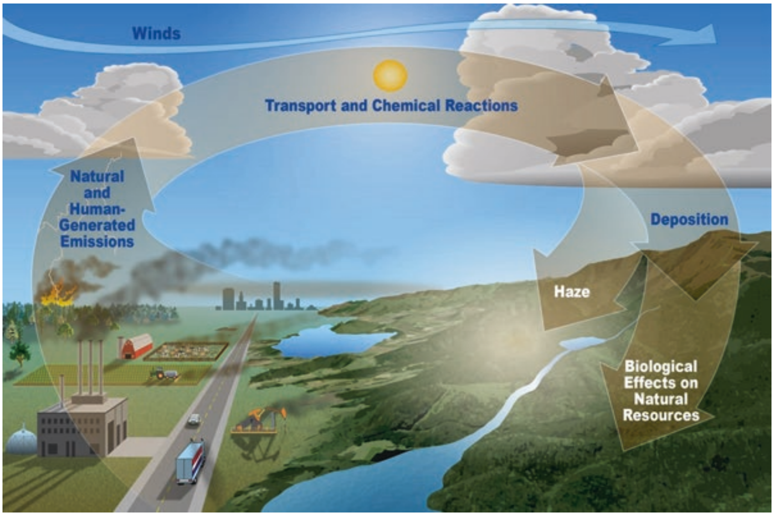

Fig. 9.3 Wind can move air pollutants short or very long distances before they cause harmful impacts. (Adapted from NPA 2018)

and Iqbal 2004; Iqbal et al. 2010a, b; Qadir et al. 2016, 2019). These pollutants have shown visible as well as an invisible injury on vegetation. In this case also, the extent of injury depends on the concentration of gases, fumigation frequency, exposure duration and other prevailing environmental conditions. Additionally, fly ash is another inorganic product obtained by the combustion of organic coal in boilers at power stations. Some reports have shown that fly ash when applied to soil at low doses increased plant growth and decreased at high doses (Pandey and Singh 2010; Shaheen et al. 2014; Yao et al. 2015). However, in terms of positive response, these studies warranted to evaluate the potential risk caused by the presence of heavy metal in fly ash; thus, its feasibility to use in agricultural practices need detailed investigations. Further, it has also been reported that some plant species have been used for remediation and/or mitigation of pollutants from air, soils and water (Nivane et al. 2001; Iqbal et al. 2015; Wei et al. 2017). In this situation, usually plants assimilate, degrade or modify the toxic impact of pollutants to less toxic ones and plants are able to utilize them. Thus, these plant species could be utilized in passive monitoring or mitigation of air pollution in a particular locality.

A number of pollutants (carbon monoxide, nitrogen oxides, sulphur dioxide, ammonia, methane, nonmethane volatile organic compounds, particulate matter and toxic heavy metals) are released by vehicles (Bell et al. 2011). Out of these, toxic metals such as lead, cadmium, manganese, molybdenum, copper, antimony, zinc, arsenic, platinum, palladium and rhodium are the principal pollutants and have been observed as the main contaminants (Wang and Zhang 2018; Khalid et al. 2018). It has also been reported that roadside plantation reduced particulate matter pollution as they are deposited on the leaf surface (Heisler et al. 1995; Steffens et al. 2012; Brantley et al. 2014; Tong et al. 2016; Baldauf 2017; Khalid et al. 2019). In this connection, leaf types, leaf thickness, presence of leaf hair or trichomes, epicuticular wax, etc. are important in terms of pollution load reduction. Baldauf (2017) reported that roadside plantation influenced nearby air quality, both in a positive and negative way. Thus, if appropriately planned, plantation barriers can be used to upgrade on-road or near-road air quality status, either alone or in combination with some kind of solid noise barriers.

In the light of the above-mentioned discussion, the present chapter was undertaken to understand and assess the current advances in the development of plant response to major air pollutants, with special reference to structural, functional, biochemical/metabolic responses, gene expression and yield attributes.

2 Responses of Plants to Air Pollution

Gaseous air pollutants are absorbed by the leaf surface or stomata (Jean-Pierre 2020) (Fig. 9.4). Additionally, these pollutants, in very low concentrations, may also enter through stems and trunk. Depending on the type of leaf surface (leaf structure, thickness, presence of leaf hair or trichomes, epicuticular wax, water

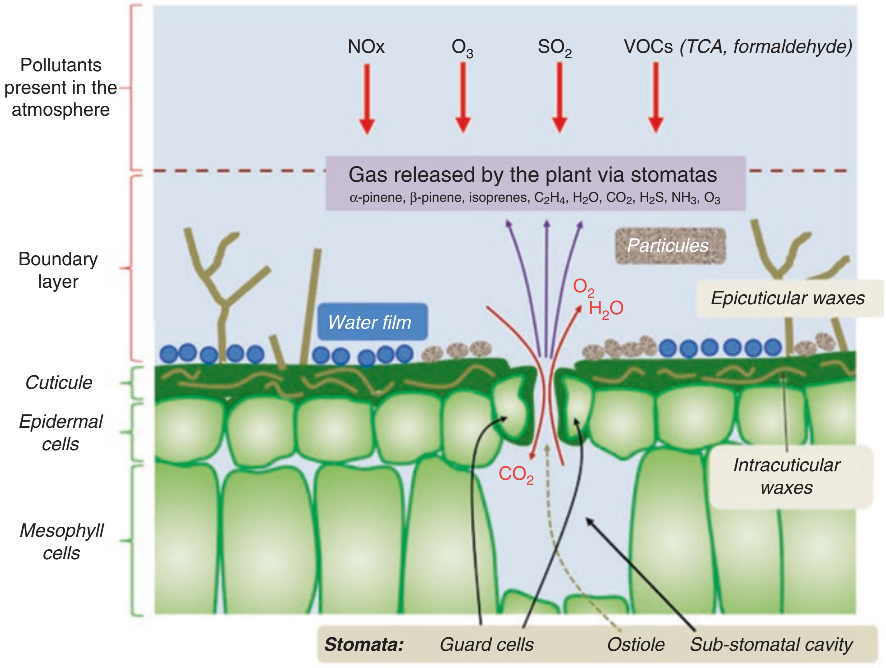

Fig. 9.4 Plant leaf surface and stomata – preferred site of gaseous pollution exchange. (Adapted from Jean-Pierre 2020)

film, etc.), concentration/type of air pollutant, they may penetrate and/or react on the leaf surface.

Occasionally, the reaction of air pollutants on the leaf surface forms acids which are more toxic than the pollutants (Smith 1990; Husen 1997). During these exercises, plants may experience temporary or even permanent damage, for instance chlorosis, bleaching, mottling and necrosis (Husen et al. 1999; Cavanagh and Clemons 2006). For instance, normal (pollution-free site; Jamia Hamdard, New Delhi, India) and polluted (maximum pollution load area of Badarpur Power Plants, New Delhi, India) sites were chosen for comparative investigation. In this experiment, *Datura innoxia* plants grown in polluted area/sites have shown various symptoms on the leaf as presented in Fig. 9.5. Overall, exposure to sulphur dioxide, nitrogen oxides, ozone, particulate matters and some heavy metals have been reported to alter important morpho-physiological (biomass, leaf traits, gas exchange characteristics, etc.), anatomical, biochemical/metabolic and enzymatic activities (Yunus and Iqbal 1996; Husen et al. 1999; Husen and Iqbal 2004). Further, the salient findings have been discussed under the following subheadings.

2.1 Response to Sulphur Dioxide Pollution

Sulphur dioxide is produced by combustion of coal, fuel oil and gasoline (because these fuels contain sulphur), and in the oxidation of naturally occurring sulphur gases, for instance, volcanic eruptions. However, the largest source of sulphur dioxide in the atmosphere is the burning of fossil fuels by coal-based power stations and other industrial amenities.

Sulphur dioxide has been investigated more extensively than the other pollutants. Sulphur dioxide shows acute visible injury to plant leaves at high concentrations (Jacobson and Hill 1970; Husen 1997) and invisible injury, involving physiological and biochemical changes at low concentrations (Husen 1997; Husen et al. 1999; Husen and Iqbal 2004; Nighat et al. 1999, 2008). It has also been noticed that sulphur dioxide is the major air pollutant produced during the combustion of coal (Smith 1990; Iqbal et al. 2000). In fact, plants growing in the vicinity of a coal-based power station are exposed to an array of air pollutants which interact and affect plant morphology and metabolism. For instance, let us compare a case study: in *D. innoxia* (Husen 1997), the number of leaves per plant was slightly reduced but leaf length, single leaf area and total leaf area per plant were significantly reduced in the vicinity of a coal-based power station, compared to those at a normal site. In *D. innoxia* plants, the biomass of leaf, stem and root were increased significantly under the polluted condition (Husen 1997). This increase might be due to the greater availability of minerals and trace elements of fly ash origin, namely, sodium, potassium, calcium, magnesium, boron, sulphate (Elsewi et al. 1981; Wong and Wong 1989), copper, zinc, molybdenum and selenium (Furr et al. 1978) and a negligible amount of carbon and nitrogen (Carlson and Adriano 1993) to the growing plant. Some studies confirm that plant biomass may increase due to the presence of fly ash

Fig. 9.5 *Datura innoxia* leaf from (**a**) normal site (pollution free) and (**b**) polluted sites (maximum pollution load) showing the difference in size, and symptoms like necrosis, chlorosis, curling surface and lesion of burn. (Adapted from Husen 1997)

in the soil (Khan and Khan 1996; Singh et al. 1997). In the upper epidermis of *D. innoxia*, stomatal density, stomatal index and size of stomatal pore increased at the polluted site, showing a significant per cent variation. The epidermal cell density, trichome density and trichome size, however, showed a significant loss, whereas the loss was insignificant for stomatal length (Husen 1997) (Fig. 9.6).

In the lower epidermis of *D. innoxia*, stomatal density, stomatal index and size of stomata as well as stoma increased at the polluted site and showed a significant

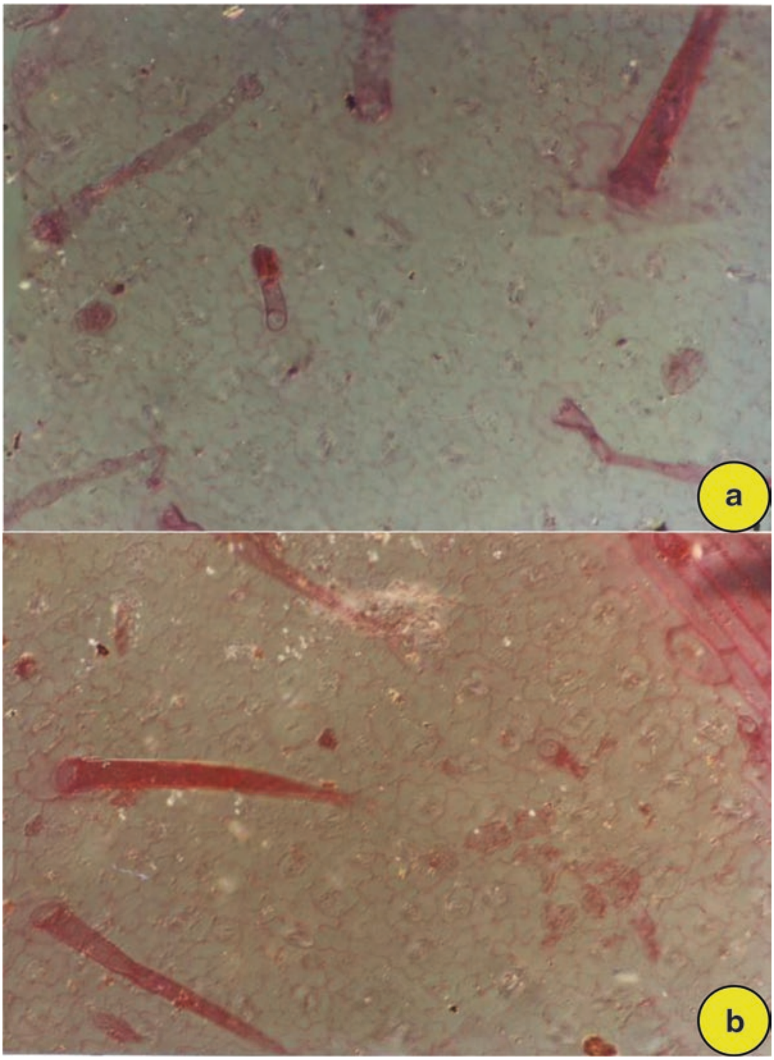

Fig. 9.6 Upper epidermal peel mount from *Datura innoxia* leaf showing the difference in size and shape of epidermal cells as well as size, number and aperture of stomata from normal (pollution free – **a**) and polluted sites (maximum pollution load – **b**). Epidermal cells decreased in the polluted sample, whereas stomata with increased size and aperture were more in number in the polluted sample. (Adapted from Husen 1997)

variation, while epidermal cell abundance, trichome length and trichome density underwent a reduction which was insignificant for the last parameter (Husen 1997) (Fig. 9.7). In rice plants, exposure to sulphur dioxide at concentration have also shown foliar injury at different levels (Agrawal et al. 1982).

Further, in *D. innoxia* plants, the studied metabolic activities (proteins and carbohydrates) also varied, in different plant parts at the normal and polluted sites.

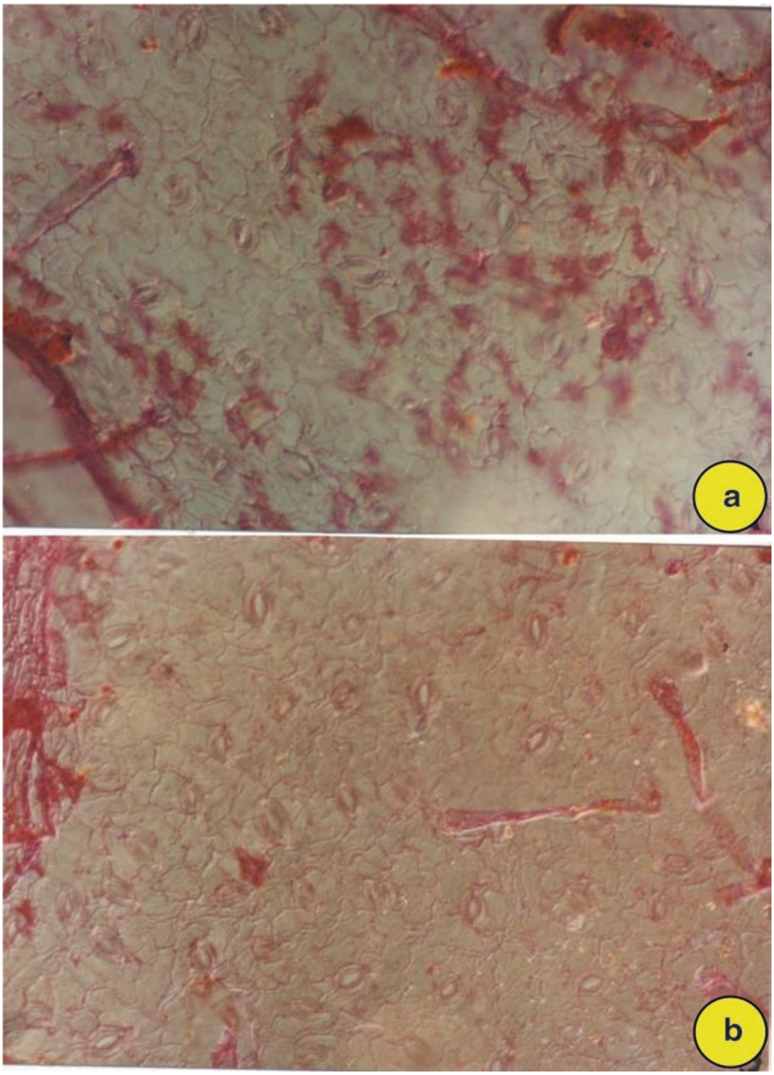

Fig. 9.7 Lower epidermal peel mount from *Datura innoxia* leaf showing the difference in size and shape of epidermal cells as well as the size, number and aperture of stomata from normal (pollution free – **a**) and polluted sites (maximum pollution load – **b**). Epidermal cells decreased in the polluted sample, whereas stomata with increased size and aperture are more in number in the polluted sample. (Adapted from Husen 1997)

Soluble protein in *D. innoxia* leaves at the pollution stress site was noted; this might be due to the toxic effect of sulphur dioxide levels on protein synthesis. This could be due to the decreased rate of photosynthesis, protein synthesis inhibition and/or enhanced protein degradation (Sij and Swanson 1974; Constantinidou and Kozlowski 1979; Husen et al. 1999). A reduction in the content of protein due to exposure to sulphur dioxide has also been detected in many other species. It is known that sulphur dioxide fumigation inactivates enzymes involved in protein synthesis (Nandi et al. 1990; Agrawal and Deepak 2003; Hamid and Jawaid 2009). A reduction in the nitrate reductase activity of *D. innoxia* leaves under pollution stress (Husen 1997) might also be associated with the rate of photosynthesis. Protein, amino acids and certain enzyme activities in leaves, buds and shoots show qualitative as well as quantitative variation with drought, salinity and pollution stress conditions (Parui et al. 2001; Rezanejad 2009; Husen 2010; Getnet et al. 2015; Embiale et al. 2016; Husen et al. 2014, 2017, 2018, 2019; Hussein et al. 2017; Sheng and Zhu 2019). In *D. innoxia*, reducing sugar increased in roots but significantly declined in leave and stem at the polluted site might be due to fly ash deposition in soil (Husen 1997).

Stomatal conductance in the leaves of *D. innoxia* was significantly reduced at the polluted site, confirming some earlier findings (Field et al. 1995; Kull et al. 1996; Kellomäki and Wang 1997; Nighat et al. 2000) which could be because of the reduced rate of photosynthesis (Farage et al. 1991). The photosynthetic rate was significantly suppressed (63.92%) at the polluted site (Husen 1997). Chloroplast disruption could be the reason for the decrease in the net photosynthesis at low concentrations of sulphur dioxide such as 0.035 ppm (Black and Unsworth 1979). Sulphur dioxide may directly affect the process of photosynthesis because its various intercellular derivatives and photo-induced oxidizing free radicals interfere with the metabolic pathway (Malhotra and Khan 1984). Inhibitory effects of sulphur dioxide and oxides of nitrogen pollutants on photosynthesis and carbon dioxide exchanges of plants are well documented. Dust in stomata may prevent stomatal closure which tends to increase the uptake of gaseous air pollutants and water loss (Fluckiger et al. 1979). Both the intensity and direction of stomatal response to carbon dioxide may change due to environmental influence (Morison and Gifford 1983; Mansfield and Atkinson 1990). The intercellular carbon dioxide concentration was raised under pollution stress. In *D. innoxia* plants, the amount of chlorophyll a, b, total chlorophyll and carotenoids decreased significantly under pollution stress conditions (Husen 1997). Chlorophyll loss due to sulphur dioxide pollution has been reported for other species too. Chlorophyll damaged by sulphur dioxide is mainly observed either by its conversion to pheophytin (Rao and LeBlanc 1966) or production of superoxide radicals by the reaction of sulphite with chlorophyll under illumination (Shimazaki et al. 1980). In *D. innoxia* plants, damage to chlorophyll 'a' was relatively greater than that to chlorophyll 'b' in the polluted atmosphere, thus showing a greater degree of sensitivity for the former. However, both the chlorophylls may be equally susceptible in some other species (Singh et al. 1990a). Total chlorophyll and carotenoid contents decreased in tomato leaves with increasing sodium metabisulphate ($Na_2S_2O_3$) concentrations (Singh et al. 1990b). However, carotenoids were more sensitive than chlorophyll to the pollution hazards (Kondo et al. 1980; Khan and Usmani 1988). Sulphur content in *D. innoxia* leaves, stem, roots and seeds of the pollution-affected plants showed a highly significant increase, about 224%, 61%, 54% and 272%, respectively (Husen 1997). Accumulation of sulphur in plant tissues has been used as an indicator of sulphur dioxide stress in air pollution studies. Pollen viability of *D. innoxia* plants was significantly decreased under pollution stress thus indicating a negative effect on the reproductive capacity of the stressed plants (Husen 1997). Reduced pollen viability due to air pollution has also been reported earlier (Ostrolucka 1989; Bellani and Paoletti 1992).

Comparative data on stem anatomy of *D. innoxia* plant growing at the normal and polluted sites were examined (Husen 1997) (Figs. 9.8 and 9.9). There was a significant increase in the width of vessel elements and fibres in the stem at the polluted site, the gain being to the tune of 11% and 23%, respectively. The length of both the cell types registered a decrease which was quite significant in the case of fibres. The number of vessels per unit transverse area also decreased, though it was insignificant. Stem diameter in the second internode from the ground was greater at the polluted site. The area occupied by the cortex and vasculature was also greater. However, the area of the pith was considerably reduced showing nearly 24% loss. Additionally, the comparative root anatomy of *D. innoxia* plant growing at the normal and polluted sites were also investigated (Husen 1997) (Figs. 9.10 and 9.11). The overall size of fibres and vessel elements in the root

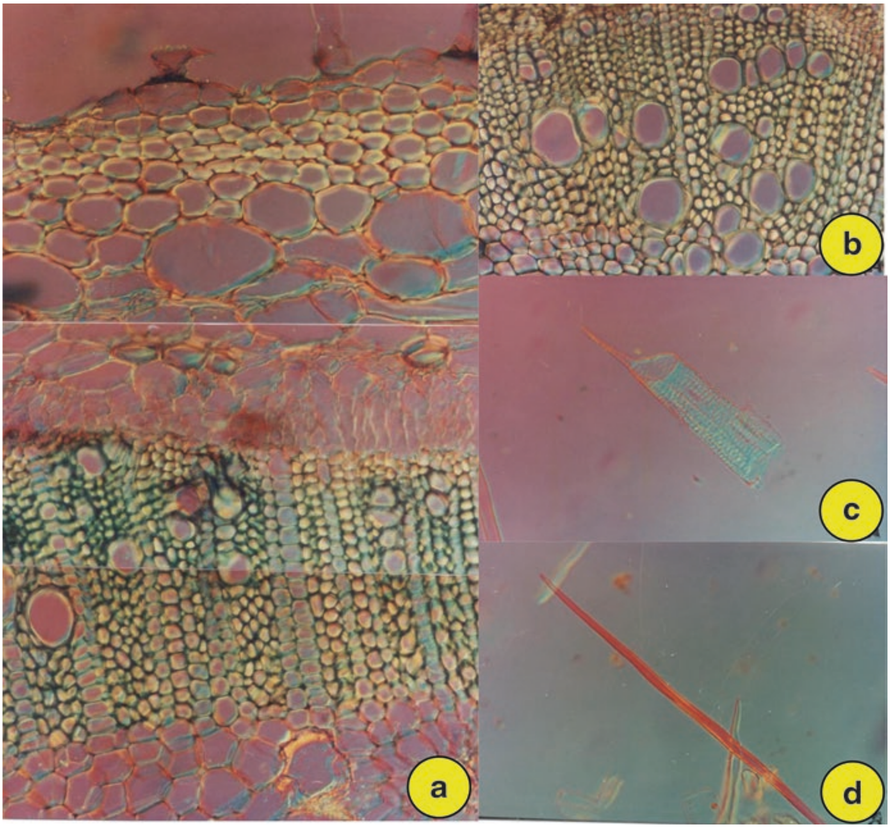

Fig. 9.8 Transverse section of normal stem of *Datura innoxia* (**a**) number and size of vessel (**b**, **c**) and fibre (**d**). (Adapted from Husen 1997)

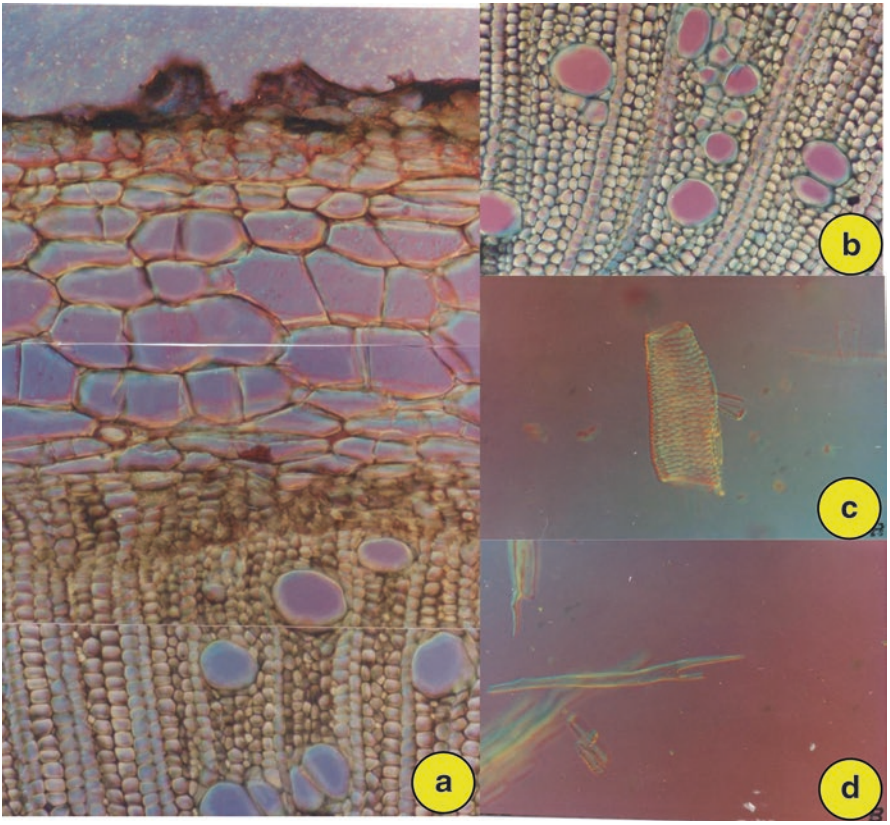

Fig. 9.9 Transverse section of polluted stem of *Datura innoxia* (**a**) number and size of vessel (**b**, **c**) and fibre (**d**). (Adapted from Husen 1997)

increased insignificantly at the polluted site. The total number of vessels per unit transverse area exhibited an insignificant increase in the stressed samples. Root diameter was significantly greater, showing about 30% gain. The area of the cortex was greatly reduced by about 57%, while areas of vasculature and pith increased more. Further, an insignificant reduction, showing only 6% variation, was observed in the vulnerability ratio (VR) of the stressed plant, hence their degree of xeromorphy correspondingly increased. Taken together, the size of the xylem cells such as fibres and vessel elements may increase or decrease due to coal-based pollution. Such studies have also been carried out both in the root and stem (Ghouse et al. 1985, 1986; Iqbal et al. 1986, 1987a, b; Iqbal et al. 2010a, b). Further specific reason for these bidirectional variations has yet to be identified (Pozgaj et al. 1996). In *D. innoxia*, vessel frequency declined in the polluted stem and increased in the polluted root. Of the areas of the cortex, vasculature and pith, the first was significantly reduced in the root, whereas the last did so in the stem at the polluted site. A slight decrease in stem axis circumference and in the proportion of cortex and xylem was reported earlier in *Cajanus cajan* (Ghouse et al.

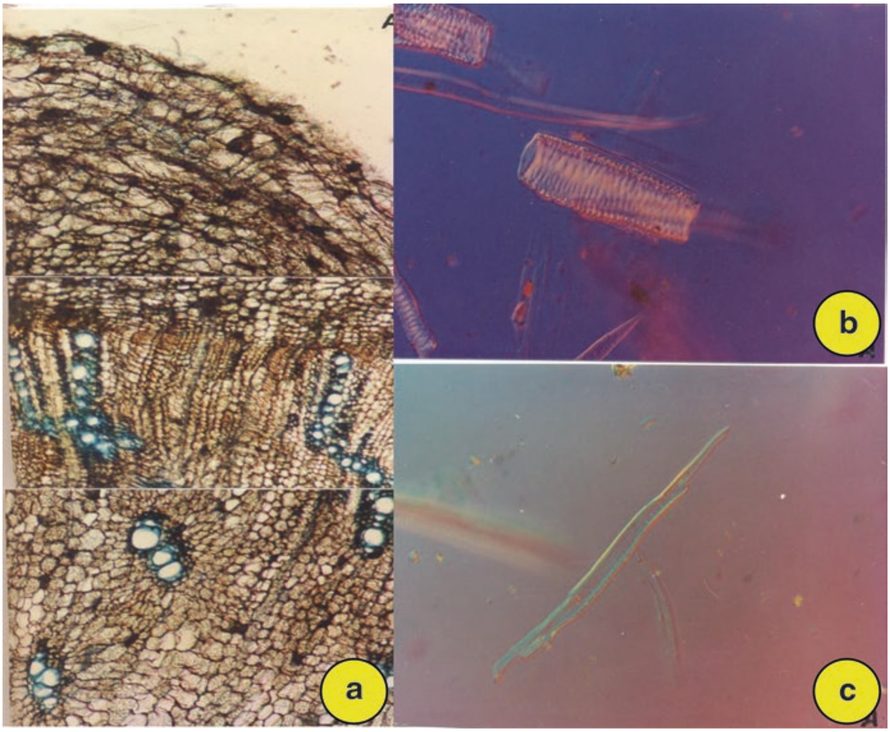

Fig. 9.10 Transverse section of normal root of *Datura innoxia* (**a**) size of vessel (**b**) and fibre (**c**). (Adapted from Husen 1997)

1989). Pollutants may reduce xylem increment even when visible leaf symptoms are absent (Thompson 1981). Decreased xylem increment in mature trees could be established by growth sign analysis (Thompson 1981; Pozgaj et al. 1996). Likewise, a decrease in stem pith of *Xanthium strumarium* under coal-smoke pollution was observed (Ansari et al. 1993). In many cases, roots of the polluted plant show better growth though stem growth declines. This could be due to deposition and uptake of fly ash that has all mineral nutrients, except nitrogen, required for the normal growth of a plant. Ariel plant parts possibly remain away from drawing benefit from this situation because of the impact of air pollutants to which they are sensitive. Air pollution influences not only the amount but also the structure of wood (Pozgaj et al. 1996). The mesophyll as well as the VR of wood, an indicator of ecological adaptation of woody plants, decreased in *D. innoxia* under stress, thus showing a tendency of the plants towards becoming more xeromorphic in characters. Overall, several investigations have been carried out by different researchers to examine the impact of sulphur dioxide and in general other air pollutants on the plant growth and survival, foliar morphology, stem and root anatomy, and biochemical changes and various physiological aspects at contaminated sites. And, the extent of injury to plants depends on the concentration of gases, fumigation frequency, exposure duration and other prevailing environ-

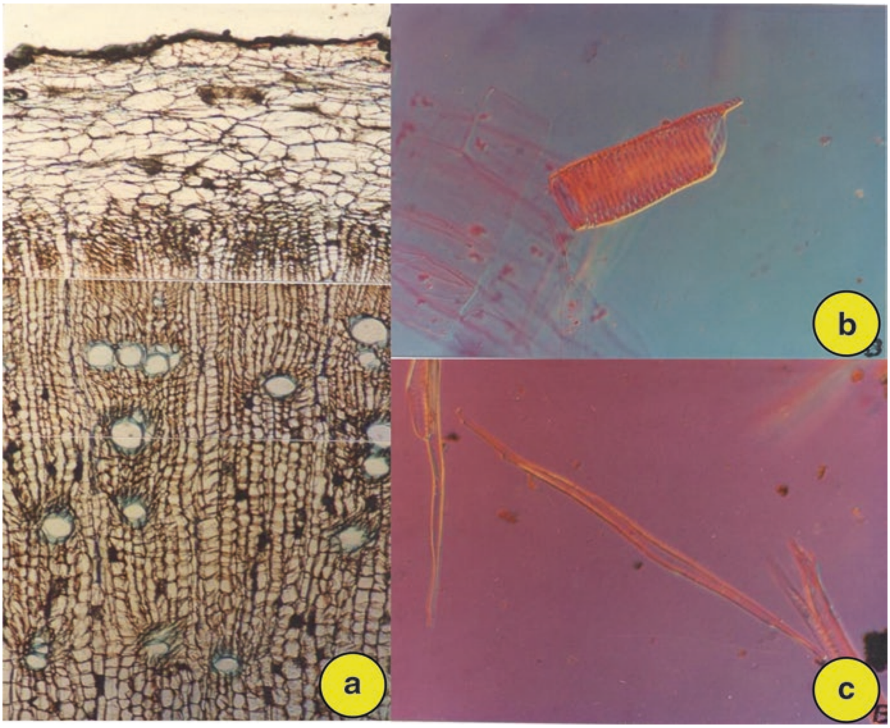

Fig. 9.11 Transverse section of polluted root of *Datura innoxia* (**a**) size of vessel (**b**) and fibre (**c**). (Adapted from Husen 1997)

mental conditions (Yunus and Iqbal 1996; Husen 1997; Husen and Iqbal 2004; Iqbal et al. 2010b; Khalid et al. 2019).

2.2 Response to Nitrogen Oxide Pollution

Nitrogen oxide and other oxides of nitrogen react with other chemicals in the air and produce nitrogen dioxide. The major anthropogenic sources are the combustion of fossil fuels such as coal, gas and oil. Additionally, it is produced from nitric acid preparation, welding and using explosives, refining of petrol and metals, commercial manufacturing and food manufacturing. However, natural sources are volcanoes and bacteria. Globally, its emission has been increasing (NASA observatory 2020) due to the higher industrial production and other associated automobile activities. It is also a precursor of secondary air pollutants, that is, ozone and particulate matter (Rahmat et al. 2013; Bermejo-Orduna et al. 2014; Marais et al. 2017). Nitrogen oxide may reach the plant system either directly through its foliar deposition or indirectly through rainwater or soil deposition. It enters the leaf, either through open stomata or the cuticles; of these, the access through the stomata is dominant. Its entry is governed by various factors like plant species, types of leaf, exposure duration and concentration. Researchers have two opinions about the plant response to nitrogen oxide. The first opinion is that, by being metabolized and incorporated in the nitrate assimilation pathway, nitrogen dioxide is able to form organic nitrogenous compounds and not harm plant leaves (Middleton et al. 1958; Stulen et al. 1998). Further, the second opinion is that many plants show both low amounts of NO_2-N incorporation into total plant nitrogen and resistance to NO_2 (Nakaji et al. 2001). In an investigation, Mansfield et al. (1982) reported that at very high levels (up to 3500 ppb) of NO_X (mainly NO) in glasshouses have reduced plant growth. Takahashi et al. (2005, 2014) and Takahashi and Morikawa (2014) recognized atmospheric NO and NO_2 as either detrimental or beneficial for plant development. Exposure to nitrogen oxide triggered physiological responses such as antioxidant enzyme activities, N metabolic activity and components/distribution of nitrogenous metabolic products in various plant tissues (Norby et al. 1989; Teklemariam and Sparks 2006; Liu et al. 2015; Vighi et al. 2017). Further, it has been reported that at a lower dose (0.1 $\mu l\ L^{-1}$ NO_2) insignificantly affected 1-year-old *Buxus sinica* seedlings' height, leaf area and dry weight (Dochinger and Jensen 1985) and at 0.5 $\mu l\ L^{-1}$ NO_2 significantly stimulated the leaf growth of Carolina poplar (*Populus canadensis* Moensch 'Eugenei') and Lombardy poplar (*Populus nigra* L. 'Italica'); nonetheless, a higher dose (1 $\mu l\ L^{-1}$ NO_2) significantly decreased stem growth (Eastham and Ormrod 1986). In a recent study, Sheng and Zhu (2019) suggested that NO_2 causes a pollution risk to plant, but the antioxidant activities play a significant role in the protection of plant against NO_2-induced oxidative damage.

2.3 Response to Ozone Pollution

The surface level of ozone (three atoms of oxygen) is formed by the reaction of gaseous pollutants in the presence of sunlight. Further, its photochemical productions are influenced by variations in solar irradiation, temperature and precursor amount and relative proportion (such as methane, carbon monoxide, volatile organic compounds and nitrogen oxide compounds). Accordingly, its surface concentration may vary from one place to another, and can be transported over long distances by wind. Thus, they may affect even productivity of plants in rural areas and on agricultural lands. Additionally, the natural ozone layer is found in the lower portion of the stratosphere (15–35 km) above the earth surface. Usually, its thickness varies geographically, and from one season to another (NOAA 2008). This is a protective ozone layer and does an important job. It absorbs the radiation (ultraviolet light) from the sun, preventing it from reaching the earth surface. Gradual thinning or depletion of the stratosphere ozone layer due to the reaction of ozone and chlorofluorocarbon gases is a major environmental problem since it increases the ultraviolet radiation that reaches the earth surface. These radiations are linked to many injurious effects in humans, animals, plants and natural ecosystem. However, technically, ozone in the troposphere is considered as a greenhouse gas which may also contribute to climate change (NASA 2018).

Plant response to elevated ozone has been investigated by many researchers (Fuhrer et al. 2016; Jolivet et al. 2016; Li et al. 2017; Yendrek et al. 2017; Mills et al. 2018; Shang et al. 2019; Peng et al. 2019; Ghosh et al. 2020). Ozone-induced damages in plants occur with stomatal entrance, lead to the production of ROS causing oxidative stress, and finally, influence the process of photosynthesis, plant growth and accumulation of biomass in various plant species (Ainsworth et al. 2012; Hassan et al. 2017). In an experiment, Rai and Agrawal (2012) showed that ozone negatively influenced the rate of photosynthesis by affecting photosynthetic pigments, chlorophyll fluorescence (Fv/Fm) and electron transport along with carbon fixation in terms of reduced Rubisco activity and quantity. It was also noticed that the photosynthate translocation and allocation also get affected due to ozone, which influenced crop yield and reproduction features such as modulation of pollen or ovule maturation, changes in the timing, rate or number of flowers produced, effects on seed and fruit development, yields, seed germinability and seedling vigour. Very recently, Ghosh et al. (2020) used two sowing dates (timely sown and late sown) to examine the impact of elevated ozone on *Triticum aestivum* cv. HD 2967 growth including biomass, leaf gas exchange rate and other yield features (i.e. the length of the ear plant^{-1}, weight of ears plant^{-1}, number of grains plant^{-1}, weight of grains plant^{-1}, husk weight plant^{-1}, straw weight plant^{-1}, harvest index, test weight of the grains and straw grain ratio). In this study, they concluded that ozone exposure affected growth and productivity; and late sowing practice is not advisable for wheat cultivation. Various studies have shown that exposure to ozone affected negatively the rate of photosynthesis and other associated physiological activities in wheat (Feng et al. 2008; Ghosh et al. 2020), soybean (Morgan et al. 2003), rice (Ainsworth 2008), radish and brinjal (Tiwari and Agrawal 2011). Reduced rate of assimilation was ascribed to decreased carboxylation efficiency, and was associated with reduced Rubisco activity (Leitao et al. 2007). Sarkar and Agrawal (2010) suggested that the degree of ozone-induced foliar injury depends on the duration and concentration of its exposure. Reduced rate of photosynthesis may also be noticed due to damage of thylakoids, which influenced photosynthetic transport of electron and is shown by a decrease in the Fv/Fm ratio. Quite often, the Fv/Fm ratio is associated with plant stress condition evaluation (Husen 2010). A decreased Fv/Fm ratio represents changes in PS II photochemistry and are related to photoinhibition. A reduction in the Fv/Fm ratio in the leaves of lettuce (Calatayud et al. 2002), rice (Ishii et al. 2004), wheat (Francini et al. 2007) and snap bean (Flowers et al. 2007) under ozone exposure has been reported. As observed by different investigators, exposure to ozone affected plant biomass, carbon assimilation, translocation and accumulation in various plant parts which can be associated with the reduced rate of photosynthesis (Grantz and Farrar 2000; Morgan et al. 2003; Fuhrer and Booker 2003; Biswas et al. 2008). In rice plants, Agrawal et al. (2002) reported a reduction in the level of RNA transcript for the small subunit of Rubisco, photosynthetic gene expression under ozone stress. Further, Sarkar and Agrawal (2010) also noticed reduced levels of mRNA (both small and large subunits of Rubisco) in the same plant under ozone stress.

2.4 Response to Carbon Dioxide Pollution

Atmospheric concentrations of carbon dioxide have also been increasing quickly due to global industrial revolution (Canadell et al. 2007). Further, it has been reported that the global concentration of carbon dioxide will increase continuously in future due to various anthropogenic activities (Yunus and Iqbal 1996). It is colourless, odourless, non-flammable gas at room temperature. However, it can be a liquid or a solid at other temperatures and pressure. Its exposure to humans causes various effects such as headaches, dizziness, restlessness, breathing problem, sweating, tiredness, increased heart rate, elevated blood pressure, coma, asphyxia, etc. Plant growth and production response to elevated carbon dioxide have shown both positive and negative impacts. In terms of positive impacts, elevated carbon dioxide accelerated photosynthesis and subsequently higher growth, biomass and plant yield (Ainsworth and Long 2005; De Souza et al. 2008; van der Kooi et al. 2016). However, in terms of negative impacts, elevated carbon dioxide has shown a reduced variety of nutrients including protein concentrations, vitamins and some macro- and micro-elements in plants (Myers et al. 2014; Fernando et al. 2015; Broberg et al. 2017; Thompson et al. 2019). Hence, it is necessary to understand the overall impact of elevated carbon dioxide on plant growth and production.

The elevated level of atmospheric carbon dioxide significantly influenced photosynthesis, metabolism and development of plant (Nowak et al. 2004; Ainsworth and Long 2005). Some researchers presumed that C_4 photosynthesis was saturated at ambient carbon dioxide and that C_4 plants might be less and/or not at all affected by the accelerated level of carbon dioxide in comparison to C_3 plant species (Pearcy and Ehleringer 1984; Bowes 1993). Perhaps, this assumption appeared on the anatomical and functional variation of C_3 and C_4 plant species and higher carbon dioxide levels in bundle sheath cells of C_4 leaves. But many investigations have shown that the variation between C_3 and C_4 is not as important as anticipated, and that C4 plants can also increase remarkably the rates of photosynthesis under elevated carbon dioxide conditions. For instance, Ziska and Bunce (1997) examined and found an increase in growth by 3–25% and stimulation of photosynthesis by 4–30% in six weedy species (*Amaranthus retroflexus*, *Echinochloa crus-galli*, *Panicum dichotomiflorum*, *Setaria faberi*, *Setaria viridis* and *Sorghum halapense*) and 4 crop species (*Amaranthus hypochondriacus*, *Saccharum officinarum*, *Sorghum bicolor* and *Zea mays*) under elevated carbon dioxide conditions. De Souza et al. (2008) reported that elevated carbon dioxide levels enhance the rate of photosynthesis, biomass and productivity, and modify gene expression in sugarcane (C_4

plant). More specifically, plants grown at elevated carbon dioxide conditions (~720 ppm) showed the rate of photosynthesis enhanced by 30%, height by 17% and biomass by 40% in comparison to plants grown under ambient carbon dioxide (~370 ppm) conditions. They also showed stomatal conductance to be lowered by −37%, transpiration rates by −32% and water-use efficiency to be increased by 62%. Further, under elevated carbon dioxide conditions, cDNA microarray studies have shown a differential expression of 35 genes on the leaves (14 repressed and 22 induced). The latter is mostly associated with the photosynthetic processes and development. However, in maize (C_4 plant) and sorghum (C_4 plant), an increase in plant productivity was not noticed in terms of grain yield and kernel number under elevated carbon dioxide and well-watered conditions (Ottman et al. 2001; Leakey et al. 2006).

Yilmaz et al. (2017) studied the role of potassium deficiency on plant growth as affected by elevated carbon dioxide; and how antioxidant defence systems respond to potassium deficiency under ambient (400 ppm) or elevated (900 ppm) atmospheric carbon dioxide conditions in durum (*Triticum durum* cv. Sarıçanak-98) and bread wheat (*Triticum aestivum* cv. Adana-99). They found that low or deficient supply of potassium induced oxidative stress, but elevated carbon dioxide had an insignificant impact on antioxidant defence systems and therefore could not alleviate the detrimental impacts of potassium deficiency. In this study, the responses in antioxidant defence enzymes were linked to the potassium nutritional status of plants rather than elevated carbon dioxide conditions. Recently, Thompson et al. (2019) studied 19 wheat genotype (five tetraploid, 11 hexaploid and three synthetic hexaploid) grain protein concentration under elevated carbon dioxide conditions. They examined whether decreased protein grain is genotype dependent and whether it is caused by biomass dilution. In most of the genotypes, the total grain protein was increased, while most genotypes exhibited decreased grain protein concentration under elevated carbon dioxide conditions. In this study, elevated carbon dioxide revealed an increase in grain biomass for all genotypes and total shoot biomass for most genotypes, with the harvest index increasing for all genotypes except for the two synthetic hexaploids CPI133814 and CPI133811. They found that most of the differences between wheat types were insignificant; and suggested that the individual genotype of wheat plants determines the response to elevated carbon dioxide rather than the wheat type.

Elevated carbon dioxide has also enhanced soil-labile C input and, therefore, more microbial carbon source, thus increasing gene abundances in N cycling, such as *nifH*, *amoA*, *nirS* and *nirK* (He et al. 2010, 2014). However, the impact of elevated carbon dioxide on plant N uptake and microorganisms is changeable due to other environmental factors (Butterly et al. 2016). Very recently, Dong et al. (2020) studied the impact of three (ambient, elevated and super-elevated) levels of carbon dioxide concentrations and two N application rates (low and high) on N uptake of cucumber plants and N cycling in a greenhouse soil in open-top chambers. In this study, elevated carbon dioxide enhanced biomass by 24% and N concentration by 4% of fine roots due to high N application, suggesting an improvement in N uptake efficiency. The improvement was greater under low N application but to a lesser extent under super-elevated carbon dioxide conditions. Further, elevated carbon dioxide and super-elevated carbon dioxide exhibited a decrease in gene abundances of soil bacterial *amoA*, *nirS* and *nosZ* in high N applications with increased plant N uptake and reduced NH_4^+, NO_2^- and NO_3^- concentrations in soils resulting in less soil N loss. They suggested that a moderate carbon dioxide enrichment increases N uptake efficiency in the fine roots of cucumber plants and decreases soil N loss associated with decreased nitrification and denitrification under high N applications. Palacios et al. (2019) assessed plant development, seed yield and composition under elevated carbon dioxide and high temperature. A network of relationships among biochemical parameters of grains at three developmental stages revealed that ambient carbon dioxide and high temperatures, as well as elevated carbon dioxide and high temperatures, *affected* significantly both carbohydrate and lipid metabolisms. Additionally, the comparison of ambient carbon dioxide/ambient temperature and elevated carbon dioxide/high temperatures showed insignificant variation in the studied parameters. Abo Gamar et al. (2019) reported that elevated carbon dioxide reduces the negative effects of high temperature and drought conditions by mitigating oxidative stress and improving water status in *Arabidopsis thaliana.* Balasooriya et al. (2020) reported that elevated carbon dioxide (950 ppm) and higher temperature (30 °C) increased the amounts of accessible bioactive compounds in strawberries. Interestingly, in a very recent experiment, Nedunchezhiyan et al. (2020) suggested that rice seed priming with salicylic acid (25 mg l^{-1}) and ascorbic acid (100 mg l^{-1}) increased germination, other seed quality parameters, α-amylase activity and antioxidant enzyme activities under stress due to elevated carbon dioxide and temperatures.

Further, it has also been reported that the elevated carbon dioxide is likely to cause changes in plant diseases (Lake and Wade 2009), tolerance to insect herbivory by pests (Lau and Tiffin 2009), changes in defence signalling (Zavala et al. 2008) and plant-to-plant interaction/competitiveness (Brooker 2006). Thus, these relationships may also lead to certain changes in ecosystems and help look for an interdisciplinary approach to manage and implement adaptive approaches specially to ensure plant production, growth, food and overall security of the ecosystem in near future.

2.5 Response to Particulate Matter Pollution

Due to rapid industrialization and other anthropogenic processes (automobiles, power plants, construction sites, unpaved roads, fields, smokestacks or fires, etc.) various types of particulate matters (also known as particle pollution) are emitted into the atmosphere. Some amounts of natural origin of dust or particulate matters have also been noticed. They are solid particles and/or liquid droplets. Some of the particles, for instance dust, dirt, soot, smoke, are visible to the naked eye. However, others are very small and can only be observed under an electron microscope. These particles can be inhaled, cause serious health problems and are well documented (Brook et al. 2003; Mcdonald et al. 2007; Thomas and Richard 2010; Ulrich et al. 2012). Vegetation in the vicinity (or in the urban area) of such kinds of pollutants (such as cement, coal-dust, fly ash, automobile exhaust and other airborne particulates) has shown remarkable impacts on morphological, biochemical, physiological and genetic status (Farooq et al. 2000; Rai et al. 2010; Younis et al. 2013; Rai et al. 2016; Yu et al. 2018, Karmakar and Padhy 2019). The deposited solid particles may alter the optical properties of leaves; due to this adverse effect, a decrease in chlorophyll content and an increase in the production of antioxidant activities are often observed. These processes finally lead to leaf senescence. Additionally, it has also been reported that some plant species improve urban air quality (Freer-Smith et al. 1997) due to the presence of specific types of foliar features such as leaf orientation, contact area, roughness, epidermal cell arrangement, types, frequency and length of trichomes and so on. Meusel et al. (1999) suggested that the foliage of plants filter many solid particles and thus can be helpful in decreasing the negative impact of particulate pollution. Sharma et al. (2005) also examined the ability of *Bougainvillea* sp. to intercept dust and its use in bio-aesthetic planning and roadside plantation as dust filters. Prusty et al. (2005) have reported that the dust interception capacity in plants depends on their canopy shape and size, leaf phyllotaxy and leaf surface features such as hairs and cuticle. In roadside plant species, the dust interception capacity has also shown seasonal variation (Prajapati and Tripathi 2008). Further, it has also been noticed that the structure and composition of epicuticular wax particles may also contribute towards the dust-capturing capacity of plants (Dzierzanowski et al. 2011). In a very recent experiment, Peng et al. (2020a, b) reported that the enclosed space had a lower particulate matter concentration than the outdoor environment; plants are able to reduce indoor particulate matter concentrations because they increased the surface area of the space. Overall, some plant species exhibited tolerance mechanisms and/or substantial degree of damage under particle pollution load leading to inhibition of photosynthetic activities, protein synthesis and so on. In this state of affairs, some plants became prone to damage caused by insects, nematodes and microbes. At the same time, some kinds of adaptation have also been noticed at the physiological, biochemical and genotoxic levels.

2.6 Response to Fluoride Pollution

Fluoride compounds are considered as another main problem due to its hazardous impact on ecosystems (ATSDR 2003; Divan Jr et al. 2008). They are released into the atmosphere in gaseous state (hydrogen fluoride and silicon tetrafluoride) as well as in solid particles. It enters the atmosphere from anthropogenic sources in large quantities by aluminium smelters, fertilizer factories, coal-burning operation and industrial activities, namely tile, pottery and cement works, ceramic, glass manufacture industries and so on (Cape et al. 2003). However, naturally at the global level, volcanic eruptions, rock dust and/or marine environment contribute very less amounts of fluoride compounds emission into the atmosphere (Barnard and Nordstrom 1982; Saether et al. 1995). In recent years, even though the fluoride emitters have been equipped with effective filters, its emission into the atmosphere continues and leads to various problems (Franzaring et al. 2006). Airborne fluoride deposition and distribution depend on several factors, like level of emission, particulate grain size, chemical reactivity and different meteorological conditions (Hara et al. 1998; Scheringer 2009; Yanchenko and Baranov 2010; Gasic et al. 2010; Walna et al. 2013). Adverse impacts of fluoride pollution in humans, plants and the entire ecosystems are well documented (ATSDR 2003; Feng et al. 2003; Divan Jr et al. 2008; Jha et al. 2011; Sharma and Kaur 2018). In the plant system, fluoride penetrates through absorption by stomata or cuticle, thus leaf is the most affected plant organ. Feng et al. (2003) reported that fluoride enters into the plant system and influences its metabolic activities. Many researchers have reported the associations between atmospheric fluoride and accumulation of fluoride in plant leaves and between fluoride in soil solution and fluoride taken up by different plant species (Klumpp et al. 1996; Karolewski et al. 2000; Fangmeier et al. 2002; Doley 2010; Koblar et al. 2011).

Cai et al. (2016) reported that higher doses of fluoride (≥ 5 mg L^{-1}) decreased the rate of photosynthesis and chlorophyll fluorescence in tea (*Camellia sinensis*) leaves. However, plant leaf has produced more epidermal hairs to reduce water loss under stress conditions. Elloumi et al. (2017) conducted an experiment on *Eriobotrya japonica* to investigate the impact of fluoride air pollution from a phosphate fertilizer factory. They found that fluoride stress negatively influenced foliar water status, photosynthetic parameters, cell membranes and photosynthetic pigments. Exposure to potassium fluoride for a period of 27 days in simulated rain was found to be extremely toxic to *Eugenia dysenterica* plants (Rodrigues et al. 2017). In this study, cell viability as indicated by anatomical leaf alterations (necrosis on the adaxial side, from the border to the centre and tissue degradation with the formation of cellular plasmolysis and elongation) and alterations in chlorophyll a fluorescence parameters was adversely affected under fluoride exposure. Further, Rodrigues et al. (2017) reported the presence of phenolic compounds and accumulation of starch in leaves exposed to potassium fluoride stress; this suggests the response of the plant to the oxidative stress caused. Oliveira dos Anjos et al. (2018) examined the response of *Spondias purpurea* to potassium fluoride using simulated fog (15 mg L^{-1} for 20 min daily up to 10 days). Plants have shown fluoride accumulation, marginal and apical necrosis, presence of phenolic compounds, anatomical alterations and leaflet abscission in young leaves. Similarly, Sharma and Kaur (2019) examined fluoride-mediated antioxidant defence responses in *Spirodela polyrhiza*, grown under hydroponic conditions. Plants were exposed to various doses of fluoride (0, 5, 10, 15, 20, 25, 50 ppm) for 24, 72, 120 and 168 h. In this experiment, accumulation of fluoride was noticed at different exposure periods which triggered the oxidative stress as observed from increased electrolyte leakage, proline, anthocyanin and phenolic content. Additionally, *S. polyrhiza* under fluoride stress responded by alterations in antioxidative enzyme activities, which reflects the tolerance ability of plants. Overall, plant response to fluoride compounds has shown a reduction in plant growth, metabolic performances and photosynthetic activity. Further, its impact on plants might be severe, acute or chronic and fluoride phytotoxicity depends on concentration, exposure duration and plant genotype.

3 Conclusion

In the modern society, air pollution is a major global concern due to rapid economic growth accompanied by increased energy consumption. Thus, its injurious link to humans, animals, plants, microbes and natural ecosystems cannot be ignored. It has been noticed that air pollutants, namely sulphur dioxide, nitrogen oxides, ozone, carbon dioxide, particulates, fluoride and various others damage plant growth and production. Their impact on plant system might be acute or chronic and depends on the concentration of pollutants, exposure duration, season and plant genotype. Tree, herb and shrubs differ in terms of physical and chemical nature, and morphology and anatomy of the leaves; thus, accordingly, they are able to escape and/or tolerate when challenged by unfriendly environmental conditions. These pollutants have several harmful effects as they affect plant growth, physiological activities, biochemical attributes, antioxidant activity and gene expression. Exposure to pollutants has shown to modulate photosynthetic pigments, the process of photosynthesis, stomatal functioning, carbon allocation, respiration, protein synthesis, nutrient contents, etc. and increase the production of reactive oxygen species which is very harmful to the metabolic activities of the plants. These changes affect the overall plant system and also disturb microbial flora and fauna associated with the plant. Thus, an integration of important molecular and physiological investigations, combined with agronomic and ecological research, is important to gain better understandings in terms of plant response to air pollution.

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Chapter 10
Physiological and Molecular Responses to High, Chilling, and Freezing Temperature in Plant Growth and Production: Consequences and Mitigation Possibilities

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Abbreviations

ABA	Abscisic acid
ACC	1-Aminocyclopropane-1-carboxylic acid
A_{net}	Net photosynthetic rate
AOP	AOX pathway
AOX	Alternative oxidases
APX	Ascorbate peroxidase
BRs	Brassinosteroids
CAT	Catalase
Chl	Chlorophyll
CKs	Cytokinins
COP	Cytochrome oxidase pathway
COX	Cytochrome oxidase
EL	Electrolyte leakages
ETC	Electron transport chain
FT	Freezing temperature
GA	Gibberellic acid
GR	Glutathione reductase
GWAS	Genome-wide association studies
HSFs	Heat shock factors
HSPs	Heat shock proteins
HT	High temperature
JA	Jasmonic acid
LEA	Late embryogenesis abundant
LT	Low temperature

MAS	Marker-assisted selection
MDA	Malondialdehyde
MLE	Moringa leaf extract
MWE	Moringa water extract
NPQ	Non-photochemical quenching
NUE	Nutrient-use efficiency
OEC	Oxygen evolving complex
PCD	Programmed cell death
PGRs	Plant growth regulators
POD	Peroxidase
POX	Guaiacol peroxidase
PSII	Photosystem II
QTL	Quantitative trait loci
ROS	Reactive oxygen species
RWC	Relative water contents
SA	Salicylic acid
SNPs	Single-nucleotide polymorphisms
SOD	Superoxide dismutase
SSRs	Simple sequence repeats
SWE	Sorghum water extract
TF	Transcription factors
WUE	Water-use efficiency
ZR	Zeatin riboside

1 Introduction

Growth and productivity of a crop get affected by both biotic and abiotic stresses, and it causes a series of morphological, physiological, and molecular changes. Some plants change their morphology to cope with these changes, some of them change their physiology or show changes in gene expression, and this alters their growing activities to withstand and tolerate such conditions (Rihan et al. 2017; Raza et al. 2019a, 2020a, b). Tolerance or susceptibility of a plant is also associated with the plant stage. Such environmental changes may affect the plant at multiple stages (Gupta et al. 2020; Raza 2020a). These changes may result in leaf wilting, reduction in leaf area, changes in relative water contents (RWC), electrolyte leakages (EL), and production of reactive oxygen species (ROS), etc. (Zhou et al. 2017; Hasanuzzaman et al. 2020).

High temperature (HT) is among the most limiting factor that not only affects plant growth and development but its production as well, which is a major threat to food security (Rai 2020; Raza 2020b; Sabagh et al. 2020). The plant can sense HT by different integral membrane proteins (i.e., channels, transporters, and receptor-like kinases RLKs) that are present in the membrane (Gupta et al. 2020). Molecular chaperones can also help in sensing these temperature extremes (Oroz et al. 2017). Under HT, there is a substantial decrease in photosynthesis due to reduced chlorophyll (Chl) biosynthesis in plastids (Jia et al. 2019). HT adversely affects DNA, proteins, and enzyme activities in the plants (Gupta et al. 2020). This extreme temperature can also cause secondary water stress by damaging cellular structures and metabolic pathways (Jia et al. 2019). Reproductive tissues are more sensitive to heat stress at the flowering stage, which lowers the grain yield (Maqbool et al. 2017).

Among abiotic stresses, low temperature (LT) is one of the critical limiting factors that affect the distribution and productivity of the plant. LT (0–15 °C), also known as chilling stress, is defined as LT above freezing point. Cold-tolerant plants have greater efficiency in maintaining a higher level of carbon dioxide assimilation (Li et al. 2020b). LT caused a wide range of changes at the physiological level and at the molecular level. At the molecular level, different microarray and RNA-Seq studies showed that almost 10–15% of genes are differentially expressed under LT treatment in different plants such as rice and *Arabidopsis* (Waters et al. 2017). Under LT, plant enhances ROS production that increases the lipid peroxidation that results in higher membrane fluidity. Membrane flexibility is also affected by the LT that increases EL (Liang et al. 2020).

Freezing temperature (FT) (<0 °C) is also a crop yield-limiting factor. Many plant species that are economically and ecologically important are affected by FT stress (Wang et al. 2020a). It harms plants either directly or indirectly; directly, it affects plant's metabolic activities and indirectly by cold-induced osmotic stress and ROS generation (Jalmi et al. 2018). As a result of cold conditions, ice forms in the extracellular, and in response to maintaining balance, the cell transport water from the intracellular to the extracellular ice phase, consequently, the concentration of the solute increase inside the cell. Moreover, root hydraulic conductance decreases under freezing that leads to reduction in turgor pressure in leaves, and it ultimately affects growth (Chen et al. 2018). During long-term freezing stress, cell water moves to intercellular apertures and undergoes the process of ice nucleation, which disturbs the osmotic homeostasis (Bao et al. 2020). If freezing period gets prolonged, all water freezes and crystals are formed, which results in the membrane rupture that eventually may lead to plant death (Sun et al. 2019). Plants exposed to FT show some visible symptoms that include wilting, chlorosis, and necrosis (Atayee and Noori 2020). To avoid its harmful effects, plants establish some pathways to prevent ice crystal formation, and sugar accumulation can play an essential role in freezing tolerance. Many plants can increase their degree of low and freezing tolerance by a phenomenon called cold acclimation (Rahman et al. 2020). This phenomenon can be defined as the exposure of plants to a low non-freezing temperature before the onset of freezing that enhances cold tolerance (do Amaral et al. 2020).

There are different approaches to cope with LT, HT, and FT. Most of the studies regarding temperature stress have been conducted on the *Arabidopsis* plant (Ritonga and Chen 2020). But some studies have also been conducted on *Brachypodium distachyon* to study molecular mechanisms of temperature stress because of the presence of cold-responsive *IRIP* and *CBF3* gene subfamily (Londo et al. 2018). The discovery of the CBF gene has been an important breakthrough in studies related to temperature stress. It has been observed that this gene is present in all field crops (Yu et al. 2020). Many studies show that this gene is present in woody and herbaceous plants (Hao et al. 2018; Rihan et al. 2017; Shi et al. 2018). CBF is strongly associated with winter temperature acclimated plants, and many variations in this gene have been reported under temperature stress (Yu et al. 2020).

Exogenous application of phytohormones is one of the best strategies to cope up with temperature stress conditions. These phytohormones include abscisic acid (ABA), brassinosteroids (BRs), salicylic acid (SA), jasmonic acid (JA), cytokinin (CK), gibberellic acid (GA), ethylene (ET), and Strigolactones (SLs) that play a significant role in protecting plants against heat stress (Barrero-Gil and Salinas 2017; Waqas et al. 2017; Khan et al. 2017; Prerostova et al. 2020; Raza et al. 2019b). ABA upregulates the expression of late embryogenesis abundant (LEA) gene that increases the tolerance against freezing (Wang et al. 2019). ABA triggers bZIP, and it also upregulates the expression of the CBF gene. CBF upregulates ABA-dependent cold responsive (*COR*) gene against temperature stress (Ding et al. 2019). It has been reported that the application of SA can enhance tolerance against LT stress in many plant species such as rice, potatoes, and maize (Barrero-Gil and Salinas 2017), while GA plays an important role in tolerance against freezing. Moreover, GA and JA are associated with *CRT/DREB* gene that confers tolerance against freezing and cold (Rihan et al. 2017; Hao et al. 2018). Moreover, plant leaf extract can also improve plant growth under different environmental constraints, including extreme temperature stresses. For instance, Sarwar et al. (2018) reported that moringa water extract (30 times diluted) prevents the cotton crop from heat-induced injury at 38/24 °C and 45/30 °C. Likewise, Afzal et al. (2015) reported higher yield production in late-sown wheat with the foliar leaf extract application of sunflower (1.5%), sorghum (3%), rice (3%), canola (3%), and MLE (3%) at tillering and booting stages.

Nevertheless, modern biotechnological tools such as marker-assisted selection (MAS), genome-wide associated studies (GWAS), quantitative trait loci (QTLs) have been explored under temperature stress. For instance, the application of MAS program under HT in rice (Dixit et al. 2017), FT in wheat (Leonova et al. 2017), and LT in maize (Lone et al. 2018) played an important role in acquiring extreme temperature tolerance. Many QTLs have been reported related to senescence under HT stress (Wen et al. 2019). Using GWAS, Pan et al. (2015) recently investigated 52 QTLs for cold tolerance at the germination and booting stages. In this chapter, we have emphasized and summarized the recent advancement in the physiological, biochemical, and molecular responses, and tolerance mechanisms of plants under HT, LT, and FT. Furthermore, several mitigations strategies, such as QTLs, GWAS, MAS, plant growth regulators (PGRs), and plant leaf extracts, have been discussed that help to enhance our understanding of temperature stress tolerance.

2 Temperature Stress: Key Factor Affecting Plant Growth and Production

2.1 *Effect on Seed Germination*

Seed germination is essential to determine the optimal temperature for sowing and restoration (Table 10.1; Dürr et al. 2015) and is a critical key transitional stage in the plant life cycle, which is strongly regulated by temperature fluctuations (Chen et al. 2019b; Hussain et al. 2019c). There is a linear relationship in germination percentage and an increase in temperature up to optimal temperature. If the temperature increases further, the germination would decrease up to zero (Parmoon et al. 2015). However, according to Dürr et al. (2015), seed germination may occur between the maximal and minimum temperature, and the highest germination rate corresponds to the optimal temperature. In this connection, Chen et al. (2019b) observed germination rate of 28 ephemeral plants at 5/1 °C, 15/5 °C, 20/5 °C, 25/5 °C, 25/10 °C, and 30/15 °C, and observed LT-responding plants, moderate temperature-responding plants, HT-responding plants, non-responding plants, and non-germinating plants at these temperatures. Moreover, they also noted that *Corispermum lehmannianum* germination is sensitive under both high and moderate temperatures. Moreover, Yi et al. (2019) reported that germination percentage increases with increasing temperature, but *Neopallasia pectinata*, *Kochia prastrata*, *Bassia dasyphylla*, *Artemisia sieversiana*, *A. scoparia*, *Artimesia mongolica*, *A. annua*, *Allium tenuissimum,* and *A. ramosum* germinated >60% at lower temperature regimes. However, Nafees et al. (2019) observed 95.3%, 93.3%, and 10% germination at 40, 10, and 25 °C, respectively.

Table 10.1 Effect of high, chilling, and freezing temperature on germination percentage

Temperature (°C)	Plant	Germination (%)	References
28/28, 10/10	*Glycine max* L.	11.1, 5	Borowski and Michalek (2014)
30	*Bombax ceiba* L.	94.0	Zheng et al. (2018)
40, 25, 10	*Lycopersicon esculentum* L.	95.3, 91.7, 93.3	Nafees et al. (2019)
13	*Zea mays* L.	58	Cao et al. (2019)
12/8	*Triticum aestivum* L.	84.34	Gu et al. (2019)
15	*Oryza sativa* L.	48.89	Fu et al. (2019b)
3, 6, 9, 12, 15	*Vicia villosa* L.	86, 94, 96, 98, 98	Yusefi-Tanha et al. (2019)
5.0 ± 1.0	*O. sativa* L.	61.00	Sohag et al. (2020)
4	*T. aestivum* L.	82	Bibi et al. (2020)
4	*T. aestivum* L.	85.56	Sun et al. (2020)
35	*Cucumis sativus* L.	92	Campobenedetto et al. (2020)

2.2 Effect on Growth and Production

High, low and freezing temperatures cause an adverse effect on plant growth, physiological functions, and productivity (Table 10.2; Liu et al. 2018a; Guo et al. 2018; Raza et al. 2019a, b). Moreover, chilling stress disturbs the respiratory metabolism, photosynthetic efficiency, and eventually hampers growth while freezing stress-formed intracellular ice crystal formation results in plant death or mechanical injury (McCully et al. 2004). Cold stress at the seedling stage causes severe negative impact on plant growth, physiology, and morphology by causing cellular damage, and diminishes the survival chances of trees (Yildiz et al. 2014).

2.3 Effect on Shoot Length

At initial stages of plant growth is more sensitive to heat injury, and seedling mortality under heat stress is a common response, and it is entirely associated with subsequent stem collapse and meristem injury. Yadav et al. (2011) reported that shoot length was significantly higher due to sufficient transpiration and translocation mechanism under normal conditions, but markedly affected under stress conditions. Extreme heat causes a negative impact on root length, plant height, grain quality, and biomass production among all filed crops (Cao et al. 2015; Waqas et al. 2015; Bahuguna et al. 2017). Kilasi et al. (2018) reported that the shoot length decreases by 16.67% under HT (39 °C). Nevertheless, the shoot length of maize was reduced under HT and LT (Moradtalab et al. 2018; Ayub et al. 2020; Hussain et al. 2019a; Hussain et al. 2020). Similarly, a reduction in wheat shoot length was also observed in response to temperature stress (Table 10.3; Kumari et al. 2018; Iqbal et al. 2019; Zencirci et al. 2019; Bibi et al. 2020).

2.4 Effect on Grain Yield

A review by Barlow et al. (2015) on the effect of extreme temperature frost and heat on wheat explored that frost caused abortion of grains and resulted in pollen sterility. Moreover, HT caused a reduction in germination and reduced the grain-filling period. Several studies have reported the adverse effect of temperature on grain yield (Table 10.4). According to Abd El-Daim et al. (2014), HT, above 45 °C, caused 80–90% seedling mortality in wheat, while Fahad et al. (2016) reported that HT decreased the panicle length and RWC of leaf in rice. Similarly, Maya and Matsubara (2013) noted that HT (30 °C) significantly reduced the root and shoot length and dry weight in cyclamen plants as compared to control (22 °C). Moreover, heat stress severely reduces the number of grains and 100-grain weight in major crops. For instance, Hütsch et al. (2019) reported a decrease in grain yield (58%) and 1000-grain weight (83%) in wheat at 30/25 °C, while Youldash et al. (2020) reported 33.9% yield

Table 10.2 General effect of high, chilling, and freezing temperature on growth and production

Temperature (°C)	Plant	Effect	References
38/28, 35/20	*Glycine max* L. *Cicer arietinum* L.	Reduction in pollen germination	Djanaguiraman et al. (2013)
50	*Helianthus annuus* L.	50% seedling mortality	Kalyar et al. (2013)
45/35	*Cicer arietinum* L.	Lower stigma activity, pollen germination, and photosynthetic rate	Kumar et al. (2013)
42	*Hordeum vulgare* L.	Lower photosynthetic rate, inhibition of quantum efficiency and functionality of PSII	Jedmowski et al. (2015)
42	*Vigna radiata* L.	Oxidative burst, lipid peroxidation, lower relative water and pigment content, higher proline concentration	Nahar et al. (2015)
10	*Hibiscus rosa-sinensis* L.	PSII damage, ETC inhibited	Paredes and Quiles (2015)
10/6	*Stevia rebaudiana* L.	Effect positively on growth development, higher quantum yield and ETR (electron transport rate)	Soufi et al. (2015)
28/35	*Oryza sativa* L.	Lower photosynthetic rate	Fahad et al. (2016)
30	*Lens culinaris* L.	Higher stomatal conductance, reduction in photosynthetic rate, and membrane permeability reduced Rubisco activity	Sehgal et al. (2017)
40	*Olea europaea* L.	Reduction in activities of Rubisco, lower carbon assimilation, and stomatal conductance	Haworth et al. (2018)
±10–15 more than ambient	*Chenopodium quinoa* Willd.	Growth drastically declined, less photosynthetic rate, and intrinsic water-use efficiency	Rashid et al. (2018)
−14, −17, −20	*Triticum aestivum* L.	Yield reduction, but no mortality (5% mortality, 30% mortality)	Zheng et al. (2018)
12	*Cucumis sativus* L.	Decreased antioxidants, increased reactive oxygen species, and decreased growth	Anwar et al. (2018)
30/25	*Brassica rapa* L.	Induced a low photosynthetic rate and reduced activities of antioxidant enzymes	Lee et al. (2020)
5.0 ± 1.0	*O. sativa* L.	Growth of plant is stunned with visible toxicity laterally with the modification of biochemical markers	Sohag et al. (2020)
38/35	*Medicago sativa* L.	Heat-induced membrane damage by reducing electrolyte leakage and malondialdehyde (MDA) content, and antioxidants activity	Wassie et al. (2020)
15 h of 0 and the minimum was −7	*T. aestivum* L.	Reduced net photosynthetic rate of leaf, and reduction in plant biomass yield and height	Wang et al. (2020d)

Table 10.3 Effect of high, chilling, and freezing temperature on shoot length

Temperature (°C)	Plant	Decrease (%)	References
39	*Oryza sativa* L.	16.67	Kilasi et al. (2018)
37 ± 2	*Triticum aestivum* L.	10.1	Kumari et al. (2018)
40	*Zea mays* L.	10.25	Ayub et al. (2020)
12–14	*Z. mays* L.	57.14	Moradtalab et al. (2018)
23 ± 2.5	*T. aestivum* L.	70.59	Iqbal et al. (2019)
2, 0, −2, −4, −6, and −8	*T. aestivum* L.	34.94, 46.18, 55.89, 79.72, 91.23, and 99.73	Zencirci et al. (2019)
40, 25, 10	*Lycopersicon esculentum* L.	15.6, 15.8, 15.3	Nafees et al. (2019)
15/12	*Z. mays* L.	34.15	Hussain et al. (2020)
5/4	*O. sativa* L.	11.03	Rayee et al. (2020)
4	*T. aestivum* L.	20	Bibi et al. (2020)
5.0 ± 1.0	*O. sativa* L.	17.94	Sohag et al. (2020)

Table 10.4 Effect of high, chilling, and freezing temperature on grain yield

Temperature (°C)	Plant	Effect	References
10/5	*Triticum aestivum* L.	Grain yield spike^{-1}: 40%	Li et al. (2017a)
13–8	*Zea mays* L.	Grain yield plant^{-1}: 21.87% 1000-grain weight: 18.38%	Waqas et al. (2017)
30/25	*T. aestivum* L.	Grain yield plant^{-1}: 58% 1000-grain weight: 83%	Hütsch et al. (2019)
−14 and −17	*T. aestivum* L.	Grain yield reduction: 3.3 number of spike: 4.4 Grain yield reduction: 8.4 Number of spike: 21.6	Zheng et al. (2018)
40	*Oryza sativa* L.	1000-grain weight: 38.28% Grain yield plant^{-1}: 46.67%	Sarwar (2019)
38/30	*Z. mays* L.	Kernels row/ ear: 3% Grain yield plant^{-1}: 16.61% 1000-grain weight: 3.35%	Hussain et al. (2019a)
35/25	*O. sativa* L.	Grain yield pot^{-1}: 53%	Ali et al. (2019)
18	*O. sativa* L.	Total grains plant^{-1}: 26.29% Yield Hill-1: 30.97	Zhang et al. (2019b)
12–20	*O. sativa* L.	Seed setting: 18.0% Grain yield plant^{-1}: 13.0%	Siddik et al. (2019)
35/21	*Z. mays* L.	Kernels number ear^{-1}: 24.26% Grain yield plant^{-1}: 33.09%	Wang et al. (2020b)
23 ± 2.5	*T. aestivum* L.	Grain yield (m^{-2}): 33.9% Grain weight (mg): 4.3% Harvest index: 28.0%	Youldash et al. (2020)

reduction at 23 °C. Similarly, Sarwar (2019) revealed 46.67% grain yield reduction in maize at 40 °C. However, according to Hussain et al. (2019a), 38/30 °C temperature decreased the kernel row (3%), 100-grain weight (3.35%), and grain yield (16.61%) in maize. Further, Wang et al. (2020b) reported 33.09% grain yield reduction in maize at 35/21 °C. Moreover, Ali et al. (2019) observed 53% grain yield reduction in rice at 35/25 °C. LT stress also hampers the grain quality and grain yield reduction in crop plants (Dreccer et al. 2018). For instance, LT at booting and jointing stage of wheat significantly reduces the number of productive tillers (Li et al. 2015), and severely affects the development of young spike (Thakur et al. 2010). Ghadirnezhad and Fallah (2014) investigated the effect of 13 °C (cold stress) for 15 days at flowering stage of rice cultivars and observed that LT had a significant impact on the number of the filled, empty and total number of grains, number of panicle and length of the panicle. It is established that chilling stress reduces yield percentage in different plants, such as 40% wheat yield reduction that was observed at 10/54 °C (Li et al. 2017a), 21.87% in maize (13/8 °C) (Waqas et al. 2017), and 26.29% and 13% in rice at (18 and 12–20 °C, respectively) (Zhang et al. 2019c; Siddik et al. 2019).

Under LT, many species of tropical and subtropical origin get demolished or typically injured and show severe symptoms due to their inability to adapt freezing stress (Sanghera et al. 2011), while cereal species develop strategies to deal with winter condition. Lei et al. (2019) observed the effect of chilling and freezing stresses on *Brassica napus*. They provided 2 and 4 °C (chilling stress) and −2 and −4 °C (freezing stress) along with control (22 °C) and noted the negative consequences of LT. Similarly, Zhang et al. (2019c) experimented on the effect of −2, 0, 2 °C for 24 h and 4 °C for 60 h by developing stress in artificial climate chamber by using wheat as experimental plant and observed the number of grains at booting stage. They observed that the development of wheat spikelet gets inhibited, while floret growth is delayed at LT stress. However, the activity of enzymes involved in sucrose metabolism was dynamically altered. Sucrose synthase activity and sucrose phosphate synthase significantly increased at 2 and 4 °C, respectively, while the activity of invertase and sucrose synthase decreased at LT. Moreover, 1000 grain weight and the number of grains per spike showed a decreasing trend with a decrease in temperature. In this consistency, Zheng et al. (2018) reported 3.3 and 8.4% grain yield reduction at −14 and −17 °C, respectively. They observed that sensitive cultivars died at freezing temperature, while they noticed no obvious morphological differences in both chilling and freezing stress in tolerant cultivars.

3 Physiological Responses in Plants under Temperature Fluctuation

Changes in morphological attributes are the result of changes in the physiological traits of plants. These changes are noted in fundamental physiological aspects including photosynthesis, respiration, nutrient acquisition, water-use efficiency, and assimilation of hormonal partitioning regulation, as discussed below.

3.1 Photosynthesis

The relationship between temperature and photosynthesis is not linear in general, but a bell-shaped curve can be observed (Yamaguchi et al. 2019); the maximum photosynthetic rate can be observed at an intermediate/optimum temperature while lower at HT and LT; therefore, temperature response toward photosynthesis varies between different temperature regimes within the same species. Moreover, growth at different temperature regimes also affects the maximum photosynthesis without changing the temperature response curve (Hikosaka et al. 2006; Yamori et al. 2014). Similarly, Dusenge et al. (2019) reported that short-term changes in temperature have a great impact on the plant, and considerable variation in kinetic properties of Rubisco was obtained in several studies, which mainly focuses on the effect of temperature-based photosynthetic responses (Hikosaka et al. 2006; Silva-Pérez et al. 2017).

According to Posch et al. (2019), photosynthetic processes are susceptible to HT, and net photosynthetic rate (A_{net}) increases at HT (peaking at an optimum and then decline) while studying wheat responses toward varying temperatures. They suggested that this decline is associated with photosynthetic CO_2 reduction. The photochemical processes of carbon metabolism in the stroma and the thylakoid lamellae (Wang et al. 2018), and the site of photochemical reactions are more sensitive to HT (Hu et al. 2020). HT also caused damage to the acceptor side of photosystem II (PSII), electron transport chain (ETC), oxygen-evolving complex (OEC), and affected the PSII (Chen et al. 2008; Li et al. 2009), thus resulting in lower photosynthetic efficiency. Similarly, Camejo et al. (2005) reported that PSII is very unstable and reduced its activity at a higher temperature, and causes OEC dissociation, which results in an imbalance between electron flow from OEC toward PSII acceptor side (De Ronde et al. 2004). Moreover, Balfagón et al. (2019) reported that chloroplast structure and the expression of the proteins that are involved in photosynthesis change under HT, especially the transcripts of PSII and D1 protein. Additionally, Wang et al. (2018) confirmed the breakdown of Chl by increasing the activities of Chl-degrading peroxidase and chlorophyllase under HT.

Change in carbon assimilation rate is the determinant of growth and ultimate yield. Chovancek et al. (2019) reported that 38 °C day temperature and 20 °C night temperature decreased the photosynthetic rate up to 40% in wheat. Hu et al. (2020) reported that HT induces inactivation of Rubisco, impairment of protein translation, Chl breakdown, and inactivation of PSII in response to HT. Meanwhile, the chloroplast protein plays a vital role in proteostasis; however, the chloroplast generates protein chaperons to protect PSII. Moreover, they also deduced that chloroplast also takes part in retrograde signaling pathways that maintain cellular integrity under HT stress. Likewise, the activation of APG6 chaperon mediates thermotolerance to the chloroplast by regulating internal thylakoid formation during plastid differentiation under extreme temperature (Myouga et al. 2006). It is reported that under HT, HSP26 (heat shock proteins) improved chloroplast formation in maize by interacting with specific proteins (Hu et al. 2015). Another holdase chaperone known as orange (Or) protein regulates the synthesis of carotenoids (Kang et al. 2017) that increases the Chl content and efficiency of PSII in transgenic *Arabidopsis* (Kang et al. 2017; Park et al. 2016).

Interestingly, despite all above-mentioned heat responses, plant hormones also play a key role in photosynthesis under HT. In this connection, Islam et al. (2018) revealed that ABA-induced stomatal closure resulted in lower A_{net}. Moreover, the synthesis of JA was involved in the translocation of lipid intermediates from chloroplast to peroxisomes and cytoplasm (León 2013). Balfagón et al. (2019) reported the involvement of JA in regulating the transcriptional responses unique to heat and light stress that maximized the efficiency of PSII (Fv/Fm) and quantum yield of PSII in JA-deficient mutant (*aos*). In leaves, direct heat shock accelerates the JA and ACC (1-aminocyclopropane-1-carboxylic acid), albeit not significantly (Prerostova et al. 2020). However, according to Dubois et al. (2018), the accumulation of ACC (precursor of ethylene) activates the inhibition of photosynthesis. Moreover, exogenous application of zeatin riboside (ZR) increases the Chl synthesis by reducing the protease level in bentgrass under extreme temperature, suggesting the involvement of ZR in increasing the photosynthesis in HT treated plants (Veerasamy et al. 2007; Hu et al. 2019). Another way of increasing the stress tolerance is the acclimation process. For example, acclimation for 1 h followed by 2 h at 37 °C significantly improved the photosynthetic ability of *Arabidopsis* (Prerostova et al. 2020).

On the other hand, the Chl fluorescence dynamics curve showed that chilling causes inactivation of PSII reaction center in *B. campestris* (Wang et al. 2020a). Chilling stress significantly reduced CO_2 assimilation, PSII activity, and photosynthetic and photochemical ability in different plants (Ruelland and Zachowski 2010). LT decreased the photochemical quantum yield of PSII and had a direct impact on the kinetics of carbon-fixing enzymes, and prolonged exposure to HT increased the darkly sustained thermal energy dissipation (Li et al. 2018b; Cheng et al. 2019a). According to Hou et al. (2016), photosynthesis is the first physiological target of chilling injury, which decreases the Chl biosynthesis (Fariduddin et al. 2011; Muscolo et al. 2015). However, Wang et al. (2020a) observed higher Chl *a* content in tolerant *Brassica* cultivars. Conversely, Rubico activity is not very sensitive under chilling conditions, but its increased activity was associated with chilling tolerance in maize (Salesse-Smith et al. 2020). Contrarily, Allen and Ort (2001) demonstrated that reaction center was overly excited under chilling temperature, which caused severe oxidative damage to the ETC and carbon supply, and also inhibited the closure of stomata and decreased activity of Rubisco.

Chilling stress deteriorates the photosynthetic efficiency and causes severe damage to the chloroplast. Li et al. (2014) revealed that redox state of P700, energy distribution of PSII, photo-oxidizable P700, and maximum quantum yield of PSII (Fv/Fm) significantly changed in oilseed crop under LT. Chilling stress altered the enzymatic activities of the chloroplast, changed the membrane state, reduced the photosynthetic efficiency, thus causing photoinhibition in PSII and PSI, which affected the Calvin cycle and initiated ROS signaling (Liu et al. 2018b). Moreover, Hajihashemi et al. (2018) confirmed a lower photosynthetic rate in *Stevia rebaudiana* during cold conditions. LT dramatically declined photosynthesis up to 88% in two native species of Antarctic plants, including *Dianthud chinensis* and *Colobanthus quitensis* (Clemente-Moreno et al. 2020). Sharma et al. (2005) concluded that hundred genes related to photosynthesis were highly downregulated in rice seedlings at 10 °C in 72 h.

The biosynthesis of the accessory pigments such as xanthophyll, carotenoids, and Chl gets stimulated to confer the photosynthetic damage (Ahmad et al. 2020). Chilling signals alter the redox state of photosynthesis, ETC, light energy absorption, and pigment synthesis (Wu et al. 2016; Morita et al. 2017). Recently, Adamski et al. (2020) observed that cold stress was more damaging for PSII as compared to PSI. They also reported that phytochemical efficiency lowers the fraction of QA in PSII and generates a large pool of electron acceptors at the PSI in tolerant rice cultivars. Chloroplast under chilling stress also responds to the chilling stress stimuli. For example, retrograde signaling from chloroplast to nucleus was responsible for chilling stress, which activated the expression of stress-responsive nuclear-encoded proteins in *Arabidopsis* (Liu et al. 2018b). Similarly, Kurepin et al. (2013) reported that cold-responsive (COR) gene and C-repeat/DREB binding factors were more sensitive to the redox state of the chloroplast. It is well known that the optimal temperature for photosynthesis is correlated with specific adaptations linked with physiological and biochemical aspects including stomatal conductance ad Rubisco activities, which are closely associated with the bioclimatic origin of the species (von Caemmerer and Evans 2015; Xiong et al. 2015; Perdomo et al. 2016). In this respect, Antarctic plants have photosynthetic optima of 15–19 °C, and at 0 °C, they maintained up to 30% (Xiong et al. 1999), which is lower than the optima of tropical species (23–35 °C), which showed a sudden decrease at 10–15 °C (Yamori et al. 2014; Cavieres et al. 2016; Clemente-Moreno et al. 2020). Göbel et al. (2019) experimented on three gramioids and concluded that as compared to others, *Kobresia pygmaea* had higher photosynthesis at 10 °C than at 20 °C air temperature. Additionally, Wang et al. (2017) reported that cold tolerance in rice is associated with photosynthesis regulation.

Similarly, FT indirectly examined its photosynthetic ability under FT in tea cultivars (Shi et al. 2019). They elaborated that maximum photochemical efficiency and D1 protein gene expression were seen in tolerant as compared to freezing-sensitive tea cultivars. Ball et al. (2002) reported that the response of evergreen leaves to the FT varied with leaf thinness, which altered the photosynthetic ability by regulating the nadir temperature of leaves. Similar findings were obtained by Jia et al. (2019) while working on evergreen plants. Primary damage of mild frost includes the disruption of energy flow toward Q_A, and further freezing accelerates dysfunction of electron flow between PSII reaction centers toward Q_A. At the same time, secondary freezing damage results in complete deactivation of PSII (Rapacz 2007). In this connection, Miralles-Crespo et al. (2011) found that FT −4 °C for 3 h decreased the photochemical efficiency (Fv/Fm) and non-photochemical quenching (NPQ) in pink oleander. Rapacz (2007) revealed that the potential quantum yield of PSII and energy trapping in PSII reaction center varies with contrasting freezing tolerance ability of winter wheat cultivars. So, generally, temperature causes a complex influence on photosynthetic reactions. Thus, HT not only facilitates electron transfer but also alters photosynthetic reactions and causes photosynthetic damage and disruption, while, on the other hand, LT (above the freezing point) does not affect the primary charge separation, but restricts electron transfer (Odahara et al. 2011).

3.2 Respiration

Respiration rate varies with changing temperature; even a slight increase in ambient temperature increases the CO_2 flux from leaves to atmosphere (Heskel et al. 2016). However, Dusenge et al. (2019) reported that respiration is more a sensitive process under HT as compared to photosynthetic reactions. Unlike photosynthetic adjustment, respiration adaption may occur rapidly (Ow et al. 2010) by changing the activities of existing enzymes and altering the composition of mitochondrial proteins (Atkin et al. 2005). Kim et al. (2007) reported that dark respiration rate increases with temperature and found maximum at 35/29 °C. Posch et al. (2019) reported that HT decreases the mitochondrial respiration and CO_2 release through the photorespiration. Over the decades, a mathematical approach has been used to demonstrate the effect of temperature on respiration. One such approach is the determination of Q10 (temperature coefficient of respiration), which describes a proportional increase in respiration with every 10 °C rise in temperature (Atkin et al. 2002). Recently, Rashid et al. (2020) investigated that HT treatment of rice about 40 °C relative to 30 °C changed the expression of eight respiration-related genes namely *ribulose 5-phosphate 3-epimerase*, *enolase*, *ATP dependent phosphofructokinase*, *phosphoglycerate kinase*, *uncoupling protein*, *alternative oxidase, and external NAD(P)H dehydrogenase*; they noted that two genes *alternative oxidase* and *external NAD(P)H dehydrogenase* downregulated more than two-fold under heat stress.

Documentation on the effect of chilling on mitochondrial ATP synthase has been sparingly studied to date (Kerbler et al. 2019). Respiratory enzymes work as regulatory elements in controlling the temperature responses of plant respiration, especially AOX (alternative oxidases) and COX (cytochrome oxidase). Similarly, differential changes in AOX pathway (AOP) and cytochrome oxidase pathway (COP) could modulate energy status and cell oxidative stress (Del-Saz et al. 2018). LT is well reputed by lowering the respiration rate and imposing ETC and TCA dysfunction (Atkin and Tjoelker 2003) and increasing the production of AOX (Heidarvand et al. 2017). Watanabe et al. (2008) confirmed this aspect by using AOX1a *Arabidopsis* mutant, with a reduced level of AOX protein. They further showed that mitochondrial respiration repressed and the activity of AOX (Kerbler et al. 2019), while NADPH oxidase increased at LT (Miller et al. 2009). Moreover, the rate of dark respiration increased exponentially in short-term cold temperature (Smith and Dukes 2013; Reich et al. 2016). The sudden decrease in temperature from 25 to 10 °C induced an immediate effect on the carbon flow, so relatively more carbon is required for respiration as compared to other phenomena (Barthel et al.

2014). Recently, Kerbler et al. (2019) observed that plant mitochondrial ATP synthase activity is differentially inhibited at 4 °C, with the other elements of the respiration pathway, resulting in limited ATP production and lower ADP: oxygen ratio in the isolated mitochondria of *Arabidopsis*. Nevertheless, an inconsistency was observed by Clemente-Moreno et al. (2020), who found that LT did not impose respiration reduction in two Antarctic native species, and the sustaining rate of respiration was recorded from 3.0 to 4.2μmol CO_2 m^{-2} S^{-1}. Additionally, mitochondrial respiration induced ROS production by dissipating reductants from mitochondria (Atkin and Macherel 2009; Florez-Sarasa et al. 2016; Hasanuzzaman et al. 2020). Similarly, Reinmann and Templer (2016) also observed reduced respiration rate in *Acer rubrum* during winter snowpack. Additionally, Atkin et al. (2000) investigated greater Q_{10} value in cold winter days when the average daily temperature falls between 6 and −1 °C. While, Göbel et al. (2019) reported that dark leaf respiration was stimulated by soil frost in *D. flexuosa*, but remained unaffected in *K. pygmaea*, which had lower temperature optimum for photosynthesis. Moreover, according to them, sedge did not upregulate dark leaf respiration in frozen soil at −2 °C soil and 10 °C air temperature. Furthermore, according to Vyse et al. (2020), sub-lethal freezing injury increased the respiration rate as a tolerance mechanism. Similarly, Sperling et al. (2015) deduced that near-freezing temperature respiration rate poses as a tolerance mechanism to adapt the mangroves to frost stress.

3.3 Water-Use Efficiency

The increase in water-use efficiency (WUE) from deserts to tropical regimes well explained the differences in temperature (Sherwood and Huber 2010; Tardieu 2013), with a gradual transition of heat stress (Mbava et al. 2020). For instance, when daily mean temperature rose by 2.2 °C, the pea WUE dropped up to 30% (Xiao et al. 2009). They also revealed that an increase of about 1.4 °C temperature decreased the WUE up to 26.1%. Similarly, Ben-Asher et al. (2008), while working on maize, also found that WUE decreases from 14 to 5 g (CO_2) kg^{-1} (H_2O) with increasing temperature treatment. Moreover, it is a well-known concept that WUE of CAM plants is much higher as compared to C_3 and C_4 plants, but contrarily, Neales (1973) noted that high night temperature dropped the WUE of *A. americana* normally associated with non-crassulacean plants WUE. However, Eustis et al. (2020) revealed that WUE depends on the genotype and varying temperature level while studying quinoa genotypes as an experimental plant. In fact, HT increased stomatal conductance and soil water availability to maintain the evaporating cooling (Hall 1992), which resulted in lower WUE, when net photosynthesis is lower than stomatal conductance. Typically, ample water supply is required for heat avoidance mechanisms, which leads to the severe reduction in WUE (Camejo et al. 2005; Sakata and Higashitani 2008). Similar inference was observed by Kaminski et al. (2014) while working on *Solanum tubersome* L. Additionally, Zhang et al. (2015) emphasized that maximum WUE reaches at the warm, dry environment, while minimum WUE was observed during wet warm temperature ranging from 29% to 55.5%, thus suggesting the role of precipitation during hot weather conditions.

On the other hand, WUE also reduces significantly in *Santalum album* after 48 h of cold stress (Zhang et al. 2017c). Similarly, Hajihashemi et al. (2018) also observed reduced WUE in *S. rebaudiana*. In this connection, Adamski et al. (2020) observed higher WUE in rice (chilling-tolerant) cultivars. Moreover, Ball et al. (2002) opined that ultimate freezing damage of evergreen leaves is not associated with the leaf three dimensions, but on the other factors especially linked with leaf water content. Navarrete-Campos et al. (2013) hypothesized that genotypes with higher WUE would have higher resistance against freezing stress while working on *Eucalyptus golbulus*. Similar findings were arrived at by Coopman et al. (2010) while studying genotypic variations of Eucalyptus under freezing.

4 Molecular Response in Plants Under Temperature Fluctuations

Plants develop various genetic strategies to cope with temperature stress by increasing the expression of different genes and the synthesis of various proteins to reduce damage. For instance, expression of heat shock proteins/factors (HSPs/HSFs), *NAC* gene, LEA protein, and antioxidant enzymes are among meaningful responses under temperature stress (Zhang et al. 2017b; Huang et al. 2019; Nedunchezhiyan et al. 2020; Sharma et al. 2019; Hou et al. 2020).

4.1 Heat Shock Factors and Heat Shock Proteins

To cope with temperature stress, increases in the abundance of proteins related to HSFs have been well reported (Wang et al. 2015; Shah et al. 2020). HSFs are responsible for the upregulation of HSPs (Wu 1995). The production of heat stress-related proteins such as HSPs to cope up with the temperature stress had been reported in various studies (Sharma et al. 2019; Niu et al. 2020; Gupta et al. 2010). During the stress period, an increase in cytosolic Ca^{2+} can promote the production of HSPs (Kaur and Gupta 2005).

For example, Feng et al. (2019) demonstrated that Hsp20s play a protective role in *Capsicum annuum* plants to withstand under HT stress. The expression of these HSPs may reduce the accumulation of ROS, enhance the activity of antioxidant enzymes, and can regulate the expression of heat-related genes, thereby helping plants to withstand under heat stress. The expression of HSP23.5, also reported by Sewelam et al. (2019), revealed that it plays similar functions in *Arabidopsis thaliana* under heat stress. Similarly, Huang et al. (2019) have studied the expression of CaHSP18.4 in *C. annuum*, and reported that overexpression of these HSPs under HT enhances the ability of ROS scavenging, thereby enhancing plant tolerance to

HT stress. The expression of some other groups of HSPs such as Hsp70, Hsp90, and Hsp100 also promoted the heat tolerance in *Hordeum vulgare* by maintaining protein homeostasis (Chaudhary et al. 2019). In another study, Hasanuzzaman et al. (2013) reported that higher molecular weight HSPs (HSP40, HSP70 and HSP100) play an essential role by facilitating the protein refolding under heat stress. In a recent study, Sharma et al. (2019) reviewed that HSP100 plays a protective role in ATP-dependent process of plants, under HT. HSP100 can act as chaperones and facilitate the correct protein refolding and enhanced the water and nutrient-use efficiencies under HT stress. Similarly, Taipale et al. (2010) reported that HSP90 facilitate the protein refolding under HT. This type of HSP plays a protective role and facilitates the maturation of various proteins under stress. The members of HSP70 kDa family, located in nucleus and mitochondria, enhance plant tolerance to temperature stress, mainly by contributing to cellular homeostasis and degradation of proteins (Kosakivska et al. 2008). Under HT, HSPs can improve the membrane stability, cellular processes, assimilate partitioning, and water and nutrient-use efficiency (NUE) in plants (Sharma et al. 2019; Salim and Raza 2020). In order to withstand thermal stress, different HSPs play a protective role in plant system to enhance temperature tolerance (Table 10.5). Similarly, Reddy et al. (2011) reported that expression of *PgHsp90* from *P. glaucum* plays an adaptive or protective role to counter the HT. This type of HSP act as a chaperone, and protects other types of protein under stress.

Furthermore, Lin et al. (2019) found the overexpression of various HSPs such as Hsp70, Hsp80, Hsp90, and Hsp100 in *Solanum tuberosum* stored under cold conditions, and reported that these HSPs enhance the stress tolerance by preventing the cellular damage. Nagaraju et al. (2020) reported that Hsp20 can maintain disaggregation of proteins and participate in diverse cellular functions in *Sorghum bicolor* under HT (40 °C) and LT (4 °C). Likewise, Jiang et al. (2020) reported that *RcHSP70* significantly resulted in better photosynthetic performance, higher electric conductivity, and more proline content, which ultimately improved crop tolerance to LT. In conclusion, HSPs enhance the tolerance to HT, LT, and FT mainly through alteration in protein structures.

4.2 The Role of NAC Genes Under Temperature Stress

NAC-type transcription factors (TF) played an essential role in plant development and against temperature stress responses. The expression of NAC type factor genes has been reported under LT and HT stresses (Hegedus et al. 2003; Olsen et al. 2005; Hou et al. 2020). Baloglu et al. (2012) proved that the NAC-type factor gene, *TaNAC69-1,* is strongly expressed under HT stress. The authors suggested that the expression of *TaNAC69-1* shows a vital role in the growth and development of plants under stress conditions. Similarly, in the same study, the expression of another NAC type gene *tNAMB-2* has been reported in wheat under LT stress (Baloglu et al. 2012) having the same functions, and plays an important role in developmental

Table 10.5 Different heat shock proteins and their protective role in coping with high, chilling, and freezing temperature

Heat shock protein	Plant specie	Temperature (°C)	Functions	References
HSP100, HSP70, and HSP40	*Arabidopsis. thaliana*	4 and 38	Helps in the release of high molecular weights HSPs, and facilitates the protein refolding	Swindell et al. (2007) and Hasanuzzaman et al. (2013)
HSP70	*Rumex patienta* L. and *Rumex tianshanicus*	2 and 40	The members of the HSP70 kDa family enhance tolerance to the temperature stress mainly through contributing to cellular homeostasis	Kosakivska et al. (2008)
HSP100	*Vicia faba* L.	38	Enhances protein stability under heat stress	Kumar et al. (2016)
HSP90	*A. thaliana*	22–29	Under heat stress, HSP90 acts as a co-regulator of heat stress related to signal transduction complexes. Also, it helps in managing of protein folding	Wang et al. (2016)
Hsp23.5	*A. thaliana*	45	Plays protective roles through reducing the production of ROS in plants under heat stress	Sewelam et al. (2019)
Hsp20s	*Capsicum annuum* L.	38	Helps plant to avoid the negative impact of heat stress by increasing antioxidant enzymes activities	Feng et al. (2019)
CaHSP16.4	*C. annuum* L.	40	Enhances the ability of ROS scavenging, thereby increased plant tolerance to heat stress	Huang et al. (2019)
Hsp70, Hsp90, Hsp100	*Hordeum vulgare* L.	42	Promoting thermotolerance by maintaining protein homeostasis	Chaudhary et al. (2019)
Hsp70, Hsp80, Hsp90, Hsp100	*Solanum tuberosum* L.	15, 4, 0	Prevents from cellular damage under cold stress	Lin et al. (2019)
Hsp20s	*Sorghum bicolor* L.	4 and 40	Maintain disaggregation of proteins under stress conditions	Nagaraju et al. (2020)
RcHSP70	*Rosa hybrida* L.	4	Enhanced plant tolerance through better photosynthetic performance, higher electric conductivity, and more proline content under cold stress	Jiang et al. (2020)

processes under LT stress. Tran et al. (2009) reported the expression of another group of NAC-factor (*GmNAC* genes) under LT. The researchers demonstrated that stress tolerance associated with *GmNAC* expression is mainly due to the improvement in physiological traits. In another study conducted by Meng et al. (2009), they reported that the *GhNAC* gene is expressed under LT and helps to enhance plant tolerance. These are involved in signal transduction cascades and hormonal-dependent signaling transduction under stress conditions. Moreover, differential expression of NAC gene (*ONAC045*) was identified in response to cold stress (Zheng et al. 2009; Baloglu et al. 2012). The studies suggest that *ONAC045* as transcriptional activator significantly enhanced plant tolerance to cold stress. The novel genes, *TaNAC4* and *TaNAC8,* play an important role in response to LT by enhancing plant growth and developmental processes (Xia et al. 2010), and the expression of *CarNAC1* gene under cold stress has been reported by (Peng et al. 2010), which plays a vital role in plant physiological metabolism. However, overexpression of *SNAC2* increased germination rates, promoted the growth, enhanced cell membrane stability, thereby enhancing the plant capacity to cope with LT (Hu et al. 2008). The expression of *CocNACs* also plays a vital role during plant development and enhances tolerance against cold stress in *Coffea canephora* (Dong et al. 2019b). The authors mentioned that this type of NAC gene plays an essential role, mainly during seed developmental processes. Another type of NAC genes, *CsNAC,* isolated from citrus, also plays an important role in response to LT and HT stress by increasing ethylene signaling (Fan et al. 2007).

A study conducted by Chen et al. (2019a) reported the expression of *BpNACs* in *Betula pendula*, and found that expression of this NAC promotes the cell growth and cellulose synthesis under LT stress (6 °C). Pang et al. (2019) reported that the overexpression of *AmNAC11* significantly contributes to enhancing LT (4 °C) tolerance in *A. thaliana*. The *AmNAC11* transgenic plants showed less leaf wilting, and ultimately led to more tolerance as compared with wild-types plant. In a recent study, Hou et al. (2020) demonstrated that expression of *CaNAC064* resulted in lower the EL and malondialdehyde (MDA) contents, and through this way significantly enhanced the tolerance of *C. annuum*. Additionally, Liu et al. (2020) identified the unique types of NAC genes (such as *PgNAC05-2, PgNAC41-2, PgNAC48, PgNAC56-1,* and *PgNAC59*), and reported that these genes play an important role in enhancing tolerance against LT (4 °C), by significantly enhancing the MDA content in cold-treated *Panax ginseng* plants. Similarly, Moraes de Freitas et al. (2019) identified other types of NAC genes (such as *OsNAC9, OsNAC10* and *OsNAP*) and reported that these genes increase the photosynthesis efficiency, reduce the respiration rates, and enhance plants tolerance against LT. *GhNAC4*, another type of NAC gene, also plays a vital role in enhancing the tolerance of cotton against LT and HT (Trishla et al. 2020). Duan et al. (2020) reported the expression of NAC family (*AgNAC63* and *AgNAC47*), and demonstrated that these genes play a protective role in *Apium graveolens* under LT and HT. However, authors did not mention the specific roles of these genes in developmental processes in plants. In conclusion, the above-discussed studies have suggested that NAC-type TFs play an important role during plant growth, development, and respond to HT, LT, and FT.

4.3 Late Embryogenesis Abundant Proteins

Late embryogenesis abundant (LEA) proteins accumulate during maturation of embryogenesis and play an important role in response to temperature stress (Zeng et al. 2018; Shi et al. 2020). Based on amino acid compositions, LEA proteins have been classified into different distinct subgroups: SMP proteins (located in the cytoplasm), dehydrin (located in mitochondria and nucleus), LEA1 (located in the nucleus and chloroplast), LEA2 (located in the cytoplasm), LEA3 (located in the chloroplast), LEA4 (located in mitochondria and nucleus), LEA5, and LEA6 (Zeng et al. 2018; Shi et al. 2020). The potential role of LEA proteins as stress tolerance has been well studied (Table 10.6; Imamura et al. 2013; Huang et al. 2019). During stress conditions, LEA proteins help in membrane stabilization, antioxidant activation, act as hydration buffering, and show binding affinity with metal ions, thereby increasing protection against abiotic stresses (Table 10.6; Zeng et al. 2018).

The role of LEA proteins to enhance thermal stress tolerance in plants has been well documented in various studies (Reddy et al. 2010, 2011, 2012). The expression of *PgLEA* protein provided a protective role in *Pennisetum glaucum* plants against HT (Reddy et al. 2012). Another group of LEAs, *PgHsc70*, have been reported for their protective role to cope with HT (Reddy et al. 2010). According to their findings, these proteins play an essential role in various cellular pathways and are also involved in re-folding of stress-denatured polypeptides under stress.

In another study, Lin et al. (2019) reported the expression of *CsLEA* genes and reported that these types of LEA not only enhance the crop growth and development but also increase the tolerance of *Camellia sinensis* plants under LT. Huang et al. (2019) studied the expression of *TaLEA* in wheat (*Triticum aestivum*) and reported that this group of LEA protein enhances stress tolerance against HT. However, the specific mechanism underlying stress tolerance still needs more exploration in future. Another type of LEA protein, *SbLEA*, also helps the *Sorghum bicolor* plants to cope with HT (Nagaraju et al. 2019). This type of LEA protein acts as a chaperone and helps in stabilization and denaturization of proteins under stress. *StLEA2-14*, *StLEA2-31, StLEA3-3, StASR-1,* and *StDHN-1* also upregulate under LT (4 °C) and HT (35 °C) and protect the plants from oxidative damage (Chen et al. 2019c).

Zeng et al. (2018) had identified the expression of LEA proteins in *Gastrodia elata*, which significantly enhances plant tolerance to LT stress. Besides, the expression of LEA1 and LEA3 from *A. sinica*, and LEA3 from *Z. mays* showed great tolerance to temperature stress (Liu et al. 2016; Zhao et al. 2016). These studies have demonstrated that LEAs protect the activity of lactate dehydrogenase, and cell membrane permeability, thereby enhancing plant tolerance to cold stress. Moreover, Kim et al. (2005) demonstrated that the expression of *CaLEA6* genes significantly enhanced tolerance against LT stress by reducing the Chl loss in *C. annuum* under stress.

The role of dehydrins in cold stress tolerance has been well reported. Peng et al. (2008) demonstrated that overexpression of the SK2 acidic dehydrin and *RcDHN5* enhances the tolerance against frost in transgenic *Arabidopsis* plants. In this study,

Table 10.6 The protective role of different LEA proteins under high, chilling, and freezing temperature. Abbreviations are explained in the text

Stress	LEA proteins	Crop	Function/protective role	References
Low temperature				
LT (4 °C)	Dehydrins (RcDHN5, COR410, DHN24, ShDHN, GtDHN1, SbDhn1, and MusaDHN1	*Arabidopsis thaliana*; *Strawberry fragaria*; *Cucumis sativus; Solanum lycopersicum*; *Sorghum bicolor*	The expression of these genes enhances tolerance against LT through increasing antioxidant enzyme activities, more proline accumulation, and reducing MDA contents	Houde et al. (2004), Yin et al. (2006), Peng et al. (2008), Shekhawat et al. (2011), Imamura et al. (2013), Liu et al. (2015), and Halder et al. (2017)
LT (4 °C)	PmLEAs	*Nicotiana tabacum*	The expression of *PmLEAs* enhances crop tolerance by reducing the oxidative damage under cold stress	Bao et al. (2017)
LT (5–10 °C)	LEA1 and LEA3	*Artemia sinica*	The expression of these types of LEAs protects the activity of lactate dehydrogenase, and cell membrane permeability, thereby enhancing plant tolerance to cold stress (5–10 °C)	Zhao et al. (2016)
LT (4 °C)	*CsLEA*	*Camellia sinensis* L.	Improves the crop growth, development, and enhanced tolerance to cold stress	Lin et al. (2019)
LT (4 °C) and HT (35 °C)	*StLEA2-14, StLEA2-31, StLEA3-3, StASR-1,* and *StDHN-1*	*Solanum tuberosum* L.	Enhances crop defense to heat and cold stress by reducing the oxidative damage	Chen et al. (2019c)
High temperature				
HT (40 °C)	*SbLEA*	*Sorghum bicolor* L.	The expression of such type of genes plays an essential role during stress condition	Nagaraju et al. (2019)
HT (42 °C)	*TaLEA*	*Triticum aestivum* L.	Plays a protective role under heat stress	Huang et al. (2019)

the authors mentioned that *RcDHN5* dehydrins rescue the activities of enzymes which are involved in osmoticum adjustment. Similar findings were reported by Houde et al. (2004); they observed that overexpression of *COR410* enhances the tolerance by improving membrane stability and nutritional quality of grains in wheat under frost stress. The higher expression of *DHN24* was also reported to enhance tolerance against cold stress, through promoting the activity of glucosyl transferase (Yin et al. 2006). Moreover, SK3-type dehydrin and *ShDHN* were also shown to enhance tolerance against LT, by increasing ROS scavenging and enhancing plant capability to withstand stress condition (Liu et al. 2015). Similarly, *GtDHN1* and *GtDHN2* from *Gentiana trifloral* are also helpful for enhancing tolerance, as these factors significantly enhance the activities of antioxidant enzymes (such as APX and GR) under cold stress (Imamura et al. 2013). Shekhawat et al. (2011) reported that expression of *MusaDHN1* significantly enhances the tolerance by increasing proline accumulation and reducing MDA content under cold stress.

4.4 Antioxidant Enzymes Activities

Temperature extremes (HT, LT, and FT) induce oxidative stress for plants. During stress conditions, ROS gets highly accumulated in plants, which triggers the programmed cell death (PCD) (Mittler et al. 2011; Singh et al. 2019; Nedunchezhiyan et al. 2020; Hasanuzzaman et al. 2020) and can cause oxidative stress (Gudkov et al. 2019; Hasanuzzaman et al. 2020). The expression of antioxidant enzymes are positively correlated with higher tolerance to HT and LT (Table 10.7). As stress tolerance, plant alleviates the heat stress by scavenging the excess ROS production through antioxidant enzymes such as CAT, SOD, APX, glutathione reductase (GR), peroxidase (POD), and guaiacol peroxidase (POX) (Hasanuzzaman et al. 2020). Various studies also reported the increased activities of antioxidant enzymes under heat stress. For instance, Zhang et al. (2017a) studied the effect of HT (40 °C) on rice, and reported increased activities of SOD, POD, APX, and CAT. Similarly, Badawi et al. (2007) also reported the improved activity of CAT, SOD, APX, and GR under HT. Furthermore, Luo et al. (2018) demonstrated that HT (40 ± 0.5 °C) also led to enhance the activities of CAT, and APX in wheat. Enhanced activity of SOD, POX (Gupta et al. 2013; Ibrahim et al. 2013), and CAT were also reported under HT (Gupta et al. 2013). Moreover, Kumar et al. (2013) reported higher SOD activities in wheat plants under HT, which showed more tolerance against abiotic stresses. However, Wang et al. (2014) reported the unchanged values of SOD and GR under HT. The involvement of different genes in the regulation of antioxidant enzymes has been reported. For example, Kumar et al. (2013) reported SOD-transcript in wheat under HT. In plants, various developmental processes and environmental signals have regulated the SOD genes (Scandalios 2005). The expression and involvement of *APX* genes under temperature stress have been reported in different studies (Bonifacio et al. 2011). It was also well demonstrated that *GPX* genes resulted in enhancing the tolerance against HT (Lu et al. 2013) through maintaining the redox homeostasis.

Zhang et al. (2017d) reported increased activity of SOD, POD, and CAT under LT (12/6 °C, day/night temperature) in melon plants. Similarly, Wani et al. (2018) also reported the increased activities of CAT, SOD, POD, and GR in *Capsella bursa-pastoris* seedling grown under cold stress (10 °C). Similar findings were observed by Ignatenko et al. (2019) while studying wheat under cold stress (4 °C). Moreover, Janmohammadi et al. (2012), also reported enhanced activity of SOD,

Table 10.7 Summary of experiments indicating the protective roles of various antioxidant enzymes under high, chilling, and freezing temperature

Antioxidant enzymes	Stress condition	Increase/ decrease	Plant	Specific role	References
CAT	12/6 °C (day/night) for 7 d	Increased	*Cucumis melo* L.	Increased activity of CAT helps to cope with oxidative stress	Zhang et al. (2017b)
	10 °C (120 h)	Increased	*Capsella bursa-pastoris*		Wani et al. (2018)
	4 °C for 7 d	Increased	*Triticum aestivum* L.		Ignatenko et al. (2019)
	4 °C for 20 d	Increased	*T. aestivum* L.		Janmohammadi et al. (2012)
	−5 °C for 3 h	Increased	*Camellia sinensis* L.		Li et al. (2018a)
	40 °C for 10 d (6 h for each night)	Increased	*Oryza sativa* L.	Increased activity can lead to prevention of spikelet degeneration	Zhang et al. (2017a)
	42 °C for 1 h	Increased	*Vigna aconitifolia*	More activity enhanced stress tolerance	Harsh et al. (2016)
	42 °C for 1 h, and 45 °C for 2 h	Increased	*Spinacia oleracea* and *Arabidopsis thaliana*	Increased activity of CAT improves the stress tolerance in heat-treated Spinish (42 °C for 1 h) and *Arabidopsis* (45 °C for 2 ha) plant	Qi et al. (2019)
	40 ± 0.5 °C for 24 h	Increased	*T. aestivum* L.	Improves stress tolerance	Luo et al. (2018)
POD	12/6 °C (day/night) for 7 d	Increased	*Cucumis melo* L.	Increased activity helps to cope with oxidative stress	Zhang et al. (2017b)
	10 °C for 120 h	Increased	*Capsella bursa-pastoris*		Wani et al. (2018)
	4 °C for 7 d	Increased	*T. aestivum* L.		Ignatenko et al. (2019)
	40 °C for 10 d (6 h for each night)	Increased	*Oryza sativa* L.	Prevents spikelet degeneration caused by heat stress	Zhang et al. (2017a)

(continued)

Table 10.7 (continued)

Antioxidant enzymes	Stress condition	Increase/ decrease	Plant	Specific role	References
	42 °C for 1 h for Spanish, and 45 °C for 2 h for *Arabidopsis*	Increased	*Spinacia oleracea* and *Arabidopsis thaliana*	Increased activity of POD significantly enhances the stress tolerance in heat-treated Spinish and *Arabidopsis* plant	Qi et al. (2019)
SOD	12/6 °C (day/night) for 7 d	Increased	*Cucumis melo* L.	Increases the activity of CAT and improves the stress tolerance	Zhang et al. (2017b)
	10 °C for 120 h	Increased	*Capsella bursa-pastoris*		Wani et al. (2018)
	4 °C for 7 d	Increased	*T. aestivum* L.		Ignatenko et al. (2019)
	4 °C for 20 d	Increased	*T. aestivum* L.		Janmohammadi et al. (2012)
	−5 °C for 3 h	Increased	*Camellia sinensis* L		Li et al. (2018a)
	40 °C for 10 d (6 h for each night)	Increased	*O. sativa* L.	Under stress, prevents spikelet degeneration, and increases stress tolerance	Zhang et al. (2017a)
	42 °C for 1 h for Spanish, and 45 °C for 2 h for *Arabidopsis*	Increased	*Spinacia oleracea* and *A. thaliana*	More accumulation improves plant tolerance under heat stress	Qi et al. (2019)
	42 °C for 1 h	Increased	*Vigna aconitifolia*	Improves stress tolerance	Harsh et al. (2016)
APX	4 °C for 20 d	Increased	*T. aestivum* L.	Helps to cope with oxidative stress	Janmohammadi et al. (2012)
	−5 °C for 3 h	Increased	*Camellia sinensis* L.		Li et al. (2018a)
	40 °C for 10 d (6 h for each night)	Increased	*O. sativa* L.	Increased activity prevents spikelet degeneration, and promotes tolerance to stress	Zhang et al. (2017a)
	42 °C for 1 h for Spanish, and 45 °C for 2 h for Arabidopsis	Increased	*Spinacia oleracea* and *A. thaliana*	More accumulation of APX prompts more tolerance against heat stress in Spinish and *Arabidopsis* plants	Qi et al. (2019)
	40 ± 0.5 °C for 24 h	Increased	*T. aestivum* L.		Luo et al. (2018)

	10 °C for 120 h	Decreased	*Capsella bursa-pastoris*	Did not play a specific role under stress condition	Wani et al. (2018)
GR	10 °C for 120 h	Increased	*Capsella bursa-pastoris*	Reduced the toxic effects of ROS	Wani et al. (2018)
	−5 °C for 3 h	Increased	*Camellia sinensis* L.		Li et al. (2018a)
POX	4 °C for 20 d	Increased	*T. aestivum* L.	Reduced oxidative stress-induced damage	Janmohammadi et al. (2012)
	42 °C for 1 h	Increased	*Vigna aconitifolia*		Harsh et al. (2016)

Abbreviations are defined in the text

CAT, APX, and POX under LT. The expression of *CAT* genes in rice has been reported on exposure to LT (Matsumura et al. 2002), by scavenging of H_2O_2. Similarly, Turk et al. (2014) reported the SOD, CAT, POX and GR activities under FT (−5 °C for 3 h) *Camellia sinensis* (Li et al. 2018a).

5 Approaches to Enhance Stress Tolerance

Abiotic stresses, mainly changing temperature, are the major constraint for crop production, so finding new strategies to increase the stress tolerance is crucial to overcome food security (Raza et al. 2019a, b, 2020). Temperature stress causes significant crop losses by affecting plant growth and crop productivity. Plants differ in their tolerance level according to HT, LT, and FT (Zhang et al. 2019c). Therefore, in this section, we have documented the current and widely adapted mitigation approaches to enhance temperature tolerance under the changing climatic conditions.

5.1 Conventional Breeding Platforms

Conventional breeding for adaptation to abiotic stress is a more complicated technique than breeding for other traits. In conventional breeding, best-defined characters of tolerant genotypes are established in sensitive genotypes. However, for each stress tolerance, there may be several mechanisms and different levels to cope with stress conditions, which can be associated with plant phenological stage and cause divergent responses (Anwar and Kim 2020).

Meanwhile, these traits are controlled by various quantitative trait loci (QTL) that generate continuous variations (Islam et al. 2019). Conventional breeding has been reportedly accepted to develop new heat-tolerant genotypes, for instance, a variety of broccoli has been established with improved head quality hank before the onset of heat stress (He et al. 2020).

Another basis of conventional breeding for HT and LT tolerance is associated with QTL mapping responsible for the tolerance, and their association to linked morphological markers, which are being used for valid selection through marker-assisted selection (MAS) (Gantait et al. 2019). Numerous studies have been conducted related to QTL, for example, heat tolerance in rice (Barik et al. 2019; Donde et al. 2019), barley (Gantait et al. 2019), and maize (Tiwari and Yadav 2019). The new genomic approaches have overcome many of the restrictions for the detection and characterization of QTL responsible for HT tolerance (Daware et al. 2020). These technologies provide a wide array of tools to increase temperature tolerance; however, the phenotyping protocols are essentially required for evaluating large population in terms of both selection processes and source identification of tolerance (Ortiz 2018). HT and LT are the major causes of yield reduction, so traditional breeding is also a successful technique for developing LT-tolerant genotypes (Frukh et al. 2020).

5.2 Modern Breeding Approaches

5.2.1 Marker-Assisted Selection

Molecular markers are portions of DNA-linked biological traits, which could be controlled through genetic tools, and can be inherited into next generations under stress conditions (Mascher et al. 2019; Bohar et al. 2020). Molecular marker exhibited selection based on genetic differences among species related to specific stress. Mainly, it does not specify the particular genes and acts as chromosomal landmarks of genes to facilitate the identification of the target gene of desirable traits (Seifi and Shelp 2019). Some QTLs for LT have been identified in tomatoes by using polymorphic molecular markers (Tian et al. 2017). Yuan et al. (2018) determined that the introgression of QTLs enhanced LT tolerance in rice (De Leon et al. 2017). The two species of Asian-cultivated rice showed differences in LT tolerance. Japonica cultivars possess stronger LT tolerance than Indica cultivars (Sang and Ge 2007).

Several molecular markers have been used in MAS; however, single nucleotide polymorphisms (SNPs) and simple sequence repeats (SSRs) are being used extensively. These markers were used in pyramid genes conferring resistance to abiotic stresses, that is. FT, LT, and HT in spinach (Li et al. 2019), tomatoes (Hu et al. 2019), okra (Phornvillay et al. 2020) and strawberry (Ergin et al. 2016). In another study, heat tolerance was improved by deploying MAS approaches in barley (Gous et al. 2016). The application of MAS program under temperature stress in various crops was reported, that is, HT tolerance in rice (Dixit et al. 2017), FT tolerance in wheat (Leonova et al. 2017), LT tolerance in maize (Lone et al. 2018), and sorghum (Rao et al. 2016), etc. Similarly, tolerance to freezing and chilling was improved using MAS in switch grass (Poudel et al. 2019) and *B. oleraceae* (Song et al. 2018) breeding. However, reports for improving tolerance to heat are scanty in rice (Lang et al. 2015).

5.2.2 Qualitative Trait Loci Mapping

Qualitative trait loci (QTL) mapping is a statistical procedure used to distinguish the complex plant traits into their components (Gupta et al. 2019). It controls the heritable variations in crop plants. It is also helpful to learn the genetic architecture of plants to improve them for desirable traits during the course of their evaluation (Gupta et al. 2019; Dong et al. 2019a). To identify the temperature stress-resistant QTLs, a lot of work has been done by plant biologists, but identified QTLs proved unstable across different environmental conditions due to their complex inheritance mechanism of abiotic stress tolerance (Mugabe et al. 2019; Schläppi et al. 2017).

To overcome the heat-related stresses, plant breeders have mapped many QTLs in various important crops. In order to improve the crop productivity of rice under HT. Many QTLs have been reported that were related to senescence under HT stress (Wen et al. 2019). Similarly, Zhao et al. (2016) reported an important QTL on chromosome 9 in Indian rice cultivar that explained up to 50% phenotypic variation, which was related to HT tolerance and amylose content. Similarly, in bread wheat, QTLs for HT tolerance were mapped by using different heat-related traits such as a decrease in canopy temperature (Prasad et al. 2019), senescence (Zhang et al. 2019a), and FT stress (Kaloki et al. 2019). Moreover, four QTLs (Qhr1; qhr3-1qhr4-3qhr8-1) associated with HT tolerance at the flowering stage in rice were reported by Cao et al. (2020), and two minor QTLs (qHTSF1.1 and qHTSF4.1) controlling the spikelet fertility under HT conditions were mapped in rice (Liu et al. 2019). HT decreases spikelet fertility and disturbs membrane stability, so keeping these traits in mind. Talukder et al. (2014) investigated QTLs (qHTSF1.1, qHTSF4.1) related to spikelet fertility in HT. Additionally, root conductivity is an important trait that can be used as an indicator to QTLs of LT tolerance in cereals (Akram et al. 2019). LT tolerance can be controlled by controlling the biological mechanism taking place in plants, that is, cold sensing, transcriptional regulations, and post-transcriptional modifications (Cheng et al. 2019b). Different researchers have explained the molecular and cellular mechanism of LT; however, its genetic mechanism is not understood yet. Among cereals, rice is the most affected cereal by LT stress, so by broadening the rice gene pool through introducing LT tolerance traits and its related genes in wild rice, its production can be enhanced (Muthu et al. 2020). Three more QTLs (qPSST-3, qPSST-7, and qPSST-9) were verified from ten chilling-tolerant lines of rice with spikelet fertility of 51–81% compared to 7% (chilling-sensitive parent) and 73% (chilling-tolerant donor). LT-related QTLs have been mapped in lentil (Mane et al. 2020), maize (Fu et al. 2019a), ryegrass (Vines 2019), Sorghum (Mace et al. 2019), and faba bean (Abd El-Fatah and Nassef 2020).

5.2.3 Genome-Wide Association Studies

Genome-wide association studies (GWAS) consisted of a genomic-wide set of genetic variants in different varieties to identify trait-associated variants (Tam et al. 2019). GWAS mainly emphasize the associations between traits and SNPs, for instance, DNA of plant varieties is compared with different phenotypes related to a specific trait (Pantaliao et al. 2016). A GWAS is a widely used powerful tool in breeding programs due to its ability to efficiently analyze complex traits under different environmental conditions (Tam et al. 2019). In rice, GWAS-based high-density SNP arrays have been used for detecting trait-associated loci for LT tolerance (Pantaliao et al. 2016). Similarly, Zhang et al. (2008) successfully mapped 66 QTLs for LT tolerance in 294 rice accessions, which were genotyped with the 44 K SNP chip at the seedling stage. Likewise, Lv et al. (2016) mapped 529 rice accessions and identified 132 QTLs for FT and LT in rice. Additionally, Pan et al. (2015) used the GWAS technique for mapping 52 QTLs for LT at booting and germination stages while working on 172 Chinese rice accessions, which were genotyped with 273 simple sequence repeat (SSR) markers. In this connection, Fujino et al. (2015) identified 17 QTLs in 63 Japanese varieties at the germination stage of rice that were genotyped with 115 SSR markers. Moreover, it has been reportedly accepted that FR-A2 locus on chromosome 5A in wheat is associated with FT, which consists of a minimum of 11 CBF genes and is located at approximately 30 cM near VRN1 (Vágújfalvi et al. 2003). Interestingly, QTLs separation for HT in wheat has been done at the grain filling stage by using bi-parental mapping populations (Maulana et al. 2018; Vijayalakshmi 2007). However, Talukder et al. (2014) identified many minor and major QTLs at vegetative and reproductive stage in wheat chromosomes; for example, five QTLs for HT have been identified in wheat on chromosomes 7A, 6A, 2B, 1D, and 1B, and two QTLs were detected on chromosomes 5B and 2B in spring wheat population (Butler 2002).

5.3 Application of Plant Growth Regulators to Enhance Stress Tolerance

Plant hormones, phytohormones, or PGRs play a key role in plant growth and development and have an essential function in plant interactions with the environment (Raza et al. 2019b, 2020c). Several PGRs, such as ABA, JA, CKs, GA, SA, ET, auxin, and BRs, play a crucial role in plant development under HT, LT, and FT conditions (Table 10.8; Kumar et al. 2011; Waqas et al. 2017; Khan et al. 2017; Prerostova et al. 2020). These PGRs modulate plant responses to temperature stress at cellular, tissue, and organ levels (Waqas et al. 2019). Prerostova et al. (2020) proved their role under HT stress, by evaluating the phytohormones profile of *A. thaliana* after applying direct heat shock (45 °C, 3 h). Similarly, Kumar et al. (2011) reported that 50μM application of ABA increases germination, growth rate, and Chl content and antioxidant system in wheat under HT (45/35 °C day/night for 12 h/12 h). Likewise, Zhou et al. (2014) observed higher NADPH oxidase activity by treating tomato plants with 50μM ABA under HT stress (42 °C for 6 h); a similar increase in NADPH oxidase activity was also found by treating plants with 24-epibrassinolade (200 nM) under HT (Zhou et al. 2014). Interestingly, 100μmol L^{-1} ABA foliar treatment increases the pollen viability at pollen mother cell at the mitotic stage of rice under HT stress (Islam et al. 2019). However, Li et al. (2020a) reported negative regulation of ABA by increasing the leaf temperature and energy homeostasis under HT stress.

Moreover, SA (0.5 mM, 1 mM and 0.01% concentration) increases the HT tolerance of tomato and wheat respectively by improving growth and development and increasing photosynthetic and antioxidant enzyme activities (Jahan et al. 2019; Afzal et al. 2019; Wassie et al. 2020). Clarke et al. (2009) suggested that JA can improve thermotolerance in plants. They applied low dose of methyl jasmonate (MeJA) and noted improved cell viability by controlling the EL in *Arabidopsis* under HT stress.

Additionally, GA confers HT and LT stress by reducing conductance and stomatal density (Plaza-Wüthrich et al. 2016). Similarly, a foliar spray of 0.1% SA and 50 mM SA increased LT tolerance while promoting hormonal metabolism, signal transduction, energy supply, photosynthetic rate, transpiration, enzymatic activities and crop yield (Waqas et al. 2017; Li et al. 2017b). According to Tian and Li (2018),

Table 10.8 Summary of experiments documented the beneficial role of PGRs to enhance high, chilling, and freezing temperature tolerance in plants

Plant growth regulators	Plant	Concentration	Temperature	Protective role and mechanism	References
High temperature					
Abscisic acid	*Triticum aestivum* L.	50µM	45/35 °C day/night (12 h/12 h)	Increased germination, growth, Chl contents, and antioxidant enzyme activity while reduced H_2O_2 concentration	Kumar et al. (2011)
24-epibrassinolide; Abscisic acid	*Solanum lycopersicum* L.	200 nM; 50µM	42 °C for 6 h	Increased expression of *RBOH1*-gene, induced NADPH oxidase activity and apo-plastic hydrogen peroxide accumulation	Zhou et al. (2014)
(Cytokinin's) 6-benzylaminopurine	*T. aestivum* L.	10 mg L^{-1}	35/20 °C for 2 d	Increased growth and yield but decreased GA and ABA contents	Yang et al. (2016)
Salicylic acid	*Solanum lycopersicum* L.	1 mM	42 °C for 36 h	Increased photosynthesis activity and antioxidant enzyme functions	Jahan et al. (2019)
Salicylic acid	*T. aestivum* L.	0.01%	Plastic sheet tunnels temperature range 15–20, 20–22, 25–31, 32–35 °C during January, February, March, and April, respectively	Improved growth and development and yield with higher antioxidants and relative water contents and minimizing oxidative damage	Afzal et al. (2019)
Brassinosteroid, Methyl Jasmonate, Salicylic acid	*Brassica rapa* L.	200 nM, 200 nM, 2 mM	28–30 °C d/22–25 °C night for 5 d	Reduced physiological damage and enhanced the activity of the antioxidant enzymes	Lee et al. (2020)
Salicylic acid	*Zea mays* L.	50 mg L^{-1}	Late sown	Improved photosynthetic pigment, stability index of membrane, relative water content, growth and yield of crop	Iqbal et al. (2020)
Salicylic acid	*Medicago sativa* L.	0.5 mM	38/35 °C day/night temperature for 3 d	Improved leaf morphology, plant height, biomass, Chl content, photosynthetic efficiency, and antioxidant enzyme activities	Wassie et al. (2020)

Chilling and freezing temperature					
Gibberellic acid	*Z. mays* L.	100 mg L^{-1}	10 °C lower than optimum temperature	Improved germination and growth with increasing total sugars and higher α-amylase activity	Afzal et al. (2008)
Salicylic acid	*Oryza sativa* L.	100 mg L^{-1}	8 °C for 4 d	Improved antioxidants, relative water content, and increased root and shoot length	Pouramir-Dashtmian et al. (2014)
Gibberellic acid	*T. aestivum* L.	100µM	0 °C (October), −10 °C (November), and −25 °C (December)	Decreased the ABA content, resulting in lower soluble sugar and protein content and aggravated oxidative damage	Wang et al. (2015)
6-benzylaminopurine	*Solanum melongena* L.	10µM	10/5 °C for 120 h	Improved antioxidants and reduced ROS	Chen et al. (2016)
glycine betaine	*Prunus persica* L.	10 mM	0–20 °C for 3 d	Induction of energy status, and proline contents which prevented membrane damage	Shan et al. (2016)
Salicylic acid: brassinolide	*O. sativa* L.	1 (SA) (mmol/L): 2 (BRs) (mg/L)	13 °C for 4 d	Increased seedling survival, leaf area, height of seedling and weight, root morphology and by reduction in lipid peroxidation and increased antioxidant enzymes	Mo et al. (2016)
Gibberellic acid	*Solanum lycopersicum* L.	0.5 mM	4 ± 1 °C for 28 d	Reduced chilling injury index	Zhu et al. (2016)
Salicylic acid	*O. sativa* L.	100 mg L^{-1}	18 °C d and night for 48 h	Higher starch metabolism, lesser lipid peroxidation, and greater antioxidative defense system	Hussain et al. (2016)
Salicylic acid	*Z. mays* L.	50 mM	13 °C for 7 d	Hormones metabolism and signal transduction were promoted and increased activities of antioxidant enzymes	Li et al. (2017b)

(continued)

Table 10.8 (continued)

Plant growth regulators	Plant	Concentration	Temperature	Protective role and mechanism	References
Salicylic acid	*Z. mays* L.	0.1%	8–13 °C till harvesting	Improved crop growth, yield and quality of grains with higher photosynthetic and transpiration rates	Waqas et al. (2017)
Abscisic acid	*Z. mays* L.	10^{-5} M	14 ± 0.5 °C and 5 ± 0.5 °C (day and night) and the light time was 12 h	Enhanced root biomass, increased enzyme activities such as phenylalanine ammonia-lyase and polyphenol oxidase and enhanced flavonoid and phenolic contents	Tian and Li (2018)
24-epibrassinolide	*Cucumis sativus* L.	0.1μM	12 °C for 7 d	Improved antioxidant enzyme activities and reduced reactive oxygen species which enhanced growth	Anwar et al. (2018)
Ethylene	*Pyrus* × *bretschneideri*	100μL L^{-1}	0 ± 0.5 °C for 5 h	Improved antioxidant defense systems and reduced reactive oxygen species	Wei et al. (2019)
24-epibrassinolide	*Vitis vinifera* L.	0.1 mg L^{-1}	4 °C for 12 h	Improved the antioxidant defense activity	Chen et al. (2019d)
Salicylic acid	*Moringa oliefera* L.	50 mg L^{-1}	14–18 °C till harvesting	Enhanced growth, Chl contents, phenolics and membrane stability index	Batool et al. (2019b)
Brassinolide	*Z. mays* L.	1 mg L^{-1}	4 °C for 2 d	Increased the germination rate and improved antioxidant systems and reduced reactive oxygen species	Sun et al. (2020)
Salicylic acid	*T. aestivum* L.	100μM	15 h of 0 °C and minimum was −7 °C	Improved the capacity of photosynthesis, antioxidants which led to reduce the negative effect on growth and yield	Wang et al. (2020d)
Salicylic acid	*T. aestivum* L.	100μM	−2 °C for 24 h	Induced freezing tolerance and ABA synthesis and reduced H_2O_2 accumulation	Wang et al. (2020c)

10^{-5} M ABA increases LT tolerance at 14/5 °C (day/night) by improving root biomass and increasing phenylalanine ammonia-lyase and polyphenol oxidase enzyme activities, which significantly increases the total phenolics and flavonoid contents. Yadav et al. (2011) reported that 100μM ABA-primed plants prevents LT stress exposure (10 d at 4 °C) with 100% survival rate. Additionally, 24-epibrassinolide at 0.1μM and 0.1 mg L^{-1} level also mitigates LT stress (Anwar et al. 2018; Chen et al. 2019d).

Additionally, Shibasaki et al. (2009) observed the role of LT stress (4 °C for 8–12 h) on gravity and found that gravity responses inhibited up to 50% under LT stress, suggesting that LT stress inhibits the intracellular trafficking of auxin carriers, so proving its negative consequences under LT stress. Moreover, ET as a gaseous hormone improved antioxidant system at 0.5 °C in pear (Wei et al. 2019). Furthermore, Sun et al. (2016) reported that ET response varies in different species under LT. They observed that LT increases ET production in grapevine. They also noted that the exogenous application of 1-aminocyclopropane-1-carboxylase (precursor of ET) improves LT tolerance. In contrast, application of aminothoxyvinylglycine (ET biosynthesis inhibitor) reduced LT tolerance in grapevine, suggesting the involvement of ET in improving LT tolerance. Another hormone, JA, plays a vital role during FT and LT tolerance. In this connection, Kolaksazov et al. (2013) experimented on *Arabis alpina* (a member of the Brassicaceae family) and observed the JA level under different temperatures. They concluded that all sensitive and tolerant plants had a high level of JA under normal conditions (22 °C). In contrast, after 4 °C LT, the tolerant plants did not show any considerable change in JA content, while JA content reduced up to 10-fold in sensitive plants. However, upon exposure to FT (0 °C), the sensitive plants had nearly the same level of JA, while in tolerant plants, JA content dropped drastically, suggesting that JA may be the principal mediator of JA under cold stress. Moreover, Du et al. (2013) deduced that in LT stress, genes are involved in JA synthesis and signaling, while HT stress suppresses its gene expression in rice plants.

On the other hand, 100μM SA increased FT tolerance (− 2/− 4 °C) in wheat by enhancing ABA synthesis, antioxidant activities and photosynthetic efficiency, while decreasing H_2O_2 accumulation (Wang et al. 2018, 2020d). Wang and Li (2006) also reported that SA increased FT tolerance (−3 °C for 3 h) by increasing the activities of MDHAR, DHAR, APX, AsA/GSH pool, and by maintaining the Ca^{2+} homeostasis in *V. vinifera*.

5.4 Application of Aqueous Extract of Crops in Mitigating Extreme Temperature Stress

Several experiments have been carried out to decipher the potential role of pretreatment of crops with protein hydrolysates and extracts in improving plant growth under different temperature constraints (Table 10.9). Sarwar et al. (2018) reported that moringa water extract (MWE) (30 times diluted) prevents the cotton crop from

Table 10.9 Effect of crop water extracts on plants in mitigating high, chilling, and freezing temperature

Crop water/leaf extracts	Plant	Concentration	Stress condition	Protective role and mechanism	References
High temperature					
Moringa leaf extract	*Zea mays* L.	1 (moringa): 30 (water)	28–35 °C at sowing time; late sown	Improved seedling establishment but also yield performance of spring maize through physiological improvement	Mahboob et al. (2015)
Sorghum water extract; sunflower water extract; brassica water extract; moringa leaf extract	*Triticum aestivum* L.	3%	Glass canopies were 4–2 °C higher than the ambient temperature	Improved growth and yield	Farooq et al. (2017)
Moringa leaf extract	*Chenopodium quinoa* Willd.	3%	7–10 °C more than ambient; 76 d after sowing till harvest	Enhanced photosynthetic rate, intrinsic water-use efficiency due to improved leaf Chl and antioxidant defense system	Rashid et al. (2018)
Sorghum water extract; sunflower water extract; brassica water extract	*T. aestivum* L.	1:10; 1:10; 1:10	Glass canopies were 4–2 °C higher than the ambient temperature	Improved growth and yield with higher accumulation of proline, soluble phenolics, and glycine betaine	Farooq et al. (2017)
Moringa leaf extract; Sorghum water extract	*T. aestivum* L.	3% 0.075%	Plastic sheet tunnels temperature range 15–20, 20–22, 25–31, 32–35 °C during January, February, March, and April, respectively	Improved growth, development, and yield due to high activities of antioxidant enzymes and relative water contents and minimizing oxidative damage	Afzal et al. (2019)

(continued)

Table 10.9 (continued)

Crop water/leaf extracts	Plant	Concentration	Stress condition	Protective role and mechanism	References
Moringa leaf extract	*Z. mays* L.	3%	10 °C more than ambient temperatures; 10 d	Improved photosynthetic pigment, carotenoids, crop growth and yield	Batool et al. (2019a)
Moringa leaf extract	*Z. mays* L.	3.3%	27–32 °C at sowing time; late sown	Improved photosynthetic pigment, membrane stability index, relative water content, crop growth and yield	Iqbal et al. (2020)
Chilling and freezing temperature					
Moringa leaf extract	*Z. mays* L.	3%	12 ± 1 °C at sowing time; early sowing in field	Improved germination and growth with improved Chl content, amylase activity, and total sugar contents	Afzal et al. (2012)
Moringa leaf extract; sorghum water extract	*Z. mays* L.	3% 10 mL L^{-1}	13 °C for 15 d	Improved germination and growth	Imran et al. (2013)
Sugar beet root extract; moringa leaf extract; aloe vera leaf extract	*Lens culinaris* L.	2% 3% 2%	10 ± 1 °C for 1 week	Improved germination and growth with superior α-amylase activity and sugar contents	Imran et al. (2014)
Moringa leaf extract	*Z. mays* L.	3%	0–12 °C at sowing time; early sowing	Improved stand establishment, Chl and phenolic contents with improved yield	Bakhtavar et al. (2015)
Sorghum water extract; moringa leaf extract	*Z. mays* L.	3% 3%	8–13 °C till harvesting	Improved crop growth, yield and quality of grains with higher photosynthetic and transpiration rates	Waqas et al. (2017)
Moringa leaf extract	*Moringa oliefera*	3%	14–18 °C till harvesting	Enhanced growth, Chl contents, phenolics and membrane stability index	Batool et al. (2019a)

HT-induced injury at 38/24 °C and 45/30 °C. Additionally, sunflower, *Brassica* and sorghum water extract (SWE) also gave promising results in wheat under LT stress (2–4 °C higher than ambient) by improving growth and yield and enhancing the accumulation of proline, soluble phenolics, and glycine betaine (Farooq et al. 2017). Afzal et al. (2019) applied 3% moringa leaf extract (MLE) and 0.075% SWE on wheat under HT stress and reported higher RWC and antioxidant enzyme activities with improved growth and production. In this connection, (Iqbal et al. 2020) also extended their studies on the use of MLE, and explored improved photosynthetic efficiency, RWC, membrane stability index, and higher crop growth and yield production in late-sown maize plants. Moreover, application of *Ipomoea cairica* aqueous leachate (0.025 g mL^{-1}) as soil supplementation improved germination in *B. compestris* and *Raphanus sativus* L. at HT (26 °C). Afzal et al. (2015) reported higher yield production in late-sown wheat with the foliar leaf extract application of sunflower (1.5%), sorghum (3%), rice (3%), canola (3%), and MLE (3%) at tillering and booting stages.

On the other hand, seed priming with chitosan showed promising results in enhancing seed germination and seedling growth under LT stress (Guan et al. 2009; Hussain et al. 2019b). Similarly, Waqas et al. (2017) applied SWE and MLE to improve the LT tolerance of autumn maize. They observed that SWE and MLE increased the plant height, leaf area duration, leaf area index, crop growth rate, total dry matter, biological yield, grain yield, and 1000 grain weight under LT stress, whereas MLE enhanced grain starch, oil and protein content as compared to control plants. Moreover, enhanced crop water productivity was also reported in MLE-treated maize plants. Waqas et al. (2017) also noted higher growth and production of maize with the application of 3% MLE and SWE under LT stress (8–13 °C till harvest). Similarly, (Batool et al. 2019a) applied 3% MLE on maize, and reported improved pigment content with higher yield production under LT stress (10 °C higher than ambient). They also noted higher Chl, phenolics content with application of MLE.

6 Conclusion

Climate change is the leading cause of environmental stresses and alarming the ecosphere by hindering agriculture and its products. Plants are exposed to various environmental stresses, and among them, temperature (HT, LT, and FT) is the most important environmental stress that poses drastic effects on agricultural sustainability, and hinders to achieve a goal of “zero hunger” proposed by FAO. Moreover, HT, LT, and FT reduce the growth and development of plants, alter mineral uptake, hinder photosynthesis, and affect various important yield attributes. Change in the optimum temperature causes an oxidative outburst that leads to ultrastructural alterations even at the organelle level. These alterations can be physiological, biochemical, morphological, and genomic forms together with transcriptional and post-transcriptional levels. The plant can only tolerate a certain extent of temperature by adjusting compatible solutes and antioxidant defense system, or by maintaining membrane stability. Notably, it has been reported that the world population is anticipated to be around 9.8 billion in 2050 and 11.2 billion in 2100; thus, crop production must be significantly increased to feed to growing population and to achieve a goal of “zero hunger”.

To overwhelm the food supply in near future, it is very crucial to develop climate-resilient crops. The methods to overcome this problem and the approaches we should adapt are still vague. During the past few decades, conventional and modern breeding platforms, including MAS, QTL, and GWAS, have made tremendous progress for the development of temperature-resistant plants. Likewise, several PGRs (ABA, JA, SA, ET, SLs, etc.) and aqueous leaf extracts of crops have gained the attention of researchers to alleviate stress and enhance tolerance in plants. Furthermore, when developing transgenic plants, the researchers should be very careful that the transgenic plant can withstand and acclimatize the adverse temperature precisely at the whole-plant level. A more holistic method is required that needs data from numerous biological kinds of research to study temperature stress. Nonetheless, plant biotechnology plays a dynamic role in the development of stress-resistant genotypes. In the near future, the integration of -omics approaches, such as transcriptomics, proteomics, and metabolomics, could aid us to recognize stress-related genes, proteins, metabolites, and other regulators, that ultimately lead to manipulate the particular genes for the development of stress-resilient plants. Additionally, an influential genome-editing method such as CRISPR/Cas system together with conventional and modern breeding methods can be exploited to benefit plants to withstand the adversities of HT, LT, and FT stress and to improve the crop quality for sustainable agriculture. Speed breeding is another exciting approach that can be coupled with the CRISPR/Cas system to enhance the plant growth and production under harsh environmental conditions in a short time.

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Chapter 11
Physiological and Molecular Responses to Salinity Due to Excessive Na⁺ in Plants

Varucha Misra, A. K. Mall, and Mohammad Israil Ansari

Contents

1 Introduction

Salinity is a crucial abiotic stress condition that hinders the growth and production of any crop (Long et al. 2020), particularly in arid and semi-arid regions (Munns and Tester 2008). This problem is relatively becoming higher due to problems of climate change, especially global warming. Misra et al. (2020b) had revealed that contribution of such soils in the world is 7%, having increased salt content and difficulty in leaching out of water (Zhao et al. 2007). Agricultural lands covering large areas under this abiotic stress cause heavy losses in economy of the world (Chaitanya et al. 2014). In India, saline soils cover a total area of about 6.73 million ha (of five states, Gujarat, U.P., West Bengal, Maharashtra and Rajasthan). Gujarat covers the highest area (2.23 million ha) of saline soil followed by U.P. (1.37 million ha), Maharashtra, West Bengal and Rajasthan (Sharma and Singh 2015). Sharma et al. (2014) had revealed that approximately 75% of soil in India belongs to saline (40%) and sodic (60%) categories. This amount is expected to increase thrice its present value to 20 million ha by the upcoming year 2050 (Sharma et al. 2014). The abiotic

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stresses prevent the plants to explore out their fully inherited potential of high yielding, leading to less crop yield (Cramer et al. 2011; Misra et al. 2020a; Ansari and Silva da 2012; Jalil and Ansari 2018; Jalil and Ansari 2020b). Amongst these abiotic stresses, salinity is a serious issue which is increasing day by day (Rogers and McCarty 2000). Saline soil can be defined as the one comprising of chloride and sulphates of four ions, viz., sodium, calcium, magnesium and potassium (Rani et al. 2019). There are many causes of elevation of sodium ions in soils. They are as follows: natural means through weathering of parental rocks (Szabolcs 1998), salt deposition in marine through wind and rains, anthropogenic activities, i.e. use of poor-quality war for irrigation of crops, global warming, etc. According to tolerance or sensitivity, plants are also grouped into glycophytes and halophytes. Zakharin and Panichkin (2009) had revealed that glycophytes are the ones which are sensitive towards salt-stress condition and majority of plants belong to this category. These plants even have slower growth rate when salt concentration in soil exceeds 0.01% (Dajic 2006). Regarding halophytes, these plants are bestowed with natural ability of tolerating high salt content, i.e. greater than 300–400 mmol NaCl (Cheeseman 2015).

In certain cases, salt stress also occurs in combination with other stresses creating a secondary salinity. Salt stress along with waterlogging is one amongst them which is becoming a crucial problem in Indian soils, chiefly in north western states (Singh et al. 2010). The losses caused due to these have resulted in monetary losses of Rs. 1669 million in Haryana (Datta and De Jong 2002). Munns and Tester (2008) had even showed that combination of nutrient imbalance and salt stress causes strong impact on photosynthesis resulting in chlorosis of plants. Parvaiz and Satyavati (2008) had shown that leaf senescence is another aspect which limits plant growth. Studies had reported that cotton plants exposed to salt-stress condition have poor growth germination and reduced seed yield. Furthermore, the quality of fibre of such plants is also low (Dong et al. 2009; Higbie et al. 2010). At times, salt stress even causes death of plants and it is known that plant growth is negatively affected when the range of salt stress lies from 0.2% to 0.5% (Yu et al. 2012). Considering the increasing problem of salt stress and its negative influence on plant growth, this chapter will highlight the physiological response in plants due to high accumulation of sodium ions as well as the response of various genes at molecular level under such a situation.

2 Physiological Response Under Increased Sodium Ions in Plants

When salt levels in soil get increased, it reduces plant water uptake (Maser et al. 2002). Once root uptakes a large amount of sodium and chloride ions from soil, the photosynthetic rate is declined and metabolic processes undergo alterations resulting in harmful effect on plant growth, irrespective of the growth stage (Maser et al.

2002). Plants exposed to high salt concentration undergo many alterations in physiological processes and are explained below.

1. *Photosynthesis Rate and Water Potential*: Photosynthesis is considered as a sensitive physiological aspect when sodium ions are excessive in plants. High amount of sodium ions in plants results in damage of photosynthetic apparatus due to dehydration of cell membrane resulting in closure of stomata. This in turn causes reduction in CO_2 permeability (Piotr and Giles 2009). Munns et al. (2006) had revealed that metabolic hindrance also occurs during photosynthesis in leaves when sodium ions are present in large amount in plants. Besides, when plants adapt to salt-stress condition, at times it changes its photosynthetic cycle which requires water for opening of stomata during night (Zhu and Meinzer 1999).
2. *Ionic Homeostasis and Compartmentalization*: In such a condition, sodium ion is transported from cytoplasm to vacuolar region via sodium hydrogen antiporter. Vacuolar type H^+-ATPase (V-ATPase), a type of H^+ pump, helps in regulating ion homeostasis and compartmentalization as well as its survival under salt-stress condition (Polash and Hossain 2019). Otoch et al. (2001) had revealed that V-ATPase activity is enhanced while vacuolar pyrophosphatase (V-PPase) activity is suppressed in cowpea hypocotyls under high sodium ions condition.
3. *Solute Accumulation*: Solute biosynthesis and accumulation get increased under salt-stress condition. Glycinebetaine, proline, trehalose, sugars, etc., are the solutes which are known to enhance their production and accumulation when sodium ions concentration gets increased (Ashraf and Foolad 2007; Tahir et al. 2012; Kerepesi and Galiba 2000). These solutes do not hinder with reactions occurring under normal condition (Hasegawa et al. 2000; Zhifang and Loescher 2003). Increased proline content under salt-stress condition is known to be seen in plants like sugar beet, *Brassica juncea*, tolerant sugarcane variety, etc. (Ghoulam et al. 2002; Yusuf et al. 2008; Vasantha and Rajlakshmi 2009). Biosynthesis and accrual of these solutes cause protective shield for the plant cells exposed to such a situation and help in maintaining the osmotic balance through incessant water supply (Hasegawa 2013).
4. *Enzyme Activity*: Inhibition in enzyme activity takes place when plants are exposed to salt-stress condition. Booth and Beardall (1991) had reported that the ratio of sodium to potassium is increased under salt-stress condition which results in inactivity of enzyme. This in turn causes changes in cellular metabolism and interruption in uptake of potassium ions. Furthermore, partition in the cells is also affected. On an overall basis, salt-stress condition causes an influence on opening of stomata due to which there is reduction in plant growth (Nawaz et al. 2010). Protein synthesis in such plants is also affected that results in reduction in leaf growth or at times may causes death of leaf (Ashraf 2004; Munns 2005).
5. *Ionic Balance*: Due to the excessive sodium ions in the root region of the plant, interruption in water uptake and nutrients is seen. This also contributes to alteration in plant metabolism (Munns 2002; Lacerda et al. 2003). Nutrient imbalance (due to higher Na^+, Cl^- ions accumulation) and deficiencies (due to interruption

in uptake of K+, Mn^{2+} ions, etc.) have been reported in plants exposed to salt-stress conditions (Karimi et al. 2005).

6. *Hormonal Balance*: Plants exposed to salt-stress condition have an imbalance of hormones due to reduction in osmotic potential (Khan and Weber 2008), changes in metabolism of nucleic acid, proteins and enzyme activity (Gomes-Filho et al. 2008; Yupsanis et al. 1994; Dantas et al. 2007).
7. *Nutrient Balance*: Under salt-stress condition, plants show an imbalance in nutrients. Several studies had shown that there was a decrease in uptake of nutrients along with its accumulation in salt-stress condition (Hu and Schmidhalter 2005; Jalil and Ansari 2019). This may even lead to nutrient deficiency or disorder at times in plants (Khorsandi and Anagholi 2009). Association of nutrient uptake and nutrients accumulation has been reported to be hampered under salt-stress condition because of two reasons, one being the composition of soil and other being the competition between various salts occurring due to sodium accumulation under salt-stress condition (Khorsandi and Anagholi 2009). There is also a reduction in accumulation of nitrogen under increased sodium ions due to Na^+ and NH_4^+ interaction and/or between NO_3^- and Cl^-. This results in reduction in yield and in plants like sugarcane, growth of the plant also gets influenced by salt stress (Rozeff 1995). Further, another nutrient, phosphorus is also revealed to be deficit in saline soils. This is so as activity of phosphate ion gets decreased. Epstein (1983) had shown that reduction in potassium, magnesium and calcium ions are seen in plants exposed to salt-stress condition which causes imbalance of nutrients. Furthermore, deficiency in micronutrients is also seen due to high pH values (Zhu et al. 2004). Chaitanya et al. (2014) had revealed that increase in sodium ions due to salt stress causes induction of potassium deficiency as plants selectively absorb these ions in comparison to sodium ions.
8. *Other Parameters*: When sodium and chloride ions are high, osmotic potential in soil is reduced which in turns results in water absorption by plant roots (Isayenkov 2012). Furthermore, increase in respiration rate and increase in ion toxicity are also observed in plants grown under salt stress. Besides, calcium displacement by sodium ions and permeability property of membrane cause membrane instability in plants of such condition.

3 Salt Overly-Sensitive (SOS) Stress-Signalling Pathway

Under salt-stress conditions, studies showed that salt overly-sensitive stress signalling is important for ion homeostasis as well as providing tolerance towards salt. There are basically three major proteins, viz., SOS 1, SOS 2 and SOS 3, involved in this signalling pathway that perform different functions. SOS 1 protein is responsible for controlling efflux of sodium ions at cellular level and long length of transportation from roots to shoot. It encodes Na^+/H^+ antiporter of plasma membrane.

Furthermore, this protein is reported to provide salt tolerance, if over-expressed in plants (Shi et al. 2002). SOS 2 protein consists of two terminal domains, N terminal which is the catalytic domain and C terminal which is the regulatory domain. This protein is known to encode serine/threonine kinase and is activated by combination of SOS 3 protein and Ca^{2+} ions (Liu et al. 2000). SOS 3 protein is also referred to as myristoylated Ca^{2+} binding protein. This protein has myristoylation site at its N-terminus, known to play important role in providing tolerance against salt stress (Ishitani et al. 2000).

The SOS signalling pathway is depicted in Figure 1, which illustrates that SOS signalling gets activated when SOS 2 protein (particularly regulatory domain of C terminus) initiates kinase by interacting with calcium-binding ions of SOS 3 proteins (Guo et al. 2004) after which phosphorylation of SOS 1 protein occurs due to the activated kinase which increases the activity of transportation of ions through Na^+/H^+ antiporter (Quintero et al. 2002). Martinez-Atienza et al. (2007) had revealed that this rise causes efflux of sodium ions into the cells making sodium ion toxicity ease out (Fig. 11.1).

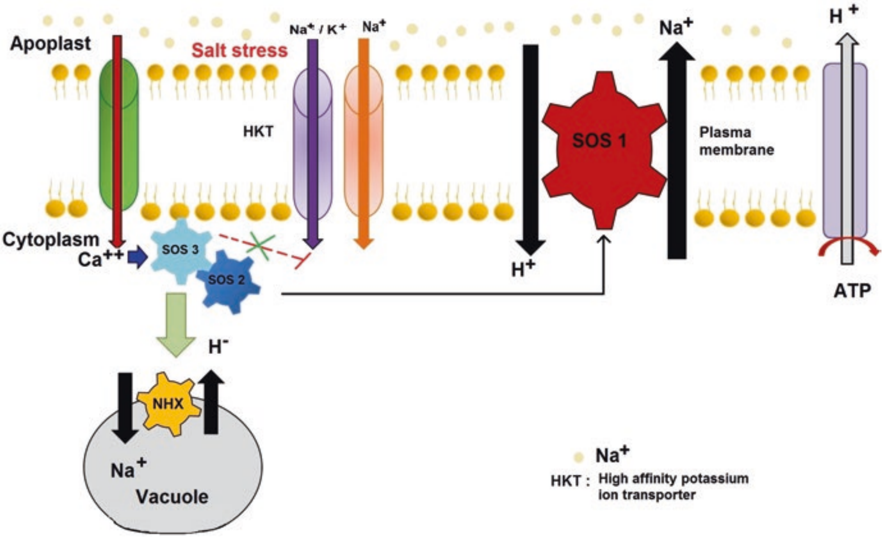

Fig. 11.1 SOS pathway model in plants exposed to salt stress. Under salt-stress condition, when sodium ions are high at plasma membrane, it induces calcium ion influx. On influx of calcium ions, SOS 3 gene alters its conformation and thereafter interacts with SOS 2 for its auto-inhibition. SOS 2 in complex with SOS 3 phoshorylates SOS 1. The complex of SOS 3 and SOS 2 inhibits HKT1 activity while SOS 2 activates activity of NHX. This in turn causes Na+/H+ antiporter to get activated for efflux of excess sodium ions

4 Halophytes: Tolerance Capability Under Increased Sodium Ions

Halophytes are the plants which have the property to survive under such saline environment and this salt increase helps in their growth and development. In *Suaeda salsa*, role of V-PPase is not much in salt environment while V-ATPase activity is upregulated. Halophytes are known to tolerate excessive sodium chloride ions either by salt-tolerant mechanism or by salt-avoidance mechanism. In salt-tolerance mechanism adopted by halophytes, studies have illustrated that reduction of sodium ion influx, excretion of sodium ions and compartmentalization are the three strategies involved (Flowers and Colmer 2015; Misra et al. 2020b) while in salt avoidance, strategies involved are shedding, secretion and succulence (Aslam et al. 2011; Shabala et al. 2014). Another way of halophyte to survive under saline environment is sequestration of salts into cell vacuoles which occurs via transporters. These transporters help in maintaining the ratio of potassium and sodium ions in cytosol (Kronzucker and Britto 2011; Sreeshan et al. 2014). High production of osmolytes such as proline, polyphenols, etc., also acts as osmo-protectants in halophytes which provides the capacity to tolerate such condition (Lokhande and Suprasanna 2012; Patel et al. 2016). In respect to genes imparting tolerance to such condition, halophytes regulate through mechanism of ABA dependent or ABA independent. There are two ways by which halophytes survive under such condition. They are as follows:

1. *Salt-Avoidance Mechanism*: In halophytes, salt-secreting structures such as salt hairs or salt glands are present. In certain halophytes, excess salt is secreted in liquid form which takes crystal formation when it comes under contact of air. These crystals appear on leaves of the plant. Balsamo et al. (1995) had reported that these crystals are washed off during heavy rains or in tides, thus, preventing the reabsorption of it into the cells of leaves. In shredding strategy, older leaves of the plants are shredded so as to avoid toxicity of salt (Mishra and Tanna 2017). Several studies had reported this method of mechanism for tolerance adaption in halophytes (Rozema et al. 1981; Waisel et al. 1986; Shabala et al. 2014).
2. *Salt-Tolerant Mechanism*: In plants several physiological aspects such as water status, transpiration, leaf area, antioxidant production, transpiration use efficiency, etc. contribute to tolerate salt stress (Ashraf 2009; Barbieri et al. 2012; Harris et al. 2010; Maggio et al. 2007). Munns and Tester (2008) had revealed that there are three mechanisms by which plants undergo salinity tolerance. These are: ion exclusion, tissue tolerance and shoot ion-independent tolerance. In ion exclusion, toxic ions from shoot are excluded out. In tissue tolerance, toxic ions are compartmentalized into particular tissues, cells and subcellular organelles. In shoot ion-independent tolerance, growth of the plant and water uptake by the plant is independent of the sodium ions accumulate under salt-stress condition (Fig. 11.2).

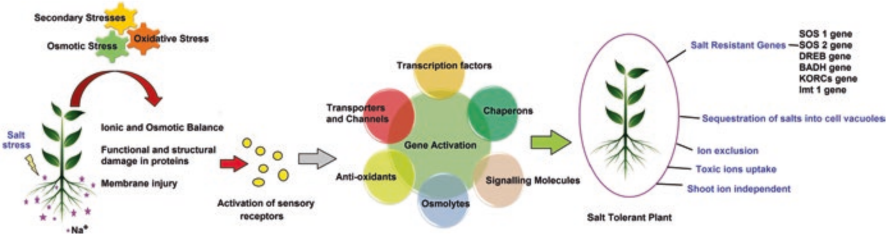

Fig. 11.2 Salt tolerant mechanism in halophytes under salt-stress condition

5 Molecular Response in Plant: Tolerance to Saline Environment Condition

Expression of many plant genes has been showed to regulate transcriptional and post-transcriptional process under salt-stress condition (Jalil and Ansari 2020a; Long et al. 2020). Understanding the molecular mechanism involved under such a condition is difficult as revealed by several studies (Munns and Tester 2008; Zhu 2001; Zhu 2002). The most important gene that plays a role under salt-stress condition is SOS 1 gene which is known to be upregulated (Oh et al. 2009; Shi et al. 2000). In certain plants like *Thellungiella*, genes associated with photosynthesis process do not show much changes under such condition (Wu et al. 2012); however, in plants like *Oryza sativa*, such genes play a role in recovering from stress (Zhou et al. 2009). Characterization of expression of genes and proteins under salt stress has also been reported in several plants like *Oryzae sativa, Nicotinum tobaccum, Medicago truncatula, Triticum aestivum,* and *Arabidopsis thaliana* (Sobhanian et al. 2010; Capriotti et al. 2014; Ghaffari et al. 2014). Heat shock proteins also play a role in plants exposed to salt-stress condition. Manaa et al. (2011) had revealed the upregulation of heat shock proteins in tomato plants exposed to salt-stress conditions. Long et al. (2020) had shown that heat shock protein (70 kDa) was upregulated in Zhongmu-1 (S28), but downregulated in Jemalong A17 (T26). Besides, Wu et al. (2012) had revealed that genes responsible for photosynthesis processes do not vary much under such a condition in plants which are tolerant to it like *Thellungiella,* whereas in rice, variation has been observed but it has been correlated with stress recovery (Zhou et al. 2009). Furthermore, Sewelam et al. (2014) had illustrated that there are many stress-responsive genes which are expressed due to combination of salt and osmotic stress, as ionic and osmotic stresses are the secondary stresses induced by excessive salt content. Salt stress solely generates 932 genes in *Arabidopsis* while 435 overlapping genes are expressed along with 367 repressive genes solely by salt stress and 154 overlapping genes (Sewelam et al. 2014).

Certain plants are also capable of tolerating salt stress. As a response to salt stress, high affinity potassium ion transporter 1 (HKT1) is an important determinant considered for such a condition. Studies had revealed that this gene helps in improving salt-tolerance capability as it lowers accumulation of sodium ions in tissue of shoot (Horie et al. 2009; Møller et al. 2009). In *Arabidopsis* plant, htk1 mutant expresses higher sodium ions in shoots while lesser in roots under salt-stress condition (Rus et al. 2004; Davenport et al. 2007). Møller et al. (2009) had also showed that HKT1 gene expressed in tissues of vascular bundle or pericycle are known to increase salt tolerance in plants. Furthermore, hkt1 mutations are known to suppress hypersensitive phenotypes associated with this stress (Rus et al. 2001; Rus et al. 2004). Studies had also revealed that HKT proteins are also important in plants as a response towards salt stress during developing new plant genotype through breeding (Asins et al. 2013; Ariyarathna et al. 2016). Yang and Guo (2018) had illustrated that there are other unidentified and SOS genes which are expressed in specific tissues under such condition for improving tolerance power against salt stress.

6 Conclusion

Salt stress is causing severe problems to agriculture and productivity. It is affecting physiological processes as well as alteration in osmotic and ionic balance has also been reported that leads to decline in biomass production. Salt stress does not affect the plant on a single growth stage rather it causes adverse effect on any plant growth stage at which it strikes. Salt stress also causes other secondary stress like osmotic stress leading to more severe impact on the plant growth. Several physiological responses have been known to cause alteration in plants, such as photosynthetic rate, hormone imbalance, and ionic imbalance. Since last two decades, salt-tolerance genes have also been identified using molecular approaches for coping with such condition. Genomic studies have also been reported in salt-tolerant plants. Identification and cloning of several genetic loci which are playing role in salt stress have been done. Transgenic plants are being developed for tolerating such situation and enhancing productivity under field conditions. In order to enhance tolerance towards this stress, it is vital to identify and characterize determinants and mechanism behind regulation of these determinants. There is a need to know molecular mechanism mediated by salt-responsive genes for regulating the developmental process of plant. Furthermore, there is a need to identify the markers for salt-tolerance capability for breeding programmes.

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Chapter 12
Physiological and Molecular Responses to Drought, Submergence and Excessive Watering in Plants

Namrata Verma, Prachi Sao, Aashna Srivastava, and Sachidanand Singh

Contents

1 Introduction

Ecological stress is diverse and, for the most part, explicit, which causes enormous harvesting misfortunes. They include expanded UV-B radiation, high saltiness, water stress, extreme temperature, hypoxia (limited oxygen is provided in waterlogged and compacted soil), lack of mineral supplement, harmful metals, fungicides, herbicides, contaminated air, topography and light temperature (Pradhan and Mohanty 2013). It can also be presented as the rapid change in atmospheric conditions that expand the recurrence of abiotic stresses like drought, floods, heavy metals or high salinity, cold and high temperatures, which cause a sudden decrease in efficiency of plant production and yield (Wang et al. 2003). The total populace is

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anticipated to ascend by 31 million every year going up to 9.1 billion by 2050, turning into a significant danger to food security (United Nations, Population Division 2002). It was assessed that there would be 70% high food prerequisite by 2050, forcing a more prominent workload on plant raisers to grow high-yielding cultivars that can withstand this high requirement. Among the abiotic stresses, water stress is intermittent and a key restricting element for development and improvement of yields (Araus et al. 2002; Dinesh et al. 2016).

Environment-based connections towards plant growth and its different interchangeable reactions are significantly connected with water (Fukao et al. 2019). Plants represent many physiological, morphological, molecular, and biochemical connections under water stress (Sourour et al. 2017). Water stress antagonistically impacts numerous plant parts physiologically, particularly photosynthesis proportions. The chances of plant development and its efficiency are severely impaired if stress last longer. The physiological and atomic components are widely contemplated for their relationship with water-stress resistance and water-use effectiveness. Furthermore, we explore how the plant functions at an atomic level to resist stress, preserve the hormone balance and its reactions and prevent excessive light damage. An understanding of the way in which these frameworks are regulated and the impact of water stress on plant viability would provide data to improve the resilience of the plant through biotechnology while preserving plant supply and nature (Bhatt and Rao 2005; Osakabe et al. 2014).

There are mainly two kinds of water stress that focus on the plant's involvement with it in general. One is when water is not in an adequate amount, mentioned as water shortage, while the other one is when water is accessible and in abundance called waterlogging/submergence. Water shortage influences plants through the decline of leaf water potential, which results in the closing of the stomata and loss of cell turgor, leading to a reduced rate of photosynthesis and transpiration and eventually resulting in plant's poor development and later wilting. Then again, waterlogging happens when the soil has a high number of the pore openings, which are engaged by water which constrains the dissemination of oxygen and gas trade between the plants, its surrounding soil and climate, followed by poor root development and their activity, therefore, influencing the plant development and endurance negatively (Pradhan and Mohanty 2013).

2 The Effect of Water Stress on Plant Growth and Its Productivity

Ecological stresses alter a wide assortment of plant reactions, extending from the metabolism of the cell and modified gene expression to changes in development and yield (Anjum et al. 2011).

2.1 Drought

In India, it was evaluated that there would be exhaustion of over 40% of accessible water by 2025, prompting a drought for horticulture crops. To understand stress better, the definitions related to various abiotic stresses are expressed thus. Heat stress is characterized as ascending in temperatures typically 10–15 °C above ideal conditions, which cause permanent harm. Low-temperature stress incorporates freezing pressure (<0 °C) or chilling pressure (<20 °C), leading to crystallized plasma layer, and when a plant's water potential and turgor are sufficiently diminished to hinder common plant activity, it is water stress (Hsiao et al. 1976). In contrast to the observational crop stand, the harvests developed in crude condition experience numerous unpredictable stresses which are responsible for the tremendous yield misfortune (Dinesh et al. 2016).

Out of all these stresses, drought or water deficit is particularly one of the terrible factors responsible for poor plant development and efficiency (Noorka and Tabasum 2015). There are various sorts of plant responses to drought: (i) stress resilience; (ii) stress escape and (iii) stress avoidance. Water deficit is an intricate character contingent upon seriousness, length of the stress phase and the plant development period (Sourour et al. 2017).

Drought is a significant ecologically restricting element at the adolescent phase of plant development and initiation. Actually, seed germination is the principal phase of development that is fragile to water shortage. Subsequently, seed germination, its vitality and sheath protecting young shoot tip of coleoptile length are beneficial for the foundation of a plant. During critical water inadequacy, elongation of the cells of higher plants may be suppressed by interference of the water stream from xylene to the extended cells (Nonami 1998). Water deficiency causes weakened mitosis; cell lengthening and expansion contributes to decreased growth and yields (Hussain et al. 2008).

Drought lessens the number of leaves per plant and individual leaf size, leaf life span by diminishing the water potential of the soil. Leaf part development relies upon leaf turgidity, heat intensity and acclimatizing flexibly for development. Water-deficit-stress encouraging the reduction of the leaf part is attributed to the concealment of the leaf extension by the reduction of photosynthesis (Rucker et al. 1995; Scott 2000).

Water-deficit stress decreases the number of days in a plant life cycle, which leads to complete flowering, shoot length and a most important decrease in the production of fresh and dry biomass (Farooq et al. 2009; Kilic and Yağbasanlar 2010). It was finalized that the length of plants, the diameter of the stem and leaf zone diminished observably with increased water-deficit stress. The decrease in plant stature could be credited to a decrease in cell expansion and more leaf ageing in the plant undergoing water stress (Manivannan et al. 2007).

Plenty of processes in plants that decide on yield, respond to water disruption. Yield has complicatedly integrated a large number of certain techniques. It is therefore difficult to determine how plants accumulate, consolidate and explain ever-changing and unpredictable processes over the entire life-long pattern of harvesting. Plant yield is the consequence of the articulation and consortium of a few plant development segments. The insufficiency of water prompts a serious decrease in yield attributes of harvest plants, presumably by disturbing leaf gas interchanging properties which not just constrained the size of the source and submerged tissues but also the loading of the phloem, movement acclimatization and dry material distributing are likewise disabled (Farooq et al. 2009). Water-deficit stress restrains the dry substance to be produced mostly because of the great extent of its inhibitory impacts on leaf elongation, leaf growth and therefore decreased light capture (Nam et al. 1998). Water-deficient stress at blooming usually causes barrenness. However, a decrease of absorbing motion to the growing ear within certain limits is important for optimum grain development, its may not be the only reason for low yield (Yadav et al. 2004).

Peduncle length has been likewise recommended as a valuable marker of yield execution in stress conditions. A paper by Kaya et al. has mentioned a positive connection between the peduncle length and plant yield (Kaya et al. 2002). Water stress can also influence productivity and its associated properties, for example, spike number per m2, plant for each spike number, 1000 plant weight and plant weight per spike, especially in the dry and semi-dry area (Bilal et al. 2015). The impact of water stress on productivity and its productivity parameters at various development stages have been noted by a few researchers (Simane et al. 1993). Actually, drought may take place all around the developing season; it does not matter whether the season is early or late; productivity is diminished generally when water stress happens during the blossoming stages; however, its impact on reduced yield is most elevated when it happens after the flowering period. In durum wheat, water stress can highly reduce the yield (Ehdaie 1995). During development, this pressure leads to a 10% decline in productivity. However, generally, there is no effect on yield due to moderate stress if provided during the early vegetative development stages (Bauder 2001).

Maize developed at high temperature combined with serious water stress during fertilization brings about 100% yield misfortune. This might be because of the decrease in the amount and nature of produced pollen, low chances of pollen survival and silk receptivity (Hall et al. 1982; Schoper et al. 1986). Normally, the decrease in crop yield relies upon tension attributes like length of subjection, the strength of stress, blend of stresses and the number of subjections (Lobell et al. 2011).

2.2 Submergence and Waterlogging

Pressure on plants forced by flooding of the humus and more profound submergence establishes one of the major abiotic limitations on development, species' dissemination and farming efficiency. Stress due to flooding is likewise a solid driver of versatile advancement. This has brought about a wide scope of biochemical, sub-atomic and morphological transformations that authorize the development and conceptive accomplishment under rambling or for all-time overflowed conditions that are profoundly harming to most of the plant species (Jackson and Colmer 2005). Development and advancement of most vascular plant species are hindered by soil flooding and especially by total submergence, the two of which can bring about death (Pradhan and Mohanty 2013).

Submergence/flooding/waterlogging is viewed as one of the significant limitations for crop output or yields in numerous territories of the world (Kozlowski 1984; Pang et al. 2004; Conaty et al. 2008), which unfavourably influence roughly 10% of the worldwide land territory (Fao 2002). Soil waterlogging and submergence are abiotic stresses that impact species synthesis and efficiency in various plant networks around the world. Flooding is a complicated stress that forces a few frequent simultaneous difficulties to typical plant working. Deprivation of oxygen and carbon dioxide is forced by very moderate paces of dispersion across the floodwater in contrast with that in air. Partial (hypoxia) or total oxygen deficiency (anoxia) in the surrounding soil limits the development, advancement and yield, which is a significant natural outcome of waterlogging or flood stress. Submergence happens when precipitation or the supply of water to the land is stored on the surface of the soil or earth for the elongated timeframe and can likewise happen when the volume of water included through precipitation or supply is beyond what can permeate into the earth in less than 1 or 2 days. Field-grown crop plants waterlogging can happen either as ‘waterlogging of the surface’ where the top of the ineffectively evacuated soils is overflowed or ‘waterlogging of the root zone’ where the water table ascends to drench a section or whole root zone with water. In this manner, the inclination towards complete flooding has a damaging impact for almost all the terrestrial plant crops, with the exception of some resistant species, since it hampers development and can bring about early sudden death (Pradhan and Mohanty 2013) because of the quick advancement of anoxic or hypoxic conditions in water-logged soils. For nearly all variant yield, abundant water is a significant requirement to profitability in numerous districts and circumstances (Jackson 2004), unfavourably influencing plant crop (Setter and Waters 2003) and development of field species (Gibberd and Cocks 1997; Gibberd et al. 2001).

In pigeon pea, stress due to moisture brings about 50% decreases in photosynthesis at its pre-flowering stage (Choudhary et al. 2011). Yield improvement for physical stress resilience is monotonous and includes very good-quality logical information to comprehend quantitative nature of the characteristics. The plant being immobile has the capacity to start sub-atomic, physiological and structural changes to any pressure and act as indicated by it (Hasanuzzaman et al. 2013). Understanding atomic components and utilization of sub-atomic methodologies are incredibly critical to productivity improvement. In contrast to the traditional standards, the hereditary gain for each unit time has been high through sub-atomic methodologies. This prompted an expanded examination action to comprehend the scientific framework of various harvests under abiotic stresses (Cramer et al. 2011).

The current analysis or assessment is an endeavour to achieve the pathways and crosstalk engaged with reaction to various abiotic stresses and arrangements more about the progressions that happen at an atomic level.

3 Plant's Physiological and Molecular Response Against the Major Water Stresses

3.1 *Physiological Response Against Drought*

3.1.1 Photosynthesis and Chlorophyll Content

In case of drought, the predominant impact of water stress is restricting photosynthesis due to the closure of the stomata which limits uptake of the CO_2 by leaves and blocks the loss of water through transpiration which eventually leads to the decrease in leaf turgor as well as water potential (Yokota et al. 2002; Anjum et al. 2003). The restrained CO_2 accessibility is the root cause of photo damage (Cornic and Massacci 1996). Water-deficit stress controls especially photochemical productivity of photosystem PS II through the electron transport reduction, external protein removal and also by releasing ions of calcium and magnesium from their coupling (Barta et al. 2010; Zlatev and Lidon 2012). Severe water-deficit stress conditions can diminish photosynthesis because of the reduction in Rubisco activity (Bota et al. 2004). Under drought conditions, the photosynthetic electron transport chain activity is subtly adjusted towards the existence of CO_2 in the chloroplast and the changes that occur in photosystem II. Water-deficit stress ends up creating changes in the proportion of chlorophyll 'a' and 'b' along with carotenoids (Farooq et al. 2009). Chlorophyll concentration has become the ultimate source as an evaluating indicator. Actually, cultivars that are resistant to water pressure have been found to have high chlorophyll content (Sairam et al. 1997). Relating to it, Ashraf et al. found that water-deficit stress is capable of reducing concentration more in chlorophyll b than chlorophyll a (Ashraf et al. 1994).

3.1.2 Water Relation and Osmolyte Accumulation

Relative water content (RWC), water potential of the leaf, resistance of the stomata, transpiration rate, temperature of the leaf and temperature of the canopy are significant qualities that impact plant water relations (Anjum et al. 2011). Water stress is also responsible for the decrease in relative water content (Cornic 2000; Saeidi et al. 2015). Relative water content (RWC) is viewed as a proportion of water status in plants, indicator of the metabolic movement in tissues and is utilized as the most important parameter for resistance against dehydration. In fact, despite the fact that constituents of plant water relations are influenced by decreased accessibility of water, the opening and closing of the stomata is greatly influenced. In addition, alterations in the leaf temperature might be a significant element in controlling water status in leaf influenced by water-deficit stress (Anjum et al. 2011)

High relative water content or RWC is actually a process that works against water-deficit stress and is more in relation with the osmotic regulation than elasticity of the cell walls of the tissue (Ritchie et al. 1990).The osmotic change is the procedure for maintaining the turgidity in the tissue through the collection of solutes against water-deficit stress. Accumulation of solutes contributes to the osmotic modification in plants, incorporating organic acids, starches, inorganic cations and free amino acids. Potassium is the essential inorganic cation in some plants, collected during water stress and can also be the richest solute of the leaf (Jones et al. 1980; Ford and Wilson 1981). Osmotic change relies mostly on photosynthesis for the supply of suited solute. Photosynthesis is hindered bringing about less contribution of the solute for osmotic alteration. With the water constraint, osmotic modification is slowed down, yet it cannot totally prevent it from dehydration (Kramer and Boyer 1995). Osmotic modification is not perpetual, and plants frequently react quickly to decreased water presence. Osmotic regulation and turgidity maintenance allow the continuity of the root development and proficient soil moisture uptake (Sharp and Davies 1979). Even with the collection of ions and organic solutes which permit osmotic changes in meristematic and elongating activity, the shooting development may still be hindered with stress either because of osmotic changes which cannot make up for the development or because of the turgidity failure that is caused by stress (Sourour et al. 2017; Dodd and Ryan 2016).

3.1.3 Root Signalling

It is advantageous to have an immense root system to help the plant development during the early yield developmental stages and in the extraction of the water from little depths of the soil layers that is generally effectively lost due to evaporation.

Under water-deficit stress conditions, roots incite a stream of signals to the shoots through xylem, causing physiological alterations in the end, deciding the degree of transformation to the stress. Cytokinins, abscisic acid (ABA), malate, ethylene and other unidentified variables have been involved in the root–shoot signalling. This water-deficit stress ends up inducing initiated root-to-leaf signalling across the transpiration stream, resulting in closing of the stomata, which is a significant transformation to constrained supply of water in the fields (Anjum et al. 2011).

3.2 Molecular Response Against Drought

The comprehension of plant's molecular response to abiotic stresses included improvement of new devices and tools by means of gene alteration through the expression of numerous genes responsible for inducing stress. There are different kinds of proteins that will likely enhance stress resistance. Genes that encode osmolyte biosynthesis catalysts allow these osmotic compounds to work against stress, for example, the formation of proline from l-glutamic acid via D1-pyrroline-5-carboxylate (P5C) in the presence of two catalysts: P5C synthase and P5C reductase, and the degradation of proline to l-glutamic acid by these two enzymes – proline dehydrogenase and P5C dehyde. In return of drought stress, proline dehydrogenase activity is repressed while inducing P5Csynthetase, bringing about a collection of proline. Unique to plants are another set of genes which are instigated in plants when exposed to water stress. These genes which are programmed to function during growth in the desiccating seeds are named as late embryogenesis abundant genes, which are abbreviated as LEA genes. These genes in turn are responsible for encoding small hydrophilic proteins which are anticipated to ensure the protection of membranes and proteins during the dehydration of the cell. For the wheat plant, to resist or to tolerate drought stress, there are numerous genes liable for it, which produces various types of catalysts and proteins, e.g. abscissic acid (Rab), rubisco, helicase, proline, protein-rich late embryogenesis (LEA protein), glutathione-S-transferase (GST) and starch during water-deficient stress (Bray 2001).

3.3 Physiological Responses Against Submergence/Waterlogging

First primary plant reactions to waterlogging is the decrease in stomata water flow activity (Folzer et al. 2006). Plants presented to stress due to flooding have increased resistance of stomatal conductance also show restricted water uptake, prompting shortage of water internally (Parent et al. 2008). What is more, low degrees of O_2 may diminish water-driven conductivity due to hampered root penetrability (Else et al. 2001). Lack of oxygen is responsible for considerable decrease in the net rate of photosynthesis (Ashraf et al. 2011). This reduction in the rate of transpiration and photosynthesis is responsible for the closing of the stomata (Ashraf and Arfan 2005). It can also have different other factors because of which rate of transpiration is being reduced, for example, chlorophyll substance reduction, senescence of the leaf and decreased leaf volume (Malik et al. 2001).

Besides, if plants are exposed to flooding for a long time, this condition could bring about root damages which as a result leads to certain changes in the biochemical response of photosynthesis due to reduction in the photosynthetic capacity overall. The biochemical modifications consist of restrained activities of ribulose bisphosphate carboxylase (RuBPC), glycolate oxidase and phosphoglycolate (Yordanova and Popova 2001), damaged membrane of chloroplast restraining photosynthetic electron transport and effectiveness of photosystem II (Titarenko 2000). It is clear from the research that waterlogging ends up causing a noticeable decrease in photosynthetic limit in various plants, for instance, *Lycopersicon* *esculentum* (Bradford 1983; Jackson 1990), *Lolium perenne* (McFarlane et al. 2003), *Triticum aestivum* (Trought and Drew 1980) and *Pisum sativum* (Jackson and Kowalewska 1983; Zhang and Davies 1987). Flooding stress is likewise known for causing clear shifts in various fluorescence of the chlorophyll which are the characteristics of plants. Chlorophyll fluorescence has always been a fantastic physiological marker that decides the essential procedures associated with photosynthesis, for example, absorption of light, photochemical responses taking place in the PSII (photosystem II) and transfer of energy because of excitation (DeEll et al. 1999; Saleem et al. 2011). Thus, changes in the parameters of the chlorophyll fluorescence decide the working and steadiness of photosystem II (Jimenez et al. 1997; Abdeshahian et al. 2010). The plants exposed to flooding situations display certain adjustments in this physiological marker; for example, when China wingnut (*Pterocarya stenoptera*) and Cork oak (*Quercus variabilis*) were exposed to flooding stress, a noticeable reduction was observed in the maximum quantum effectiveness (Fv/Fm) (Yinghua et al. 2006). Similarly, reduction in the utmost yield of quantum of PS II photochemistry (Fv/Fm) was as well noted in field beans when exposed to differing long stretches of flooding stress (Pociecha et al. 2008). PSII photochemistry was also damaged due to flooding in Medicago sativa. The reduction in Fv/Fm showed the affectability of photosynthetic instruments to abiotic stress and furthermore failure of the plants to recover rubisco under distressing conditions (Smethurst et al. 2005).

3.4 Molecular Response Against Submergence/Waterlogging

Plants under flooding stress display notable gene regulation for a number of genes which can be up-regulated or down-regulated. Through an examination of the prompted gene expression in low-oxygen condition, the identification of some gene products becomes possible. At that point, these potential genes engaged with granting water-logging resilience can be segregated and brought into the transgenic plants so as to recognize their conceivable commitment in stress resistance. Early examinations conducted by the isotopic marking of maize roots with 35S-methionine unmistakably showed the formation of anaerobic polypeptides when plants were exposed to low-oxygen conditions (Sachs et al. 1980). The anaerobic polypeptides incorporate the proteins related to fermentation, that is, alcohol dehydrogenase, pyruvate decarboxylation and lactate dehydrogenase. Besides, there prevails a noticeable variety of potential crop's genetic reservoir for water-logging resilience. As such, it has been reported worldwide in the research literature that there are genetic differences prevalent for wheat plants against water-logging resistance (Gardner and Flood 1993; Ding and Musgrave 1995). Setter et al. demonstrated that there is a huge gene variation among 14 varieties of wheat when presented to water-logging stress under glasshouse state (Setter et al. 1999). Likewise, genetic variability has additionally been accounted for in numerous other plant varieties, such as cucumber (Yeboah et al. 2008), oat (Lemsons e Silva et al. 2003), maize (Anjos et al. 2005) and soybean (VanToai et al. 1994).

4 The Actions of the Regulatory Transcription Network and Abiotic Stress in Drought

Drought and irregular climate change influence plant development globally and that incredibly influences the plant yield. The decline in the production of plant products is a major threat to the increasing population (Bray et al. 2000). Drought has a significant impact on rice, wheat, maize and soybean production, the main staple food worldwide (Nakashima et al. 2009). Therefore, the production of crops that withstand stress, especially in areas where these stresses occur frequently, will be of great significance. Recently, some advancement has been made towards recognizable proof of pressure-related qualities possibly fit for expanding the resistance of plants to abiotic stress. In order to enhance the plant's drought-tolerance properties, molecular techniques are important for understanding the molecular mechanisms in the response to drought. In the plant, abscisic acid (ABA) is the main player for developing resistance to water-limiting conditions such as drought (Finkelstein et al. 2002; Yamaguchi-Shinozaki and Shinozaki 2006; Nakashima et al. 2009; Nakashima et al. 2014). To develop plant resistance against abiotic stress, it is very important to understand the communication between various regulatory networks and factors affecting the expression of regulatory genes. Along with ABA, transcription factors (TFs) and related genes are also known to be a key molecule in handling abiotic stress (Nakashima et al. 2009).

For example, ABRE (ABA-responsive element), a cis-element, which regulates gene expression under stress conditions, is a major TF, is found in the ABA promoter regions in *Arabidopsis*. Gene expression requires a group of ABRE or group of coupling elements (CE) and ABRE (Fujita et al. 2011, 2013). They regulate the transcriptional activity by ABA-dependent phosphorylation. To facilitate a response to a water crisis, ABRE plays an essential role in signalling the network. Therefore, overexpression of ABRE develops resistance to water-limiting stress. This regulatory network is ABA-dependent. We will look at another example of ABA-independent regulatory network and will understand how crosstalk between both impacts development of resistance against abiotic stress. Dehydration-responsive element binding (DREB) proteins is a transcription factor in the ABA-independent gene promoter region in *Arabidopsis* (Liu et al. 1998), managing stress-responsive behaviours in a large number of *Arabidopsis* genes. Research suggests that overexpression of DREB in adverse conditions improves tolerance, but in normal conditions, it leads to growth defects. (Liu et al. 1998; Kasuga et al. 1999). The chance of growth defects was, however, eliminated by DREB, regulated by another promoter, RD29A (Kasuga et al. 1999).

Research also suggests that DREB proteins interact physically with AREB proteins and that ABA-dependent DREB TF is functional as a CE for ABRE in ABA-dependency gene expression (Kim et al. 2011; Narusaka et al. 2003; Lee et al. 2010). Molecular analyses demonstrated that TFs and their crosstalk work in response to drought and tolerance. It is essential to take advantage of these properties to grow drought-resistant crops. Therefore, different combinations of TFs can produce different transgenes, specific to the particular area, depending on the weather conditions.

5 Adaptations of the Plant to Withstand Excess Water Stress

Other factors that influence crop are excessive rain, which results in waterlogging; whether it is temporary or permanent, it adversely affects the plant growth. Waterlogging leads to depletion of oxygen level, degradation of roots, changes in soil PH and redox potential (Gambrell and Patrick 1978; Ashraf 2012). Such physical and chemical changes under stress reflect aerobic respirations' shift to anaerobic fermentation. Under stress conditions, genes coding for enzymes involved in fermentation are expressed abundantly because in fermentation, each glucose produces only two ATP instead of 36 ATP, which is produced during aerobic respiration (Chang et al. 2000). Research also suggested that the plant faces oxidative damage caused by the generation of reactive oxygen species (ROS) due to the lack of oxygen (hypoxic conditions) that hinders the survival of the plant by affecting the rate of photosynthesis (Ashraf et al. 2011). In response to waterlogging, plants look for alternative pathways to save energy and withstand damages such as root hydraulic conductivity, closing stomatal conductance and change in net CO_2 assimilation rate (Folzer et al. 2006; Else et al. 2001).

In a situation of waterlogging, the plant changes its physiological processes, for example, reducing stomach conductance to reduce the water intake (Parent et al. 2008), which substantially reduces photosynthesis. Studies have suggested that abscissic acid (ABA) transport from older to younger leaves has been allocated to support the closure of the stomach (Ashraf 2012). Due to lack of water intake, hypoxic conditions result in reduced root strength and permeability; also destroys the chloroplast membrane, which eventually reduces the efficiency of photosystem II and CO_2 exchange; restricts the activity of glycolate oxidase, ribulose bisphosphate carboxylase (RuBPC) and phosphoglycolate; and controls the CO_2 exchange rate of plants (Yordanova and Popova 2001; Smethurst et al. 2005; Titarenko 2000; Ashraf and Arfan 2005; Ashraf et al. 2011; Tardieu et al. 2010).

As already mentioned, oxidative damage caused by waterlogging is handled by the plant by producing enzymes like ascorbate peroxidase (APX), glutathione reductase (GR), etc., which neutralize reactive oxygen species. Sometimes, non-enzymatic antioxidants such as ascorbic acid are also used by plants (Gupta et al. 2005). Waterlogging leads to nutritional deficiencies because of the reduction in root permeability for Na + (Barrett-Lennard et al. 1999). Studies highlight the factors that hamper the efficiency of PS II, and deficiencies of N, P, K, Mg and Ca are interconnected and they adversely affect plant survival (Smethurst et al. 2005). To survive unfavourable water condition, plants also undergo morphological change such as lenticels (Yamamoto et al. 1995), adventitious roots (Malik et al. 2001) and development of lacunae gas spaces (Aerenchyma) (Evans 2004), which try to maintain oxygen, water intake and gas exchange rate respectively to maintain homeostasis. As discussed above, waterlogging is a major problem, and the development of waterlogging-tolerant plants needs a deep understanding of genes which are produced during water-stress conditions.

6 Conclusion

The abundance of water (hypoxia/anoxia) or water supply deficiency seriously impacts plants by water stress and causes numerous physical, social, physiological and molecular changes. Drought and waterlogging are multidimensional stresses which cause a broad range of plant reactions. The analysis of the various components of stress, especially low-oxygen stress, organ expression, ion channels, ROS signalling, shooting length alterations, aerenchyma, adventitious roots, the crosstalk between pathways dependent on and independent of abscisic acid (ABA) and transcription factors play an important role in the development of tolerance at the molecular level. All these changes greatly affect the rate of photosynthesis which ultimately affect the crop yield. The challenge for today’s and future agriculture is to increase the supply of food to meet the demand of the growing population. Therefore, in-depth research on transduction, signalling events and how crosstalk between regulatory networks work at the molecular level to minimize the effects of diverse types of abiotic stresses can be helpful in understanding how the plant cell transits from stress to the recovery process and develops crops tolerant to stress.

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Chapter 13

Mitogen-Activated Protein Kinase, Plants, and Heat Stress

Jyotsna Bharti, Sahil, Sahil Mehta, Shaban Ahmad, Baljinder Singh, Asish K. Padhy, Neha Srivastava, and Vimal Pandey

Contents

Abbreviations

AMPK	AMP-activated protein kinase
APX	Ascorbate peroxidase
cAMP	Cyclic adenosine monophosphate

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CAT	Catalase
CDPK	Calcium-dependent protein kinase
DHAR	Dehydroascorbate reductase
ERK	Extracellular signal-regulated kinase
GHGs	Greenhouse gases
Gly I	Glyoxalase I
GR	Glutathione reductase
GST	Glutathione-S-transferase
H_2O_2	Hydrogen peroxide
Hsf1	Heat shock factor 1
HSPs	Heat shock proteins
JAK-STAT	Janus kinase/signal transducers and activators of transcription
KDa	Kilo Daltons
LEA	Late embryogenesis abundant
MAPK	Mitogen-activated protein (MAP) kinase
MAPKK	Mitogen-activated protein (MAP) kinase kinase
MAPKKK	Mitogen-activated protein (MAP) kinase kinase kinase
MDHAR	Monodehydroascorbate reductase
NPK2	Nucleus- and phragmoplast-localized protein kinase
NTF2	Nuclear transport factor 2
OMTK1	Oxidative stress-activated MAP triple-kinase 1
PSII	Photosystem II
ROS	Reactive oxygen species
RuBisCo	Ribulose-1,5-bisphosphate carboxylase/oxygenase
RUE	Radiation use efficiency
SIMK	Salt-induced mitogen kinase
UV	Ultraviolet
WIPK	Wound-induced mitogen kinase

1 Introduction

Stress signifies a set of conditions that deviate the organism from its “normal physiological conditions,” i.e., outside the optimum range in which the organism thrives. From seedling to the postharvest stage, plants encounter numerous stresses. The term “stress” can be categorized into two major groups, namely, biotic and abiotic stress (Gupta et al. 2020). The former one is a consequence of living disturbances, such as fungi, bacteria, viruses, algae, etc., and hampers the normal growth and development of the plants (Mehta et al. 2020). The latter one arises due to fluctuation in the plant’s physical environment (naturally occurring inanimate factors) like water, salinity, metal/metalloid toxicity, pollution, nutrient paucity, dwindling seasonal patterns, and temperature shifts (Husen 1997, 2010; Iqbal et al. 2015; Getnet et al. 2015; Embiale et al. 2016; Husen et al. 2018, 2019; Mehta et al. 2020; Pandey and Gautam 2020).

Compared to biotic stress, abiotic stresses are the first and foremost reason accounted for the loss of annual productivity rate (Sharma et al. 2019; Pandey and Gautam 2020). Interestingly, during the last five decades, one of the major global concerns besetting the crop biologists is the perpetually increasing temperature (Kaur et al. 2018; Rai 2020). The major reasons are global warming, increasing human population, overconsumption of fuel/resources, and anthropogenic activities. This is also reflected in the accumulation of greenhouse gases (GHGs) and increased heat entrapment in the immediate surroundings, famously known as global warming (Lesk et al. 2016; Yanni et al. 2020), which is supported by the data presented in Fig. 13.1. This GHGs-induced rise in ambient temperature ultimately inflicts a plunge in food production. In this chapter, we have highlighted the involvement of the plant's MAPK cascade under extreme environmental conditions, namely, heat stress. Additionally, we have also summarized the MAPK cascade's role in heat-related secondary stresses such as osmotic, oxidative, and drought.

2 Heat Stress

Biologically, a temperature condition which is hot enough for a persistent period, potentially jeopardizes the normal cellular functions, and results in a series of biochemical, morphological, physiological, and molecular changes that adversely affects the plant's normal functioning is known as heat stress (Abdelrahman et al. 2020; Azhar et al. 2020). As temperature increases from the optimal threshold, plants adapt intricate mechanisms including cellular and molecular modifications to sustain cellular homeostasis. But prolonged exposure to abnormal temperature is competent enough to cause an irreversible menace to germination, plant growth, and development, reproduction, and finally yield loss, which is precisely addressed as heat stress (Liu et al. 2019; Ali et al. 2019). The optimum temperature varies from plant to plant, and any increase in temperature from the optimum for a prolonged period is categorized as heat stress. The effect of heat stress includes various physiological modifications at multiple levels throughout its ontogeny, i.e., protoplasm shrinkage, reduction in cell size, slough off leaves/flowers/fruits, reduced net assimilation rate, disturbed fertilization, general infertility, hormonal imbalance, increased respiration, early senescence, etc. (Abdelrahman et al. 2020; Azhar et al. 2020).

At the cellular level, it influences cell division and cell cycle by altering the phragmoplast microtubule elongation, formation of microtubule asters, and microtubule organization (Parrotta et al. 2016), whereas physiologically, changes like cell size reduction, rapid stomatal closure, enhanced number of xylem vessels in the root, and water loss have been diagnosed by the researchers (Lipiec et al. 2013; Haworth et al. 2018; Aliche et al. 2020). Depending on the extent and the temperature range, at the reproductive level, the plant experiences reduction in flower bud development, failure in the germination of the pollen tube and reduced viability of

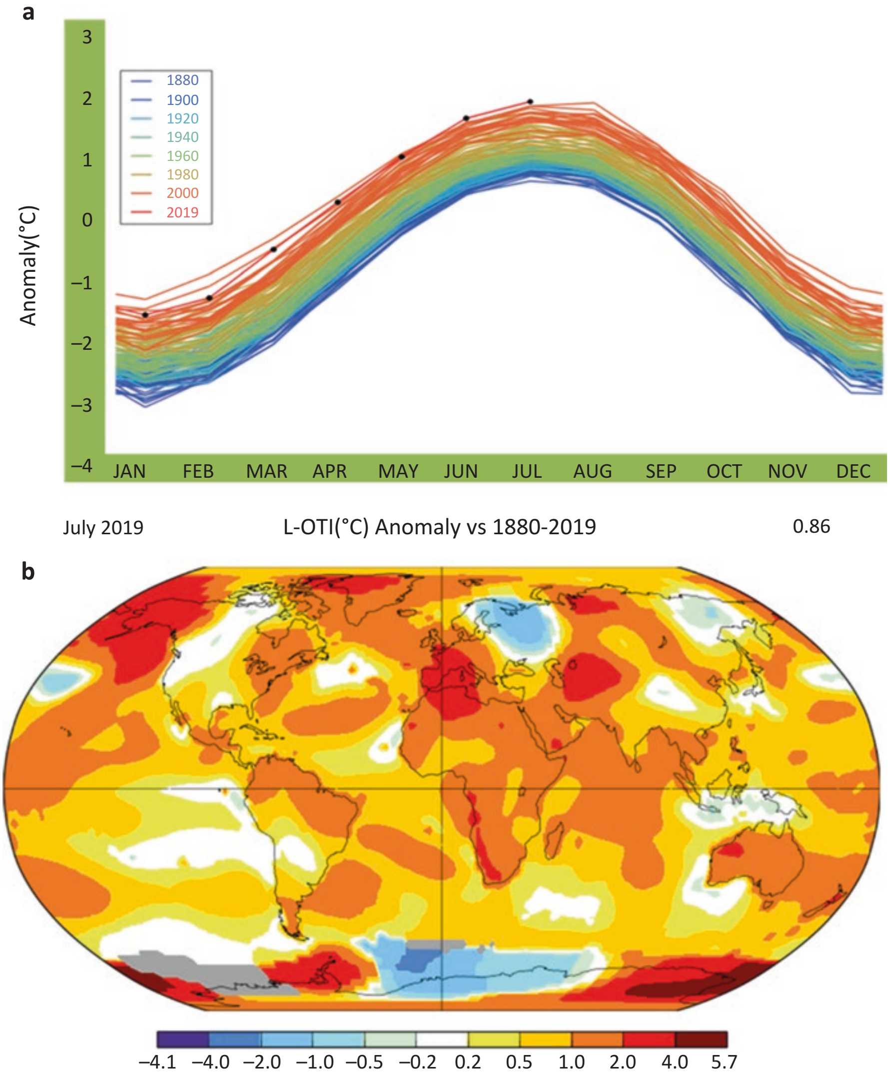

Fig. 13.1 (**a**) Graph showing the GISTEMP Seasonal Anomaly Cycle data based on MERRA2 reanalysis for the period 1880–2019. (**b**) Anomaly map depicting the globe surface temperature for the period 1880–2019. The data have been adapted from NASA-Goddard Institute for Space Studies (https://data.giss.nasa.gov/gistemp/). (Accessed on 24th January 2020)

ovule, stigma anomalous positioning, and abnormal anther dehiscence (Raja et al. 2019; Aliche et al. 2020). Heat stress often comes along with drought (Loka et al. 2020). Therefore, protective measures including seed priming are preferred along with adaptive measures undertaken in drought conditions (Banerjee and

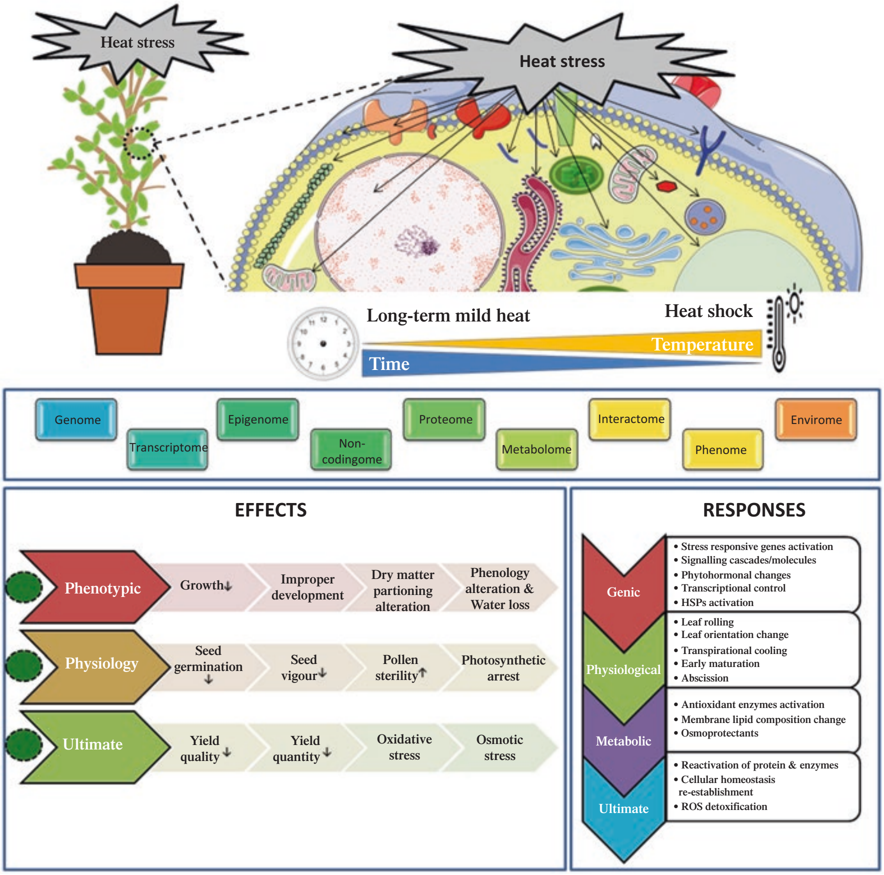

Fig. 13.2 Effect of heat stress on various plant's omics and other related parameters

Roychoudhury 2020). The overall effect of heat stress on plants and their responses are depicted in Fig. 13.2.

Additionally, the prolonged rise in temperature attenuates the photosynthetic efficiency due to many plausible reasons: (i) denaturation of the enzymes involved in the photosynthesis (e.g., RuBisCo) (Kumar et al. 2019), (ii) lipid peroxidation of chlorophyll and thylakoid membrane (Sharma et al. 2018), (iii) distortion of the grana stacking and PSII arrangement (Dongsansuk et al. 2017), (iv) disturbance of electron transport chain (Neves et al. 2019), and (v) loss of RuBP regeneration capacity (Chovancek et al. 2019). Due to all these abnormalities, Radiation Use Efficiency (RUE) of the plant reduces. On the other hand, an increase in respiration also leads to a higher rate of transpiration that causes permanent wilting and hence crop loss.

To control the water loss, plants shed their leaves, and in turn, photosynthesis is severely affected resulting in reduced grain weight (Bheemanahalli et al. 2019; Ali et al. 2019). Additionally, high temperature leads to a decrease in oil yield due to the reduction in linoleic acid content in *Brassica*, *Helianthus*, and seagrass (Beca-Carretero et al. 2018). All such injuries ultimately cause starvation, growth inhibition, reactive oxygen species (ROS) production, and ion flux reduction (Pucciariello et al. 2012; Baxter et al. 2014). In addition to all these effects, heat stress also causes both osmotic and oxidative stresses at the secondary level (Qi et al. 2011). As a result, it is one of the most challenging stresses that need to be tackled in order to achieve an optimum yield of the crop plants in the ideal case scenario where all other factors are taken care of.

3 Plant Response to Heat Stress

To maintain their cellular homeostasis in multiple natural adversities including high-temperature stress, plants have evolved various strategies during the course of time. Plants either tolerate or avoid the heat stress to some extent by some morphological and metabolic modifications (Matsui et al. 2019; Azhar et al. 2020). The mechanisms include induction of MAPK and Calcium-Dependent Protein Kinases (CDPK) cascades, scavenging the ROS, maintaining membrane stability, accumulation of compatible solutes, production of antioxidants, transcriptional activation and chaperone signaling, etc. (Fig. 13.2). All these mechanisms are regulated at the molecular level and help plants to fight against heat stress. Likewise, they also produce compatible solutes at the biochemical level, such as proline, polyols, tertiary and quaternary ammonium compounds, etc., that maintain the cell's turgor pressure and help in the redox balance. In addition, there are multiple reports in the literature which elaborate the increase of late embryogenesis abundant (LEA) proteins, dehydrins, Pir proteins, ubiquitin, and heat shock proteins in the heat stress repercussions-surviving plants (Rurek 2010; Hand et al. 2011; Priya et al. 2019; Maher et al. 2019; Yadav et al. 2020). All the changes and modifications in the metabolism happen due to the changes in the upregulation of the genes that provide the plant with a range of osmoprotectants, transporters, regulatory proteins, and detoxifying enzymes. At the expression level, this results in heat tolerance that gets translated into acclimatization (in long-term "adaptation") and depends directly on the signaling pathway. Para-heliotropism, altered membrane lipids, increased trichome density, etc., are the mechanisms undertaken by plants in heat avoidance; however, the signaling is involved here too (Thitz et al. 2017; Marcus 2019). Table 13.1 reviews the effect of high-temperature stress in different crop species.

Table 13.1 Effect of high-temperature stress in different crop species

Crops	Heat treatment	Major effects	References
Rice (*Oryza sativa*)	>33 °C, 10 days	Reduced spikelet fertility	Hurkman et al. (2009)
Wheat (*Triticum aestivum*)	37/28 °C (day/night), 20 days	Duration of grain filling shorten and decreased kernel weight	Rahman et al. (2009)
Wheat (*Triticum aestivum*)	30/25 °C (day/night)	Reduced leaf size, heading, anthesis, and maturity and drastic reduction in grains/spike number and size	Djanaguiraman et al. (2010)
Sorghum (*Hordeum vulgare*)	40/30 °C (day/night)	Decreased chlorophyll (chl) content, fluorescence, photosystem II photochemistry, and antioxidant enzymes, and increased ROS content and thylakoid membrane damage	Mohammed and Tarpley (2010)
Rice (*Oryza sativa*)	32 °C (night temperature)	Decreased grain dimensions and increased spikelet sterility	Suwa et al. (2010)
Maize (*Zea mays*)	35/27 °C (day/night), 14 days	Reduced ear expansion, hemicelluloses, and cellulose synthesis	Yin et al. (2010)
Rice (*Oryza sativa*)	25–42.5 °C	Decrease in the CO_2 assimilation rate	Djanaguiraman et al. (2011)
Soybean (*Glycine max*)	38/28 °C (day/night), 14 days	Decreased the leaf Pn and stomatal conductance, increased palisade and spongy layers thicknesses, damage in plasma membrane and chloroplast/thylakoid membranes, and distortion in mitochondrial membranes, cristae, and matrix	Tan et al. (2011)
Tobacco (*Nicotiana tabacum*)	43 °C, 2 h	Decrease in NPR and stomatal conductance and apparent quantum yield, carboxylation efficiency (CE), and antioxidant enzymes content	Gunawardhana and De Silva (2011)
Wheat (*Triticum aestivum*)	38 °C, 24 and 48 h	Decreased chl and relative water content and diminished antioxidative capacity	Hasanuzzaman et al. 2013
Yunnan poplar (*Populus yunnanensis*)	40 °C	Higher reduction in photosynthetic activity and enhanced production of ROS	Li et al. (2014a, b)
Lentil (*Lens culinaris*)	>33 °C, 36 days	Lentil genotypes exposed to full heat (unshaded) had an average grain yield 66% less than those grown under the shaded control	Delahunty et al. (2015)
Rice (*Oryza sativa*)	32 °C and 35 °C	36% decrease in yield during high night temperature stress and 25% decrease in high day temperature stress	Fahad et al. (2016)
Rice (*Oryza sativa*)	31–39 °C	A yield reduction of 30–40% during early reproductive stage	Wu et al. (2016)

(continued)

Table 13.1 (continued)

Crops	Heat treatment	Major effects	References
Rapeseed (*Brassica napus*)	30 °C day/25 °C night	Reduced seed germination and seed vigor	Rashid et al. (2018)
Chickpea (*Cicer arietinum*)	Day–night air temperatures >32 °C −20 °C), 7 days	Reduced seed yields of the heat-tolerant genotypes by 25–28% and the heat-sensitive genotypes by 4 s5–58%	Awasthi et al. (2017)
Soybean (*Glycine max*)	Day/night temp 30/22 32/24 38/26, 42/28 °C	Decline in leaf area, seed weight, total biomass, pods/pl, seeds/pl, harvest index, seeds/pod, and 100 seed weight	Jumrani and Bhatia (2018)
Quinoa (*Chenopodium quinoa*)	Day/night temp 40/24 °C	Reduced pollen viability between 30% and 70%	Hinojosa et al. (2019)

4 Signal Transduction for Heat Stress

There is an array of signaling pathways involved in conferring heat stress resistance. While some of them control the expression and synthesis of heat shock proteins (HSPs), others are involved in the production and/or activation of different effector constituents (Yadav et al. 2020; Pereyra et al. 2020). To withstand the stressful conditions, plant upregulates various genes that get translated into a battery of proteins and enzymes that are the key players of stress signaling cascades to ultimately counter the stress (Kaur and Gupta 2005) (Fig. 13.3). The signaling cascades may operate independently or maybe in cross talk with various other pathways in the cell (Nakashima et al. 2014; Dunayevich et al. 2018; Muthuramalingam et al. 2020). Depending upon the signal transduction molecules, plant type, and subjected stress, there are broad groups of molecules along with transcription factors that activate the responsiveness of genes. These groups of molecules include Ca^{2+}-dependent protein kinase (CDPKs), mitogen-activated protein kinase (MAPK/MPKs), NO, sugars, phytohormones (Azhar et al. 2020; Xalxo et al. 2020), etc. All these signaling increases the activity of antioxidants such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase, GST, CAT, glyoxalase I (Gly I), etc. (Fig. 13.2). This helps the plants to fight and survive in unfavorable conditions especially high-temperature and other-related stresses. Furthermore, various signaling pathways operate in a cell such as the AMPK signaling pathway, cAMP-dependent pathway, JAK-STAT signaling pathway, Nodal signaling pathway, Wnt signaling pathway, MAPK/ERK signaling pathway, and many more (Yu et al. 2019; Shumayla and Upadhyay 2019; Fu et al. 2020). Within all these highly conserved signaling cascades which play a central part in the heat stress conditions is the mitogen-activated protein kinase (MAPK) pathway (Yu et al. 2019; Ijaz et al. 2019). In simple words, mitogens are actually the agents that stimulate/promote cell division. Because of activation and deactivation of the enzyme by the kinases and phosphatases action, the signal passes

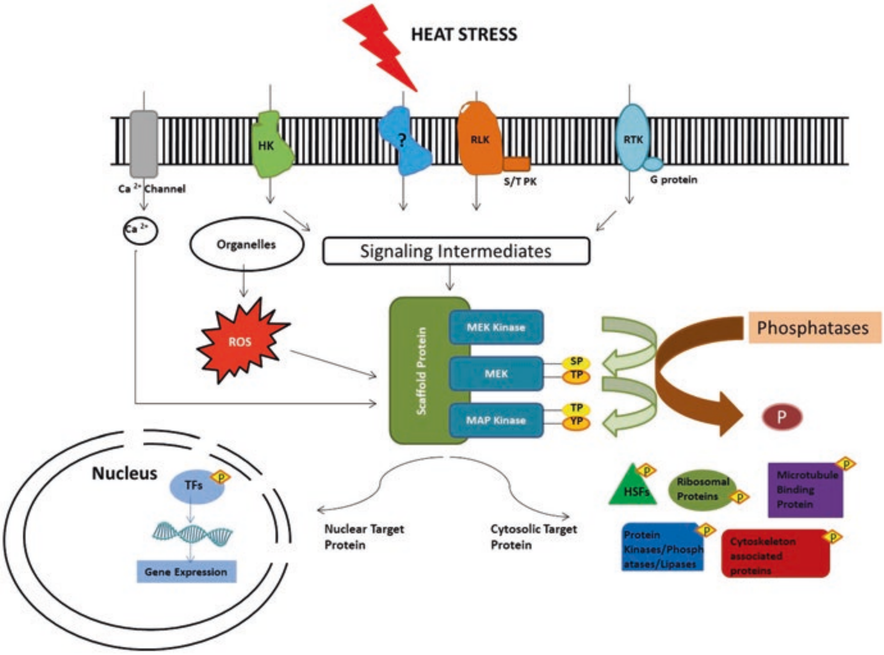

Fig. 13.3 Diagrammatic representation to show the core of MAPK pathway which contains three components MAPKKK-MAPKK-MAPK and along with that the downstream targets of the pathway. The downstream targets generally are transcription factor (WRKY), ribosomal protein (RPS), protein kinases/lipase/phosphatases, microtubule binding protein, and cytoskeleton-associated proteins

down fast. Apart from heat stress, there are many studies in the literature which point out the importance of the MAPK pathway in growth, hormone signaling, and other stress too including cold, drought, ROS, salinity, wounding, ozone, and UV radiation (Qiu et al. 2019; Sözen et al. 2019; Mahmood et al. 2020). Table 13.1 tabulates the reported MAPKKK and associated components of MAPK signaling cascades in a few plant species.

5 MAPK Pathway in Plants

A cell has multiple MAP kinase pathways that control distinct cellular responses. The pathway is composed of three protein kinases: a terminal MAP kinase and two upstream kinases, namely, MAPK kinase (MKKs) and MAPK kinase kinases (MKKKs) (Sözen et al. 2019). These kinases sequentially channelize, integrate, and amplify the cellular external environment response. MAPKs were first discovered because of their ability to phosphorylate the microtubule-associated protein-2

(MAP2), and that is why it was initially named as MAP2 kinases (Ray and Sturgill 1987). Later, it was discovered that these proteins show homology with certain mitogen-stimulated proteins (such as p42 protein), and they were renamed to mitogen-activated protein kinase (Cooper et al. 1982). With the continued research in the same field, it is now known that there are certain MAP kinases (a member of MAPKs family) collectively known as extracellular signal-regulated kinases (ERK). The first ERK (an insulin-activated protein kinase) was discovered from the Chinese hamster ovary. MAPKs need activation in the form of phosphorylation (Ijaz et al. 2019), and the activators are known as MEK (for MAPK/ERK Kinase). MEKs are in turn phosphorylated by MEKs activator, and they are known as MEKK (MEK Kinase) (Wang et al. 2015). The first MAPK pathway was characterized in *Arabidopsis,* and *At*MEKK1, *At*MKK2/MEK1, and *AT*MPK4/AtMPK6 constitute the whole pathway. It is vital for the plant's innate immunity and also regulates the response in conditions like salt, cold, and drought stress (Blanco et al. 2006; Xing et al. 2008). In interaction studies, it was established that *At*MEKK1interacts with *At*MKK2 and MEK1. *At*MPK4 interacts with both *At*MKK2 and MEK1, sometimes directly to *At*MEKK1. MEK1 primarily phosphorylates the threonine residue of *At*MPK4, but tyrosine phosphatase can deactivate *At*MPK4. This suggests that in plants either the MEK1 doesn't have dual specificity and thus tyrosine phosphorylation is simultaneously done by second MEK (Ichimura et al. 1998) or tyrosine gets autophosphorylated and thus MAPK is activated. MAPK cascade has a very important role to play in signal transduction for the multitude of stress responses (Fig. 13.3).

5.1 MAPKs

MAPKs are serine/threonine kinases activated by MEKs which either move to the nucleus to phosphorylate other specific transcription factors or stay in the cytoplasm to pass the signal to cytoskeleton binding proteins or some enzymes (protein kinases, phosphatases, phospholipases, etc.) for further signal transmission. Upon activation, MAPK disassociates from MEK and get arranged in a homodimer form to expose a domain called as MAP kinase insertion domain for facilitating active nuclear import (Pitzschke 2015; Wu et al. 2015). In MAPKs, the substrate phosphorylation occurs specifically at serine/threonine residues that are followed by a proline residue, i.e., $PX_{S/T}$ where X can be basic or neutral, but −2 position proline is not required (Clark-Lewis et al. 1991; Gonzalez et al. 1991). This mechanism provides specificity in substrate recognition, and the P + 1 loop present in the substrate-binding pocket regulates the substrate binding. Binding to the proline of the substrate is only possible when kinase is in active form (Canagarajah et al. 1997). A secondary structure called activation loop is present which forms the mouth of the active site (Zhang et al. 1995). The dual phosphorylation motif (TXY**:** threonine–X–tyrosine) is present on the activation loop in kinase sub-domain VIII (Payne et al. 1991; Gartner et al. 1992), and phosphorylation on both tyrosine and threonine residues is required for the full activation of the MAPKs; as without phosphorylation, the binding site will be blocked. Distinct MAPKs have distinct dual phosphorylation motif, and the length of the loop also varies (length of the loop controls the autophosphorylation of the protein) (Jiang et al. 1997). Mammalian MAP kinases can be divided into three families, and each family has multiple members and multiple activators (MEK and MEKK) that are present upstream to MAPK. The first family is ERK/MAP kinases, and the members are many times activated when receptor tyrosine kinase is activated by EGF (epidermal growth factor), and the activation sequence for this family is threonine–glutamic acid–tyrosine (TEY). The other family is JNK/SAPK (Jun N-terminal kinase/stress-activated protein kinase), and they are activated by stress or inflammatory cytokines with the activation sequence: threonine–aspartic acid–tyrosine (TDY). The last family is p38/Hog which is activated by cytokines, endotoxins, and osmotic stress with activation sequence: threonine–glycine–tyrosine (TGY). As EGF, which activates both ERK and JNK/SAPK pathways, extracellular stimuli may activate more than one pathway (Cano and Mahadevan 1995). Plant MAPKs shares high homology with the ERK subfamily. Plant MAPKs mainly cluster in one group which is known as PERKα, and very few (three) clusters in a group denoted as PERKβ. Based on sequence similarity, the PERKα family can be divided into five different subfamilies named as PERKα1–5. The activation loop length varies among the PERK groups which are 25, 22, and 21 amino acids long for PERKβ, PERKα5, and PERKα1–4, respectively (Ligterink and Hirt 2001).

Generally, all plant MAPKs have a TEY motif at the site of dual phosphorylation, except in *Arabidopsis* and alfalfa MAPK because they have TDY as the motif. Additional to this, the MAPKs having the TDY motif have an additional C-terminal extension (Mizoguchi et al. 1997; Schoenbeck et al. 1997) compared to the MAPKs that have a TEY motif. Generally, C-terminal (not extended) has a CD (common docking) domain which acts as the docking site for MPKKs, phosphatase, and substrate proteins (Ichimura et al. 2002). The amino acid sequence [LH][LHY]Dxx[DE]xx[DE]EPxC (where x is any amino acid residue) clearly denotes the importance of acidic residues D (aspartate) and E (glutamate) in interacting with the basic (K-lysine and R-arginine) counterparts that are present as a cluster on the MPKKs. Based on the sequence of the activation loop, the MAPKs can be divided into four groups (A, B, C, and D). Groups A, B, and C have a TEY sequence motif, whereas group D has a TDY sequence motif. Group A members are involved in environmental and hormonal responses, e.g., MPK6 (*Arabidopsis*), and its orthologs in other plants are activated by various environmental cues. Group B members are involved in environmental stress responses and cell division, e.g., MPK4 (*Arabidopsis*) is induced by both biotic and abiotic stress induction, and subgroup B2 members MPK13 (*Arabidopsis*), Ntf6 (*Nicotiana*), and MMK3 (*Alfalfa*) have cell cycle-dependent activation. Group C member MPK7 (*Arabidopsis*) shows expression that is regulated by circadian rhythm. Some group D members (BMWK1 from rice and TDY1 from alfalfa) are induced by pathogen attack and wounds. Group D members lack the CD domain, but some like MPK8, MPK9, and MPK15 (*Arabidopsis*) have a small (60–80 amino acids) N-terminal extension (Ichimura et al. 2002). Table 13.2 summarizes about the reported MAPKs and their associated activators in plant species using Google scholar (https://scholar.google.co.in/).

Table 13.2 Tabulation of the reported MAPKs and their associated activators in few plant species

Plant species	Family	Chromosome no.	Genome size (Mb)	MAPKs	MAPKKs	MAPKKKs	References
Actinidia Chinensis	Actinidiaceae	29	616.1	18	9		Wang et al. (2018a); Jiang and Chu (2018)
Amborella trichopoda	Amborellaceae	13	706	8	7	79	Neupane et al. (2019)
Amborella trichopoda	Amborellaceae	13	748		6		Jiang and Chu (2018)
Aquilegia coerulea	Ranunculaceae	7	302	11	5	141	Neupane et al. (2019)
Arabidopsis thaliana	Brassicaceae	5	135	20	10	80	
Arachis duranensis	Fabaceae	10	~2700	16	7		Purayannur et al. (2017)
Arachis ipaensis	Fabaceae	10	~1390	16	7		Purayannur et al. (2017)
Brachypodium distachyon	Poaceae	5	~355	16	12	75	Chen et al. (2012)
Brassica napus	Brassicaceae	19	1200	12	7	66	Liang et al. (2013); Sun et al. (2014)
Brassica rapa	Brassicaceae	10	485	31	14	100	Wu et al. (2017)
Cajanus cajan	Fabaceae	11	852	17	7		Purayannur et al. (2017)
Capsella rubella	Brassicaceae	8	137.1	18	11		Jiang and Chu (2018); Mohanta et al. (2015)
Capsicum annuum	Solanaceae	12	3480		5		Jiang and Chu (2018)
Carica papaya	Caricaceae	9	372	9	9		Jiang and Chu (2018); Mohanta et al. (2015)
Cicer arietinum	Fabaceae	8	750	16	7		Purayannur et al. (2017)
Citrullus lanatus	Cucurbitaceae	11	425		6		Jiang and Chu (2018)
Citrus clementina	Rutaceae	9	370	12			Mohanta et al. (2015)
Citrus sinensis	Rutaceae	9	280	12	7		Jiang and Chu (2018); Mohanta et al. (2015)
Coffea canephora	Rubiaceae	11	710		8		Jiang and Chu (2018)
Cucumis melo	Cucurbitaceae	12	375		6		Jiang and Chu (2018)
Cucumis sativus	Cucurbitaceae	14	350	14	6	59	Wang et al. (2015)
Daucus carota	Apiaceae	9	421	17	5	136	Neupane et al. (2019)
Dianthus caryophyllus	Caryophyllaceae	15	622		8		Jiang and Chu (2018)
Eucalyptus grandis	Myrtaceae	12	640	13	6		Jiang and Chu (2018); Mohanta et al. (2015)

Plant species	Family	Chromosome no.	Genome size (Mb)	MAPKs	MAPKKs	MAPKKKs	References
Fragaria vesca	Rosaceae	7	240	12	7	73	Zhou et al. (2017a); Zhou et al. (2017b)
Glycine max	Fabaceae	20	975	38	11	150	Neupane et al. (2013b)
Gossypium raimondii	Malvaceae	13	880	28	11	78	Zhang et al. (2016)
Helianthus annuus	Asteraceae	17	3600	28	10	166	Neupane et al. (2019)
Hordeum vulgare	Poaceae	7	~5300	20	6	156	Cui et al. (2019)
Jatropha curcas	Euphorbiaceae	22	320.5	12	5	65	Wang et al. (2018b)
Linum usitatissimum	Linaceae	15	318.3	24			Mohanta et al. (2015)
Lotus japonicus	Fabaceae	6	470	19	7		Neupane et al. (2013a); Purayannur et al. (2017)
Lupinus angustifolius	Fabaceae	20	924	29	10		Purayannur et al. (2017)
Malus domestica	Rosaceae	17	~742.3	26	9	123	Sun et al. (2017); Zhang et al. (2013)
Manihot esculenta	Euphorbiaceae	18	770	21	11	62	Jiang and Chu (2018); Ye et al. (2017); Yan et al. (2016)
Medicago truncatula	Fabaceae	8	~465	25	7		Neupane et al. (2013a); Purayannur et al. (2017)
Mimulus guttatus	Phrymaceae	14	322	6			Mohanta et al. (2015)
Musa acuminata	Musaceae	11	600	25	10	77	Asif et al. (2014); Wang et al. (2017)
Oryza sativa	Poaceae	12	430	17	8	75	Rao et al. (2010)
Panicum virgatum	Poaceae	9	1358	27			Mohanta et al. (2015)
Phaseolus vulgaris	Fabaceae	11	473	15	9		Neupane et al. (2013a); Purayannur et al. (2017)
Pisum sativum	Fabaceae	7	~4450	16	6		Purayannur et al. (2017)
Populus trichocarpa	Salicaceae	18	422	21	11		Jiang and Chu (2018); Mohanta et al. (2015)
Prunus persica	Rosaceae	8	265	12	10		Jiang and Chu (2018); Mohanta et al. (2015)
Ricinus communis	Euphorbiaceae	10	400	12	6		Jiang and Chu (2018); Mohanta et al. (2015)

(continued)

Table 13.2 (continued)

Plant species	Family	Chromosome no.	Genome size (Mb)	MAPKs	MAPKKs	MAPKKKs	References
Setaria italica	Poaceae	9	700	16	12		Jiang and Chu (2018); Mohanta et al. (2015)
Solanum lycopersicum	Solanaceae	12	900	16	6	89	Wu et al. (2014)
Solanum melongena	Solanaceae	12	1093		4		Jiang and Chu (2018)
Solanum tuberosum	Solanaceae	12	800	12	5		Jiang and Chu (2018); Mohanta et al. (2015)
Sorghum bicolor	Poaceae	10	730	16	7		Jiang and Chu (2018); Mohanta et al. (2015)
Thellungiella halophila	Brassicaceae	7	238.5	16			Mohanta et al. (2015)
Thellungiella parvula	Brassicaceae	7	140		9		Jiang and Chu (2018)
Theobroma cacao	Malvaceae	10	430	12	8		Jiang and Chu (2018); Mohanta et al. (2015)
Trifolium pretense	Fabaceae	7	420	19	7		Purayannur et al. (2017)
Trifolium subterraneum	Fabaceae	8	540	18	8		Purayannur et al. (2017)
Triticum aestivum	Poaceae	7	~17,000	54	18	155	Wang et al. (2016); Zhan et al. (2017)
Vicia faba	Fabaceae	6	~13,000	15	6		Purayannur et al. (2017)
Vigna angularis	Fabaceae	11	538	15	7		Purayannur et al. (2017)
Vigna radiata	Fabaceae	11	579	15	7		Purayannur et al. (2017)
Vigna unguiculata	Fabaceae	11	519.4	15	7		Purayannur et al. (2017)
Vitis vinifera	Vitaceae	19	490	14	5	62	Cakir and Kılıçkaya (2015)
Zea mays	Poaceae	10	2300	19	9	74	Kong et al. (2013a); Kong et al. (2013b)
Ziziphus jujuba	Rhamnaceae	12	437.6	10	5		Liu et al. (2017)

5.2 MKKs

MKKs are dual-specificity protein kinase which activates MAPKs by phosphorylating both tyrosine and threonine residues on the TXY motif of the activation loop. As protein kinases are generally specific for either serine/threonine or tyrosine phosphorylation, it was hypothesized that MAPK might require two protein kinases for its activation. Surprisingly, a single dual-specificity kinase (MEK) activates the MAPK by phosphorylating both tyrosine and threonine residues on the TXY motif (Matsuda et al. 1992; Pitzschke 2015). In the signaling cascade, MKKs can in turn get activated by phosphorylation on the two conserved serine or threonine residues which are present in between the domain VII and domain VIII (Alessi et al. 1995; Zheng and Guan 1994), and these conserved amino acids form a motif $^{\mathbf{S/T}}\mathrm{XXX}_{\mathbf{S/T}}$ in most MKKs. In most yeast and animal MKKs, the motif is SXXX$_{\mathbf{S/T}}$, while in plants, $^{\mathbf{S/T}}$XXXXX$_{\mathbf{S/T}}$ is the motif (Ligterink and Hirt 2001). The activity of MKKs can be regulated at the posttranslational level by phosphorylation of the residues other than the conserved serine or threonine residues that negatively regulates MKKs (Brunet et al. 1994; Rossomando et al. 1994). Along with the posttranslational regulation, MKKs can be regulated at the posttranscriptional level by differential splicing (English et al. 1995). The substrate specificity for the MKKs is restricted, and the specificity is defined by multiple domains of MAPKs, and MKKs in turn bind to the tertiary structure of the MAPKs, thus restricting the substrate specificity (Seger et al. 1992). That is why MKKs are considered to be the convergence points of the pathway as it can receive many signals that it can feed into the MAPKs pathway. A conserved N-terminal putative MAPK docking site [K/R][K/R][K/R]x(1–5)[L/I]x[L/I] (basic –K and R at the extreme N-terminal to the hydrophobic L and I at inwards N-terminal) is the docking site for the MAPKs (Bardwell and Thorner 1996), and MKKs are known to regulate the kinetics of the cascade. Specificity is enhanced when both MAPK and MEK interact with the scaffold protein (e.g., MP1; Schaeffer et al. 1998) that also linearly guides the interaction between the components of the cascade (Fig. 13.3). The complex formed by pathway components with the scaffold protein is known as signalosome, and such interactions restrict any cross talk that can happen with the multitude of different pathways and within the pathway (Chang and Karin 2001; Whitmarsh and Davis 1998). Normally, MKKKs (to perceive myriad of stimuli) are present more than MKKs, and thus, it can be hypothesized that they also function in signal integration (Ferrell 1996), and an MKK can activate multiple MAPKs (they are also in excess) in the cascade, and this is the step of signal amplification (Ichimura et al. 2002). The first-ever MKK reported in plants was from *Nicotiana,* and thus, it was named NPK2 (nucleus- and phragmoplast-localized protein kinase, renamed from *Nicotiana* protein kinase 2). Plant MKKs are divided into three subfamilies, namely, PMKK1, PMKK2, and PMKK3, from which the members of PMKK3 have additional long non-catalytic C-terminal which is not present in other PMKKs subfamilies (Ligterink and Hirt 2001). Based on new advances, the plant MKKs can be divided into four groups (A, B, C, and D). Group A members are involved in multiple abiotic stress responses, e.g., MKK1 and MKK2 (upstream of MPK4 in *Arabidopsis*), whereas PRKK (pathogen-responsive MPKK in alfalfa) involved in the transduction of elicitor signals, and MKK6 (*Arabidopsis*) along with NtMEK1 (*Nicotiana*) is involved in cell division. Group B members MKK3 (*Arabidopsis*) and NPK2 (*Nicotiana*) have an extended C-terminal, and the extended C-terminal consists of a nuclear transport factor (NTF2) for nuclear localization. Group C members are stress-responsive, and downstream, they signal group A members of MAPKs, e.g., SIMKK has both salt and elicitor-induction specificity and NtMEK2 (*Nicotiana*) can induce SIMK (salt) and WIPK (wound).

5.3 MKKKs

MKKKs are serine/threonine kinase that regulates the MKKs activation. Structurally, MKKKs are different from MAPKs and MKKs, and different MKKKs have different regulatory motifs such as Pleckstrin homology (PH) domains, proline-rich sequences involved in SH3 binding, zinc finger motifs, leucine zippers, and binding sites for G-proteins (Garrington and Johnson 1999; Pitzschke 2015). MKKKs have multiple tyrosine and serine/threonine phosphorylation sites, and thus, it can be activated by a different mechanism like it can be phosphorylated by MKKKs and PKCs, by interaction with G-protein, or by the cellular two-component system (Whitmarsh and Davis 1998; Fanger et al. 1997). This much diversity in the structure and the mode of activation provide flexibility to respond to different stimuli. MKKKs are the branching point and mediate cross talk between signaling pathways. Many MKKKs have been identified by various scientists; however, Raf is well studied and documented (serine/threonine-protein kinase). Mostly, plant MKKKs show homology with yeast MEKK/STE11 and mammalian Raf (related to retroviral oncogenes), and hence, they are known as PMEKKs (e.g., *At*ANP1 and *At*MEKK1 with a conserved sequence G (T/S) Px (W/Y/F) MAPEV) and PRaf (e.g., *AtCTR1* and *AtEDR1* with a conserved sequence GTxx (W/Y) MAPE) (Rao et al. 2010). The PMEKKs can be subdivided into three groups, i.e., PMEKK1, PMEKK2, and PMEKK3, whereas PRaf can be subdivided into two groups, i.e., PRaf1 and PRaf2 (Ligterink and Hirt 2001). Some sequences in the plant also share homology with the mixed lineage kinase (MLK), thus widening the range of diversity of MKKKs in plants (Ligterink and Hirt 2001). Ichimura et al. (2002) has also provided a way of dividing MKKKs in a plant in which group A members are MEKKK1 type and group B and C members are RAF kinase type. Group A further can be divided into five subgroups and subgroup A1 (*At*MEKKK1, *At*MEKKK2, *At*MEKKK3, and *At*MEKKK4) members active in drought, high salinity, and touch. *At*MEKKK1 is present upstream of MPK4, MKK1, and MKK2. *At*MEKKK4 has an extended N-terminal which is a unique feature as it has several domains such as a glycine-rich region, WRKY domain, paired-amphipathic-helix repeat, TIR domain, leucine-rich repeat (LRR), NB-ARC domain, and a protein kinase domain. WRKY proteins are Zn-finger transcription factors that are specific to plants as they regulate plant defense response and capacity to deal with drought condition, and WRKY domain provide the direct DNA binding capacity to the protein. Along with that, the presence of the TIR-NB-LRR domain further confirms the role of *At*MEKKK1 in plant defense. Subgroup A3 members like ANP1, ANP2, and ANP3 have a C-terminal regulatory region, and NPK1 is a positive regulator of cytokinesis (Nishihama et al. 2001) and a negative regulator of the stress response (Krysan et al. 2002). But all of these MPKKKs work in oxidative stress response as a negative regulator of the auxin-response pathway (Kovtun et al. 2000). Subgroup A4 members *At*MAP3Kε1 and *At*MAP3Kε2 are involved in cell division (Jouannic et al. 2001), and the function of subgroup A2 members is not determined. Group B members are RAF kinase such as CTR1 which is involved in ethylene signaling, and EDR1 is involved in disease resistance signaling. They have an extended N-terminal (regulatory) and a C-terminal kinase domain, whereas specifically, subgroup B2 N-terminal has PAS (Per, Arnt, and Sim) domains and PAC (PAS-associated C-terminal) domains. Group C members are also RAF kinase, e.g., ATN1 and *At*MRK1. Broadly, functions of the group members are unknown. There is some information about the domains that are present like the N-terminal of subgroup C1 members having an ankyrin like a domain that is known for protein-protein interaction. Subgroup C2 has an aspartokinase, chorismate mutase, and Try A (ACT) domain which is known for sensing amino acid concentration and then regulating the activity of many metabolic enzymes (Aravind and Koonin 1999). There is another group present in cucumber MEKKs family known as ZIK like kinases, and they have an N-terminal kinase domain having a signature sequence GTPEFMAPE (L/V) Y. ZIK like kinases are also known as WNK (with no lysine (K)) which are involved in controlling circadian/internal rhythms (Murakami-Kojima et al. 2002) and in responding to abiotic stress (Kumar et al. 2011) without showing any evident phosphorylation of the MKKs in plants (Kong et al. 2013b) such as *At*3g04910 in (*Arabidopsis*). There are chances that with further studies there will be additional groups that will add up to already mentioned groups of MKKKs in plants. Members of MEKKs have structural diversity and don't share any general structure, whereas Raf protein kinase has similar structural organization both in plants and animals, i.e., catalytic domain present at C-terminal and a long non-catalytic extension at the N-terminal (Ligterink and Hirt 2001). In addition, the non-catalytic domains both in plants and in animals are rich in serine and cysteine (Ligterink and Hirt 2001). The sequence and structural diversity of MKKKs in plants suggest that even in plants, MKKKs have a wide variety of substrates and diversity in mode of regulation (Ligterink and Hirt 2001). NPK1 forms the largest group of MKKKs plant and regulation of homologs of NPK1 in *Arabidopsis* (ANP1) occurs by differential splicing resulting in ANP1L (large) and ANP1S (small) forms and ANP1S shows higher activity than the ANP1L spliced form which highlights the role of splicing in the regulation of MKKKs in plants (Nishihama et al. 1997). The cascade does not always work in a linear direction as MAPKs and MKKs can phosphorylate the MKKKs or the upstream regulating components, and this serves as the negative feedback loop (Ueki et al. 1994). At the same time, MAPKs can interact with

MKKKs (thus activating) in the positive feedback mechanism (Zimmermann et al. 1997; Pitzschke 2015).

5.4 Upstream of MAPK Cascade

In upstream of MKKK, different effectors are known to function and activate the MAPK pathway. Several kinases act upstream of MKKKs in yeast and mammalian systems such as receptor tyrosine kinases (RTK) and G-protein-coupled receptors. When RTK is active, it can stimulate the exchange of guanosine triphosphate (GTP) for the guanosine diphosphate (GDP) on G-protein Ras. Activated Ras can then interact with potential partners including Raf (Morris 2001; Pitzschke 2015). Yeast on contrast doesn't possess RTKs and instead has two components, i.e., histidine-protein kinase and G-coupled protein receptors. Yeast and mammalian MKKKs can be divided into two subfamilies. The first one is the STE20/PAK subfamily, and it is characterized by the catalytic domain at C-terminal and putative G-protein binding motif at the N-terminal. The other subfamily is GCK/SPS1, and this subfamily has a characteristic catalytic domain at the N-terminal and a long kinase-unrelated region which is mostly activated by stress at the C-terminal (Fanger et al. 1997). In plants, RTKs are not present, but instead, receptor-like kinases (RLKs) are present, and RLKs are transmembrane serine/threonine protein kinases (Stone and Walker 1995). In the plant system, there are two putative MKKKs, i.e., BnMAP4Kα1 and − 2 from rapeseed (Leprince et al. 1999), and one MKKK, i.e., SIK1 (for stress-induced kinase1) from *Arabidopsis* which can be grouped under GCK/SPS1 subfamily. Many genomic sequences that are candidates for the plant MKKKs can be grouped under STE20/PAK. In yeast and mammals, the presence of PKC and small G-proteins to activate MKKKs somewhere indicates that similar regulation of activation exists in plants upstream of the MAPK cascade (Ligterink and Hirt 2001).

6 Role of MAPK Pathway in Heat and Other Related Stresses in Plants

6.1 High-Temperature Stress

The first report of induction of MAPKs under heat stress is from the group of Sangwan who highlighted the heat-activated mitogen kinase (HAMK) getting induced in alfalfa (Sangwan et al. 2002). Following this, there were many reports in the literature that have shown that high temperatures induce the expression of many MAPK components in varied plants. *Os*MSRMK2 is a rice multi-stress-responsive gene of the MAP kinase family (Agrawal et al. 2002). In one of the preliminary study, it was found out that *Os*MSRMK2 can sense the change in temperature as the transcripts shows enhancement (37 °C) and no induction (25 °C and 12 °C) with in a period of 15 min. Whereas it showed a transient nature because at 37 °C, the transcript level decreases at the time point of 30 min and beyond and at 25 ºC the transcripts started increasing at 30 min and then drastically decreased after that, interestingly, at low temperature (12 ºC) the transcripts started accumulating at 60 min and reached to a height at 90 min and then shown a decrease at 120 min. But a rapid accumulation at high temperature suggests that it helps the plant in sensing the adverse temperature condition and thus prepares the plant to thrive in it (Agrawal et al. 2002). Another report by Link et al. (2002) showed that the heat activation of the MAPK pathway in tomato is calcium as well as heat stress factor 1 (Hsf1) dependent. The phosphorylation of Hsf1 at the tyrosine by the involved MAPK activates Hsf1, and the activated Hsf1 further activates the Hsps which induces thermo-tolerance in the plant (Link et al. 2002). On the other hand, HAMK, a 46 KDa protein, becomes active in tobacco (*Nicotiana tabacum*) and *Sl*MAPK1 in tomato (Ding et al. 2018) at the advent of heat stress, and in *Arabidopsis,* the expression of *At*MPK6 increases during the heat stress (Li et al. 2014a; Li et al. 2014b). *At*MPK6 mediates the activation of γVPE which is a vacuolar-localized cysteine protease with a Caspase1 like activity, and it basically activates the downstream hydrolytic enzymes in the vacuole which are responsible for the induction of hypersensitive reaction. This leads to cell death and tissue senescence (Albertini et al. 2014). Thus, it was postulated by that γVPE plays a role in heat-induced programmed cell death (PCD). γVPE is expressed in guard cells of *Arabidopsis,* and Albertini et al. 2014 deciphered its involvement in water stress which is one of the secondary stress of high-temperature stress. In another report by Evrard et al. 2013, it was reported that *At*MPK6 negatively regulates heat stress by phosphorylating HSF2, which is a known heat shock factor and plays a role in heat stress response. In similar reports, it was reported that *the mpk6 Arabidopsis* mutant shows higher tolerance than the wild type. A study undertaken by Ding et al. 2008 on tomato has helped in deciphering the mechanism of action of the MAPK signaling pathway in alleviating the high-temperature stress. In the case of tomato, there is 16 putative family of *Sl*MPK which have been grouped into four major groups (A–D) (Kong et al. 2013a; Kong et al. 2013b). Silencing of MPK1/2 (*Sl*MPK) results in compromised tolerance toward heat, cold, and oxidative stress (Nie et al. 2013; Zhou et al. 2014; Lv et al. 2017). But another report from Ding et al. (2018) showed that silencing *Sl*MPK 2 can increase the tolerance of plants toward high-temperature stress. *Sl*MPK1 (ortholog of *At*MPK6, *Nt*SIPK, and *Os*MPK6) is a negative regulator of heat stress responses (Ding et al. 2018). The tomato plants with silenced *Sl*MPK1 gene show the expression of many proteins that are involved in various functions such as protein folding, lipid metabolism, translation, amino acid biosynthesis, and oxide reduction. The silenced lines show no chlorophyll degeneration as compared to the wild type. Thus, Ding et al. (2018) postulated that it is due to the activation of CPN-60 (role in chloroplast biogenesis and plastid division) (Ahsan et al. 2010), and CPN-60B is known to play a vital role in acclimatizing photosynthesis to high temperature (by protecting the thermal denaturation of RuBisCo activase). The lines that are having suppressed expression of *SI*MPK1 have accumulated redox buffers.

The main mechanism behind the attained tolerance was the reduction of the high temperature-induced oxidative damage to maintain cellular redox homeostasis (Ding et al. 2018). *Sl*MKK9 (homolog of *At*MKK9) interacts with *Sl*MPK1, and it is an upstream component of the pathway, and the downstream partner of *Sl*MPK1 is SISPRH1 (homolog of At1g04330), but it is a protein of unknown function and has a putative phosphorylation site at Ser-44 (Ding et al. 2018). Later, it was deciphered that this phosphorylation site is very important for the enzyme activity as a mutation at this residue can block the *Sl*MPK1-mediated inhibition under high temperature (Ding et al. 2018). High temperature induces inactivation of a 50KDa kinase, and the ability of this kinase to phosphorylate myelin basic protein (MBP) suggests that it is a member of the MAPK family (Heider et al. 1998). While the induction of the heat shock genes by the transcription factor Hsf1 is a general response in heat stress, this is repressed by the phosphorylation of Hsf1 by the ERK1 resulting in the silencing of heat-inducible genes in unstressed conditions (Chu et al. 1996). Most of the studies conducted by researchers confirmed MAPKs except *Cs*MPK3 and *Cs*MPK7 are overexpressed under heat and drought stress (Wang et al. 2015). It has also been studied that SlMPK3 plays a major role during various biotic and abiotic stresses. Previously, it was known that knockout of *Sl*MPK3 results in reduced drought tolerance and disease resistance to *Botrytis cinerea.* But *Sl*MPK3 also gets influenced by heat stress as its relative expression gets downregulated, and its knockout provides tolerance to heat stress (Yu et al. 2019). Both ion leakage and MDA content were significantly lower in the knockout mutants. This suggested that SlMPK3 acts as a negative regulator of heat stress whose knockout maintains the relative integrity of the cell membrane and reduces cell membrane damage. Elevated levels of SlHSP70, SlHSP90, *Sl*HSP100, and *Sl*HSFA1a, *Sl*HSFA2, and *Sl*HSFA3 were observed in *Sl*MPK3 mutants, indicating the increase in HSPs and HSFs genes' relative expression might be associated with *Sl*MAPK3-mediated heat stress response in tomato plants (Yu et al. 2019).

6.2 Oxidative Stress

Oxidative stress is the most common secondary stress in biotic and abiotic stress conditions as in most of the stressed conditions, the disruption of metabolic imbalance of cell takes place, and that hampers the cellular redox homeostasis. But this is also true that ROS plays a vital role in signaling in the lower concentrations. In support of that, investigation done by Kovtun et al. (2000) helped in understanding the effect of H_2O_2 on MAPK activation under stress condition that will aid the plant to somehow deal with the adverse condition (in this case under pathogen attack). In *Arabidopsis* protoplast study, they found out two H_2O_2-activated (independent of other activators like ethylene, SA, and JA) MBP kinases (44 and 42 KDa mass). They also elucidated that H_2O_2 activated promoters of oxidative stress-responsive gene GST6 and an HSP named HSP 18.2. The fact that H_2O_2 is involved in cell cycle under nonstress conditions and also the involvement of MAPK in cell cycle regulation instigated the idea that the tobacco cell cycle regulating MAPK-NPK1 (A class of MEK kinases) might be mediating oxidative stress responses in plant cells (Nakashima et al. 2014). The homologs of NPK1 in *Arabidopsis* MEK kinases are ANP1, ANP2, and ANP3 which can activate two MBP kinases (same molecular masses) as activated by H_2O_2. Later, it was established that ATMPK3 and ATMPK6 are the substrates of ANP1, ANP2, and ANP3. Activation of MAPK suppresses the oxidative stress. But sometimes, there are activators of ROS that don’t involve in the activation of MAPK, and this suggests that MAP kinase activation is either independent or upstream of oxidative burst. In a study conducted by Xing et al. (2007), it was found out that MAP2K inhibits the ABA-dependent activation of the CAT1 enzyme. Nakagami et al. (2006) showed that MEKK1-MPK4 cascade has a role to play in ROS metabolism. Not only the MAPK pathway mediates the oxidative stress responses but also it regulates the concentration of ROS in the system by hampering the expression of the CAT enzyme (Kong et al. 2013b). An alfalfa MAPKKK, namely, OMTK1 (oxidative stress-activated MAP triple-kinase 1), is a key response regulator, and it further regulates the downstream components that are MAPK and MMK3 (Nakagami et al. 2004). The role of MAPKs in oxidative stress was also similarly deduced by the many other researchers.

6.3 Osmotic Stress

One of the secondary stresses that come in the picture due to the high temperature with which the plant has to deal is the osmotic stress. Plants have protein kinases that deal with the changes in the osmolarity. In green algae, *Dunaliella tertiolecta* hypoosmotic stress induces a 40 KDa kinase, and this kinase can phosphorylate MBP and histone, while the hyperosmotic stress induces a 40 KDa (can phosphorylate MBP, histone, and casein) kinase and a 45 KDa (can phosphorylate MBP only) kinase (Yuasa and Muto 1996). The activity of these kinases is independent of the presence of calcium, and thus, they are not CDPKs and thus possibly can be MAPKS. But MAPKs don’t use casein as a substrate, while histone can be used as a substrate by MAPK in plants (Wilson et al. 1995; Zhang and Klessig 1997). This suggests that the 40 KDa protein kinase induced in hyperosmotic stress cannot be a member of the MAPK family, while others can be MAPKs. Another response that is evident under osmotic stress in *D. tertiolecta* cells is that the cell volume changes in response to the extracellular osmolarity, and to gain the original volume, the cell induces MAPK cascade to nullify the effect of the osmolarity changes. In several experiments where the application of protein kinase inhibitor can block the recovery process, the involvement of protein kinases in the cell osmolarity balance kinetics was established. Thus, all these instances indicate the involvement of stress-induced protein kinases in osmotic tolerance in *D. tertiolecta* (Yuasa and Muto 1996), and these protein kinases can be MAPKs. Extending the studies to the higher plants indicates that MAPKs are involved in osmotic stress tolerance in plants too. In an in vitro study where tobacco-suspension-cultured cells were given hyperosmotic stress, it resulted in the activation of MAPK like kinases. The hypoosmotic stress resulted in the activation of MBP kinases of 50, 70, and 80 KDa molecular weight (Takahashi et al. 1997). 50 KDa protein kinase exhibits all the characteristic properties of an MAPK as the activation and inactivation through phosphorylation and dephosphorylation events (Takahashi et al. 1997). Even yeast has osmosensors to sense hyperosmotic stress, and one of which is a part of a two-component regulatory system. Yeast osmosensor SLN1 gets autophosphorylated at histidine which is present at the N-terminal sensor domain. The phosphate is then transferred to YPD and then to the aspartic residue of the C-terminal sensory domain of the SSK1 which is a response regulator. Then SSK1 feeds the signal into the HOG1 MAPK pathway (Posas et al. 1996). A similar pathway or mechanism of response exists in plants as *Arabidopsis* SLN1 homolog *At*HK1 act as osmosensor in complementation studies with SLN1-deficient yeast cells (Shinozaki and Yamaguchi-Shinozaki 1997). Similarly, a pea MAPK, i.e., PsD5, can complement HOG1-deficient yeast mutant (Pöpping et al. 1996), and an alfalfa MAPK, i.e., MMK2, can complement yeast MPK1 kinase (Jonak et al. 1995). Some stress-activated MAPKs like AtMPK3 and stress-activated MAPK (previously called as MMK4) also get upregulated in drought, cold, heat, touch, and salt stress, and all these stresses result in a condition of dehydration. So this can be concluded that AtMEKK1/AtMPK3 and SAMK can deal with general dehydration conditions and thus can provide tolerance to the plant against the osmotic changes (Ligterink and Hirt 2001).

6.4 Drought Stress

The high temperature in absence of irrigation/rainfall generally results in a condition called drought. In situations of dehydration, *At*MEKK1 and *At*MPK3 are transcriptionally activated (Mizoguchi et al. 1996). A ribosomal S6 kinase is activated by MAPK after phosphorylation in the mammalian system (Sturgill et al. 1988; Gregory et al. 1989), and a homolog of the same exists in *Arabidopsis,* i.e., *At*PK19 which shows accumulation in the drought stress (Mizoguchi et al. 1996). This somewhere indicates that *At*PK19 is activated by *At*MPK3 following a similar pathway as in the mammalian system. Transcriptional and translational activation of SAMK is also reported, but no significant changes in the protein level were found (Jonak et al. 1996). The drought-stressed leaves of alfalfa show the activation of p44^{MKK4} kinase within 5 min (Jonak et al. 1996). Although the activation was transient and ABA independent (Jonak et al. 1996), after full activation, it shows a decrease in activity (after 20–30 min). But the activation of p44^{MKK4} under high temperature (37 °C) was not seen in lab experiments. The drought-like condition induces the activation of *Os*MSRMK2 and *Os*MAPK5 in rice plants. DSM1, a putative MPKKK of rice, when overexpressed can increase the tolerance of the plant toward dehydration (Ning et al. 2010).

7 Concluding Remarks and Future Prospects

Due to the fact that the MAPK cascade is the major multitier player network for stress signaling transductions involved in various environmental biotic and abiotic stresses, MAPKs and other components involved in the perception of various signals are chosen as targets by multiple biologists, breeders, and bioinformaticians worldwide. Various omics approaches such as transcriptomics, proteomics, miRNAomics, metabolomics, and bioinformatics along with high-throughput DNA sequencing have allowed precise analysis of MAPK pathway cross-networking under various abiotic stresses. Due to the increase in ambient temperature around the plants, it has posed a serious threat on the yield and productivity. As a result, a huge plethora of studies has been conducted to solve the problem of making the plants more tolerant to high-temperature stress by different means of genetic modifications in order to sustain the crop yield for every second increasing population. By implying this knowledge to wheat, ryegrass, Chinese clematis, black raspberry, and other 580+ sequenced plants, the orthologous genes can be discovered and can be used to improve every important crop plant against heat and other abiotic stresses. Consequently, as already discussed above, overexpressing the positive regulators of MAPK pathway components and knocking out or editing the negatively regulating components are the ways toward climate-resilient agriculture. In a long run to the future, the rewiring of circuits will ultimately enable the smooth cultivation of crop plants such as rice, wheat, tomato, potato, lemongrass, jute, cotton, and many more even in harsh conditions.

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Chapter 14
Cross Talk Between Heme Oxygenase 1 and Lateral Root Development for Salt Tolerance

Khushbu Verma, Shubham Dixit, and Afroz Alam

Contents

Abbreviations

AuxRE	Auxin response elements
BV-IXα	Biliverdin-Ixα
CO	Carbon monoxide
HO1	Heme oxygenase 1
IBA	Indole-3-butyric acid
LR	Lateral root
NAA	Naphthylacetic acid
TF	Transcription factors

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1 Introduction

Salinity is a chief abiotic stress which significantly inhibits plant development and reduces crop productivity (Zhu 2001). Typically, it imposes oxidative damage on plant cells. Salinity stress causes developmental changes at physiological, morphological, and metabolic levels on increasing level, affecting crop yield also (Munns 2005; Rozema and Flowers 2008; James et al. 2011; Husen et al. 2016, 2018, 2019; Hussein et al. 2017). Advancement in genomics has found the solution to cope up with abiotic stress effects. Estimation of genome sequences and identification of stress-sensitive tolerance genes have provided a global solution against these stresses, which improves crop productivity levels (Gupta and Huang 2014). Different physiological and biochemical functions have developed in plants that help them stay alive in soils with salinity condition. This adaptation involves some major mechanisms, including ion homeostasis and compartmentalization, biosynthesis of osmoprotectants and companionable solutes, commencement of antioxidant enzyme, and modulation of hormones. Apart from all these physiological and biochemical responses, there are also some crucial morphogenic responses such as enhanced lateral root formation (Pasternak et al. 2005). That's why there is a strong mechanistic action between antioxidant level, auxin metabolism, and lateral root development.

A new emerging enzyme heme oxygenase is also an antioxidant enzyme that produces CO which has been confirmed to function as a signaling agent in various physiological and metabolic processes. In the literature, it has been well documented that either HO1 or its by-products CO and biliverdin (BV) are involved in plant defense system to overcome salt stress, heavy metals, programmed cell death, and UV radiation (Noriega et al. 2004; Balestrasse et al. 2006; Yannarelli et al. 2006; Xie et al. 2008; Ling et al. 2009; Cui et al. 2011; Wu et al. 2011). In this study, we have elucidated how the response of salinity stress regulates antioxidant activity which leads to auxin metabolism resulting in LR development. It has been well elucidated that CO, being the catalytic by-product of HO, is a significant component concerned in the regulation of plant progress toward abiotic stresses (Cao et al. 2007a, b; Xuan et al. 2008a), so there is a possibility that HO1 might be regulating salinity stress-induced LR formation.

2 What Is Heme Oxygenase 1 (HO1)?

Heme oxygenase (HO, EC 1.14.99.3) was first discovered in an animal system. In its mode of action, it reacts and attaches to heme and forms a complex with a ratio of 1:1 (Kikuchi et al. 2005). This enzyme is membrane bound and has a hydrophobic C-terminal tail. Heme oxygenase has two isoform, HO1 and HO2 (Yoshida et al. 1991). In plants, this enzyme comprises a small gene family with four constituents (Emborg et al. 2006), which is classified into two classes: HO1-like genes (having

HO3 and HO4 of *Arabidopsis*) and HO2 genes. Unno et al. (2007) have reported about HO1's soluble nature in algae, cyanobacteria, and higher plants. In plant system, heme oxygenase has been identified as a catalyst to catalyze the oxidation reaction that breaks down heme into biliverdin IXα (BV), Fe^{+2}, and CO (Noriega et al. 2004; Shekhawat and Verma 2010). Free heme fits in a sandwich-like arrangement between proximal and distal helices of HO1. The proximal ending of HO1 has Histidine which is the proximal heme ligand occupied in the holding of heme (Unno et al. 2007).

Linly et al. (2006) demonstrated that HO1's basic structural folds are conserved along with diverse heme-binding pocket. On the other hand, HO protein with molecular mass of 32.6 KDa containing 55 chloroplast amino acids transports peptide in *Arabidopsis thaliana* (Muramoto et al. 1999). Study also revealed that the higher plant HOs are exceedingly homologous with each other, such as *Glycine max* HO1 (GmHO1) that has homology with AtHO1 with 71.7% similarity, although plant HOs show less homology with other biological species (Gohya et al. 2006).

Functional multiplicity of HO and its participation in numerous purposes have also been studied (Shekhawat and Verma 2010). HO1 has major role in antioxidant defense mechanism to overcome various abiotic stress. On the other hand, importance of HO has been studied within the phytochrome chromophore metabolism pathway of plant system also. BV-IXα is reduced to form phytochromobilin (PUB). PUB is the chromophore from phytochrome family (Terry et al. 1993) which has a role in photomorphogenesis with light signaling (Emborg et al. 2006). Verma and Shekhawat (2013) suggested that HO is a chief enzyme in phytochrome-chromophore synthesis and has regulatory responsibility in chlorophyll synthesis. Rao et al. (2019) reported about role of *PE-1* which is encoding HO1 on development of chloroplast of *Oryza sativa* L.

2.1 Role of HO1 in Antioxidant Defense Mechanism Against Abiotic Stress Including Salt Stress

Various reports have revealed the antioxidant importance of HO1 against abiotic stress conditions. To overcome oxidative stress, HO1 has been accredited as an important enzyme to scavenge ROS in plant system (Ryter and Tyrrell 2000; Noriega et al. 2004; Balestrasse et al. 2006). HO1 is implicated via its by-products viz., biliverdin (BV), CO, and Fe^{+2} as a member in antioxidant defense mechanism in plants (Ryter and Tyrrel 2000; Noriega et al. 2004; Balestrasse et al. 2005, 2008). Under cadmium, UV-B, and salt stress conditions, BV concentration was elevated along with HO1-enhanced expression of HO1 in *Glycine max* L. (Balestrasse et al. 2005, 2008; Yannarelli et al. 2006; Zilli et al. 2009).

Regulatory function of HO1 as an active member of antioxidant defense network in *Brassica juncea* (L.) Czern. has been studied under salt-induced oxidative stress (Verma and Alam 2015; Verma et al. 2015). Characterization study of AtHO1 promoter has been performed under oxidative stress induced by salt stress, deficiency of iron, and mercury exposure (Wang et al. 2016). In one recent study with wheat, it was demonstrated that methionine sulfoxide reductase A4.1 interacts with HO1 to induce more seedling tolerance against salt/drought stress (Ding et al. 2019). One biochemical and molecular study in *Eruca sativa* suggested the defensive function of HO 1 to overcome side effect of ROS under salt stress (Mahawar and Shekhawat 2019). Khator et al. (2020) also gave an insight into the cytoprotective role of HO1 in legume crops of Indian Thar Desert affected by NaCl-induced oxidative stress. Overall, HO1 has a huge impact as an antioxidant and protective role against various types of abiotic stress including salt stress (Verma and Alam 2020).

2.2 Cross Talk Between HO1 and Lateral Root (LR) Development

LR development regulates the indispensable tasks of making availability of water, nutrients, and physical hold up to plants. LRs play a significant role in escalating the absorptive capability of roots and to secure the plant into the soil. Consequently, consideration of the regulation of LR development has agronomic significance. Various reports and research have indicated that HO1 has regulatory connection with the induction of LR development. It may positively control abiotic stress conditions via enhancing LR development. Xuan et al. (2008b) provided pharmacological, physiological, and molecular confirmation that auxin speedily helps in the activation of HO activity, and then the by-product CO generated through HO1 enters into the signal transduction events for initiation of adventitious root development in *Cucumis sativus*.

Chen et al. (2012) performed various experiments to find out the associations between LR and HO activities. In their study, they noted any possible regulatory effect of nitric oxide (NO) [sodium nitroprusside (SNP, an NO donor)], auxin (IBA, a natural auxin), and hemin (Hm) [an HO inducer] on LR formation and HO1 activity in rice. This study suggests the requirement of HO for auxin-, Hm-, and NO-induced LR development in rice.

In *Zea mays* seedlings, the cDNA of gene ZmHO-1 that encodes HO-1 protein was cloned. In the study, it was concluded that hemin, N-1-naphthylacetic acid (NAA), and CO solution were responsible for the initiation of ZmHO-1 expression and subsequent enhancement in lateral root development. Largely, this finding revealed that a maize HO-1 is necessary for the maize lateral root development (Han et al. 2012). Kao (2013) revealed that disclosure to auxin, apocynin, methyl jasmonate (MJ), and $CoCl_2$ in rice made increment in LR development. This report provided a confirmatory screening regarding a close association of rice to HO with LR development.

HO1 and hydrogen sulfide (H_2S) regulate a variety of functions related to abiotic stress and root growth. In one study, it was observed that hydrosulfide (NaHS) [H_2S donor sodium] and the hemin (HO-1 inducer) encourage LR development in tomato seedlings. Basically, it regulates by inducing intracellular signaling key points having the initiation of tomato HO-1 (SlHO-1) and the intonation of cell cycle regulatory genes, such as SlCDKA;1 and SlCYCA2;1 upregulation with immediate SlKRP2 downregulation. HO1 might be concerned in NaHS-induced tomato LR development (Fang et al. 2014). One physiological and molecular confirmation established that both NO and HO1 were implicated in the β-CDH-induced LR formation with, at slightest partially, HO1 regulating downstream of NO signaling (Li et al. 2015). The downstream signals of HO1/CO and calcium (Ca^{2+}) in cucumber for adventitious root (AR) formation in response to auxin application was also demonstrated. The observation designates that methane-rich water (MRW) power acts as a stimulator for the development of adventitious roots which are moderately mediated via HO1/CO and Ca^{2+} pathways (Cui et al. 2015).

This is a well-known fact that lateral roots participate in the major uptake of water and nutrients. *Zea mays* heme oxygenase 1 (ZmHO1) and gibberellic acid-stimulated like-1 (ZmGSL-1) have been established to be implicated in LR initiation. In one study of heat treatment to maize, inhibition was observed in lateral root primordium (LRP) development. Downregulation was also reported in expression of genes connected to LR expansion in maize, ZmHO-1, and ZmGSL-1 which indicates connection in between LR development and HO1 activity (Zhang et al. 2018). Mukherjee and Corpas (2020) explained the significance of HO1 through its by-products viz., CO, H_2S, and NO in the regulation of root development.

2.3 Promising Association Between HO1 and Auxin Response Factor (ARF)

Auxin controls lateral root development by regulating its signal transduction pathway. Physiological state and the prevailing environmental conditions influence the development of lateral root. Researchers have discovered that CO is an important signaling molecule and mediator for regulation of lateral root development (Xuan et al. 2008b). The CO and HO1 induce lateral root development which is dependent on the auxin concentration. Formation of lateral root primordia requires regulation of auxin polar transport, confined accumulation, and reorganization. During the progression of lateral root development, auxin first formed in shoots is transferred through the stele to the root apical meristems (RAM) and reorganized to the layers of root cells. In plants, lateral root's primordia is shaped in the differentiation zone of preexisting roots by dedifferentiation of non-meristematic pericycle cells and occasionally endodermal cells (Hochholdinger et al. 2001). There is experimental evidence for some kind of functional interaction of CO and auxin, as formation of CO-induced lateral roots can be suppressed in absence of auxin. But contrary to the involvement of auxin in the development of primordial and lateral roots, CO only induces the appearance of lateral roots. Intracellular production of CO and its functions are strongly linked to the HO1. Experimental evidence suggests some kind of direct functional communication between HO1 and auxin due to interaction of HO1 with auxin via CO (Han et al. 2012). Inducible HO expression has been observed on increasing the concentration of auxin and abscisic acid. Between the two, auxin is known as the key component to control adventitious rooting and lateral root development.

ARFs are basically transcription factors (TF) that control an initiation of auxin response gene's expression (Tiwari et al. 2003). ARFs work by binding particularly to TGTCTC-auxin response elements (AuxRE) with promoters of genes repressors dimerize with ARF activators. In recent years, researchers have focused on the findings of regulatory pathways related to ARF gene/protein expression. The purpose of ARFs is to control target genes related to plant growth and development especially root development.

ARF regulation and activation are well explored (Salehin et al. 2015). At low auxin concentration in plants, Aux/IAA proteins with corepressor TOPLESS (TPL) form dimers with ARFs and inhibit ARF activity that represses the purpose of auxin-responsive genes (Szemenyei et al. 2008). On the other hand, higher auxin concentration leads degradation of Aux/IAAs by binding to its SCFTIR1/AFB complex and afterwards being converted into an ubiquitinated and degraded form with the help of 26S proteasome. This reaction makes ARF then free and participate in target auxin response transcription (Wang and Estelle 2014) (Fig. 14.1).

Few studies have reported about interconnections of CO (a by-product of HO1 activity) with NOS/NO and auxin (Nan et al. 2014; Yang et al. 2016; Li et al. 2016;

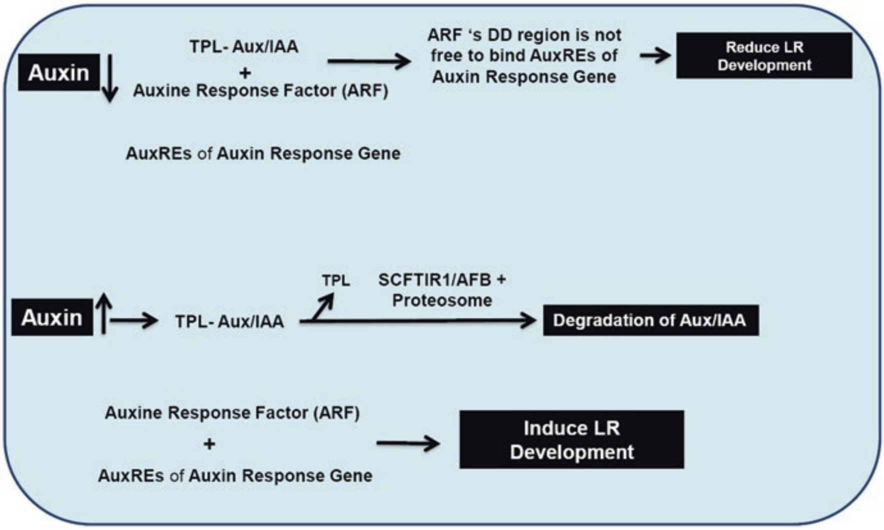

Fig. 14.1 The key events in auxin during lateral root development

Cao et al. 2016). These reports specify the possible participation of HO1 through its by-product CO to control lateral root development. Nan et al. (2014) have demonstrated that auxin regulates NO/NOS pathway and the auxin response gene transcription process. Auxin regulates NOS/NO and HO1/CO signaling pathways. NOS/NO and HO1/CO signaling pathways may be interconnected with each other and may regulate each other. Upregulation of HO1/CO might be regulated by auxin, H_2S, and methane-rich water (Xuan et al. 2008b; Lin et al. 2012; Cui et al. 2015). Further, this upregulation activates a series of events such as cyclic GMP (c GMP) through guanylate cyclase, c GMP-dependent protein kinase (PKGs), which can break down further TPL- Aux/IAA complex through its ubiquitination process and degradation. This degradation leads creation of ARF. This ARF further can bind to auxin-responsive genes for transcription initiation which is followed by LR development (Nan et al. 2014) (Fig. 14.2). Various reports have demonstrated about HO1's importance in various aspects of plant system. HO1 plays a significant part as antioxidant against various abiotic stress such as salt stress. Many reports indicate HO1 upregulation and enhanced lateral root progress under abiotic stress including salt stress. HO1/CO also regulates possibly a variety of events for LR development. Thus, this study indicates that HO1 may overcome oxidative stress induced by salt stress by enhancing LRs.

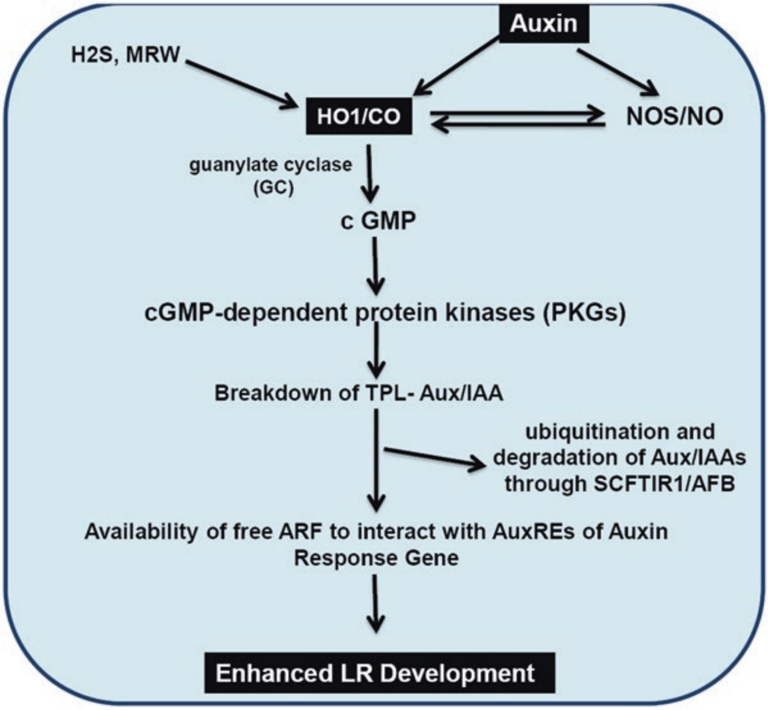

Fig. 14.2 Schematic figure of proposed regulatory pathways of HO1/CO in plants for lateral root development

3 Conclusion

HO1 has a diverse role in plant system. HO regulates the degradation reaction of free heme. A constructive function of HO1 has been demonstrated as antioxidant in plant system against oxidative stress induced by various abiotic stress. Along with this major role, HO1 also plays a regulatory task in LR development. LR enhancement during salt stress conditions indicates that this event helps to overcome stress effects. This study uncovers regulatory association among HO1 and LR development against salt stress. Along with this, possible interconnection is also present between auxin and NO/NOS pathways for signaling LR development. This study also unlocks the possibilities of more pathway's connection with HO1 for LR development in context of salt tolerance.

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Chapter 15
Salt-Tolerant and Plant Growth-Promoting Rhizobacteria: A New-Fangled Approach for Improving Crop Yield

Subhadeep Dutta, Debjoy Bhattacharjya, Sangram Sinha, and Amit Kumar Mandal

Contents

1 Introduction

Terrestrial plants face lots of environmental stresses in their entire life span starting from sprouting. There are so many abiotic factors like temperature, drought, salinity, and heavy metals directly inflicting the plants' health and crop production. Around

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90% cultivated lands are amenable to one or more abiotic factors. Thus, around 70% of total crop productivity is reduced due to abiotic stresses (He et al. 2018; Waqas et al. 2019). Abiotic stresses exhibit an adverse effect on plants' growth. Environmental stresses can limit the productivity of major economically important crops (Cohen and Leach 2019; Vishwakarma et al. 2017). About 5.2 billion hectares of fertile lands have been damaged by various types of abiotic factors globally. Among them, soil salinity is the major constrain to produce crops. Sodium (Na^+), bicarbonate (HCO^{3-}), magnesium (Mg^{2+}), sulfate (SO_4^{-2}), potassium (K^+), chloride (Cl^-), calcium (Ca), and carbonate (CO_3^{-2}) are the salt ions which contribute to soil salinity as these ions are highly soluble in water. Soil chemistry studies have estimated that electrical conductivity of a soil measuring 4 dSm^{-1} or more may be considered as saline soil (Gamalero et al. 2020). In India, approximately 7 million hectares of croplands have been affected by salinization. Excess salinity is most unfavorable for germination, plant vigor, and crop yield. It confers osmotic stress and toxicity and reduces essential nutrient uptake. Plant tissues accumulate high concentration of NaCl from soil, and as a result, the concentration of Na^+ and Cl^- ions in the plant tissue increases which in turn reduces K^+ ions uptake sometimes leading to plant death (Ketehouli et al. 2019; Marakana et al. 2018). Reactive oxygen species (ROS) like singlet oxygen ($^1O_2$), superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^-), however, are produced by different plant metabolic pathways like photorespiration, respiration, and photosynthesis routinely. Nevertheless, excess production of the same by various environmental stresses is harmful for plants. Salinity generally induces the production of H_2O_2. The ROS can destroy plasma membrane, DNA, RNA, enzymes, and different plant pigments (Ijaz et al. 2019; Tripathy and Oelmuller 2012; Xie et al. 2019). Evolution has come out with numerous ways to cope up with the various abiotic stresses including salinity stress. The soil which resides at the close vicinity of the plant roots is called rhizospheric soil. Roots always leach various types of organic components like amino acids, fatty acids, sugars, vitamins, organic acids, and other growth factors to the rhizospheric soil. These components act as chemo-attractants, which induce a high number of bacteria to colonize in the rhizospheric soil, and these bacteria are called rhizospheric bacteria. Among them 1–2% bacteria, which have been found to induce plant growth directly, are generally grouped as plant growth-promoting rhizobacteria (PGPR) (Glick 2012; Vacheron et al. 2013; Vejan et al. 2016; Beneduzi et al. 2012). PGPR has different role in crop production and amelioration of various biotic and abiotic stress. PGPRs are involved in enhancing seed germination; physical strength of plants like root length and shoot length; chlorophyll content; leaf protein content; essential plant nutrients via production of many plant phytohormones like auxin, gibberellin, and cytokine; and secretion of iron chelator like siderophore production. PGPR also involves itself in plant protection from harmful plant pathogen by production of chitinase, glucanase, antibiotics, and ROS scavenging enzymes like peroxidase (POX), superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR). Several genera of bacteria have been reported as potent PGPR like *Azotobacter*, *Pseudomonas*, *Klebsiella*, *Agrobacterium*, *Azospirillum*, *Serratia, Streptomyces,* etc. (Kumar and Verma 2018; Kumari 2015; Arora et al. 2020) (Table 15.1).

2 Salinity Stress

2.1 *How Soil Became Saline?*

In the recent times, soil salinity has become a troublesome issue around the globe. Approximately 20% of irrigated lands are salt affected throughout the world which showed harmful effects on the crop production. Generally, if the electrical conductivity (EC) of a soil is more than 4 dS m^{-1} at 25 °C, it is considered as saline soil. Normally, saline soil consists of chloride and sulfates of Na, Ca, Mg, and K. There are two main reasons to increase salinity in croplands. Climate change is the natural process for increasing the soil salinity. Besides, human activities also contribute fatal effect on soil physiology. Human activities like poor irrigation process using shallow groundwater and usage of chemical fertilizers and pesticides impart the major portion of salinity in the soil. This is called secondary salinization (Machado and Serralheiro 2017; Shrivastava and Kumar 2015).

2.2 *How Salinity Affects Plant Growth?*

Soil salinity has numerous negative impacts on crop productivity (Fig. 15.1). Due to massive evaporation of soil water in arid and semiarid region, a huge amount of salts is accumulated in the soil (Ghosh et al. 2016). Among various salts present in soil, NaCl contributes major toxicity to the crop plants. Commonly high concentration of salts is the chief obstacle for the plants to uptake water and major nutrients from the soil. These two phenomena deliver osmotic stress and oxidative stress to the plants (Li and Li 2017). Salinity stress also impedes the chief biochemical, physiological, and molecular process, like photosynthesis and protein and lipid metabolisms (Parida and Das 2005). Salinity stress also reduces seed germination percentage. Due to osmotic stress, seeds cannot absorb enough water, and the protein synthesis process of developing embryo gets hampered (Almansouri et al. 2001). Salinity stress weakens root absorption and also impedes xylem conductivity (Pessarakli et al. 2015). Higher amount of Na^+ and Cl^- ion accumulation can interfere with the absorption of N^+, K^+, Mg^+, and Ca^+ ions, leading to many deficiency syndromes. Lack of K^+ ions lowers the stomatal conductance and reduces photosynthetic efficiency and protein and starch biosynthesis. Potassium deficiency hampers the activity of many enzymes. It has a direct impact on turgor pressure and osmoregulation. Deficiency of Ca^+ and Mg^{2+} ions hampers the production of chlorophyll (Parihar et al. 2015; Osmolovskaya et al. 2019). Nitrogen is an essential element for synthesis of protein, nucleic acids, and various types of metabolites and cofactors. Nitrogen is indispensable for various types of osmoticum synthesis (free amino acids, proline, and glycine betaine) which provide a protective mechanism against osmotic stress. Deficiency of N^+ ions leads to chlorosis and directly affects photosynthetic apparatus (Ahanger et al. 2019).

Table 15.1 List of PGPRs that ameliorate salt stress and alleviate plant growth

Microorganisms	Source	Mechanisms	Result	Reference
Streptomyces *Sphingobacterium* BHU-AV3 *Pseudomonas pseudoalcaligenes* and *Bacillus subtilis* *Pseudomonas aeruginosa* (JHA6) and *Bacillus amyloliquefaciens* (ROH14) *Hartmannibacter diazotrophicus and Pseudomonas* sp. *Azotobacter chroococcum* (LMG 8756) *Azotobacter vinelandii* (DSM576) *Bacillus safensis* *Pseudomonas fluorescens* Ms-01 and *Azospirillum brasilense* DSM1690 *Bacillus* sp. (KF514117), *Zhihengliuella halotolerans (KF514119),* *Staphylococcus succinus* (KF514120), *Bacillus gibsonii* (KF514122), *Halomonas* sp. (KF514129), and *Halobacillus* sp. (KF514117)	*Triticum sp.* Agricultural field *Oryza sativa* and *Saccharum officinarum* *Capsicum annuum* *Medicago sativa* *Triticum aestivum* *Triticum aestivum* *Vitis vinifera* and *Digitaria decumbens* *Triticum aestivum*	Increase production of antioxidant Produce antioxidant significantly Possess ACC deaminase activity and produce siderophore and indoleacetic acid (IAA) Phosphate solubilization, IAA and ACC deaminase production, as well as siderophore production Increase phytohormone and other growth factors IAA production Produce IAA, ACC deaminase, and defense enzymes Auxin production, inorganic phosphate solubilization capacities, and antioxidative enzyme production Production of IAA and ammonia, N_2 fixation, phosphate solubilization, and ACC deaminase	Increases root and shoot dry weight and chlorophyll and carotene content Increase root and shoot length and chlorophyll content Increases root and shoot dry weight and chlorophyll and protein content Increase plant growth, total soluble protein, and antioxidative enzyme Increase the root length and weight, number of nodule, and chlorophyll Increase root and shoot length Increase plant growth and biotic defense Promote plant growth Increase the root and shoot length and fresh weight against salt stress	Akbari et al. (2020) Vaishnav et al. (2020) Yasmin et al. (2020) Ansari et al. (2019) Allam et al. (2018) Chakraborty et al. (2018) Kadmiri et al. (2018) Orhan (2016)
Bacillus megaterium and *Enterobacter* sp.	*Abelmoschus esculentus*	ACC deaminase and antioxidant enzymes	Higher germination percentage, growth parameters, and chlorophyll content	Habib et al. (2016)

(continued)

Table 15.1 (continued)

Microorganisms	Source	Mechanisms	Result	Reference
Enterobacter cloacae and *Bacillus drentensis* plus silicon *Bacillus amyloliquefaciens* SQR9 *Bacillus cereus* Pb25 *Pseudomonas koreensis* AK-1 (MTCC No. 12058) *Pseudomonas strains PF1 and TDK1* *Streptomyces* sp. PGPA39 *Halobacillus sp. Bacillus sp.*	*Vigna radiate* *Zea mays* Saline wastewater *Glycine max* *Oryza sativa* L. *genotypes ADT43 and IR50* *Solanum lycopersicum* *Triticum aestivum*	Produce IAA, siderophore, and ACC deaminase Produce IAA and gibberellin (GA3) Auxin production, siderophore production, and ACC deaminase and phosphate solubilization Increase proline content, stress response enzyme, and ROS scavenging enzymes Cope up salt stress Exhibit higher IAA production and phosphate solubilization in addition to ACC deaminase activity Produce IAA and siderophore and phosphate solubilization	Increase plant height, leaf area, and seed yield Promote the growth of maize seedlings and enhance chlorophyll content Plant growth promotion Induce growth promotion, reduce Na levels, but increase K levels in leaves and roots Plant height, root length, and leaf area were significantly increased. Alleviation of salt stress and plant growth promotion Root and shoot length and biomass	Mahmood et al. (2016) Chen et al. (2016) Islam et al. (2016) Kasotia et al. (2015) Sen and Chandrasekhar (2014) Palaniyandi et al. (2014) Ramadoss et al. (2013)
Pseudomonas and *Rhizobium*	*Vigna radiata*	ACC deaminase	Increase the photosynthetic rate and chlorophyll content	Ahmad et al. (2013)
Azospirillum lipoferum and Pseudomonas fluorescens	Pure culture	Increase photosynthetic pigments and proline	Increase photosynthesis and cope up salinity stress	Ahmadi et al. (2013)
Bacillus cereus	*Cynodon dactylon*	IAA production, phosphate solubilization, and siderophore	Increase height, number and length of leaves, as well as root and shoot biomass	Chakraborty et al. (2011)

(continued)

Table 15.1 (continued)

Microorganisms	Source	Mechanisms	Result	Reference
Pseudomonas sp. DW1	*Solanum melongena.*	Antioxidative enzyme	Dry matter, root length, and seed germination rate are highly increased.	Fu et al. (2010)
Pseudomonas fluorescens, Pseudomonas aeruginosa, and Pseudomonas stutzeri	*Solanum lycopersicum*	Solubilize phosphate and produce phytohormones, siderophores, and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase enzyme	Enhancement in root and shoot length, enhanced salinity tolerance in plants, and enhanced biomass production in tomato plants	Tank and Saraf (2010)
Azospirillum lipoferum Z4/1.	Pure culture	Stimulate nitrate reductase and nitrogenase activity in both shoots and roots, amino acids, sugar, and protein	Root and shoot dry weight	Hamdia et al. (2004)

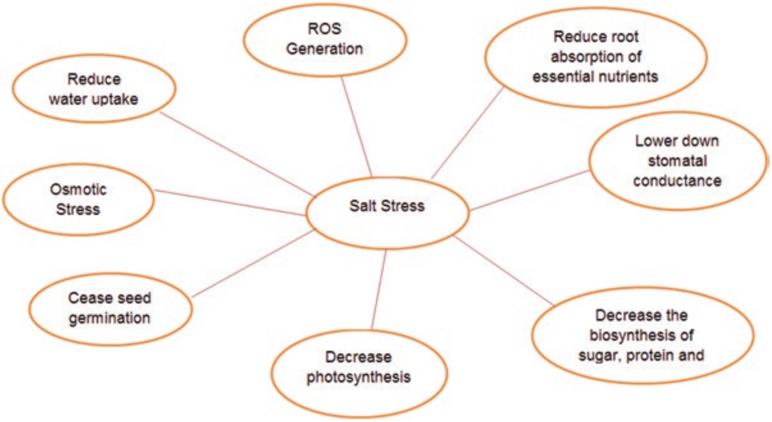

Fig. 15.1 Adverse effects of salt stress

2.2.1 What Are the Effects of Salinity Stress on Photosynthesis?

Photosynthesis is the key biochemical reaction which creates a major food chain in this planet. In this process, solar energy is converted into biochemical energy in green plants. Mainly plant leaves and sometimes other part of the plant body contain numerous photosynthetic pigments like chlorophyll, xanthophyll, pheophytin, and various carotenoids. Photosynthetic apparatus like pigments and photosystem I and II together produce NADPH and ATP in light reaction and CO_2 assimilation in dark reaction. Ultimately, the whole process is directed to produce carbohydrates which are the main energy source for all living creatures (Sudhir and Murthy 2004; Singh and Thakur 2018). Salinity has deleterious effects on photosynthesis (Sultana and Ikeda 1999). According to Heidari (2012), rising of salinity can cause a steep loss in the quantity of chlorophyll A, chlorophyll B, and carotenoids. With the increasing amount of salinity, the rate of photosynthesis gets decreased (Yang et al. 2020). Salt stress affects both the stomatal and non-stomatal factors and the enzymes which are involved in CO_2 reduction (Hnilickova et al. 2017; Shu et al. 2012). As a result, the overall production of electrons also declines. The whole electron transport system and ATP generation process collapse due to lack of electrons (Najar et al. 2019).

2.2.2 How Salinity Stress Affects Amino Acids and Proteins?

Nitrogen is one of the main constituents of amino acids, proteins, amides, polyamines, and quaternary ammonium compounds. In salt stress condition, the amount of nitrogen uptake is decreased by the plant. The salt ions like Cl^- can hamper the accumulation and transportation of nitrate (NO^{3-}) ions into the plant. Generally, it decreases the production of nitrate and ammonium-assimilating enzymes and induces hydrolytic enzymes (e.g., protease). Enzymes like nitrate reductase, nitrite reductase, glutamine synthetase, and glutamate synthase are inhibited by salt stress (Ashraf et al. 2018; Abdelgadir et al. 2005). So, the overall synthesis of protein and amino acid is disrupted by salt stress. Some recent studies also revealed that the amount of N-contents, soluble protein, and amino acids is increased in salt stress condition. Osmo-protectants like proline, arginine, ornithine, and citrulline are also increased to protect plants from osmotic stress (Khalipe et al. 2018). It is also reported that during salt treatment in soybean plants, amino acids are decreased, but leaf proteins remain unaltered (Queiroz et al. 2012).

2.2.3 How Salinity Stress Affects Lipid?

Salt stress is readily involved with the alteration of membrane lipids, sterols, and phospholipids which are the major components of cell membrane, hampering the usual membrane integrity. Thus, the routine function of the cell membrane is disrupted. Besides, the membrane transport protein is also disrupted due to the lipid alterations (Surjus and Durand 1996; Racagni et al. 2003). Some researchers, however, have reported that in some species of canola (*Brassica napus* L.), increasing amount of NaCl can increase the amount of plasma membrane sterol and phospholipids (Zamani et al. 2010). In *Zea mays* (maize), the monogalactosyldiacylglycerol (MGDG) level in mesophyll cell of chloroplast is significantly decreased under salinity stress (Omoto et al. 2016).

3 Strategies Involved in Ameliorating Salt Stress

To ameliorate salinity stress, plant develops various adaptation mechanisms. Salt-resistant plants exhibit three different strategies, that is, avoidance, evasion, and tolerance. In avoidance mechanisms, the strategies involved are as follows: (i) plants grow only in low salinity conditions and (ii) decreased the root growth and its absorption capacity; in evasion mechanisms (i) reduction of Na^+ and Cl^- ions absorption by the plant itself, (ii) compartmentalization of the toxic salt in isolated compartments, and (iii) secretion of salts to balance with environmental salinity, and in tolerance mechanism- (i) production of several osmo-protectants like proline and malondialdehyde and (ii) increments of salt-resistant cells (Batanouny 1993; Stavridou et al. 2017). In addition to plant's intrinsic mechanism to cater saline stress, several studies have come up with promising results to protect plants in salt stress condition with improved plant growth and yield. Some research showed that selenium (Se), an essential element for human, can protect plants from reactive oxygen species (ROS), which is produced mostly during salinity condition (Kamran et al. 2020). It is also reported that calcium-fortified compost animal manure (Ca-FCM) can improve plant growth and crop yields during salt stresses (Naveed et al. 2020). A study revealed that poultry manure and gibberellin significantly reduced ROS generation by increasing proline contents (Altaey 2017). Gene manipulation is another effective technique to cope up salt stress. Recombinant DNA technology is the most important tool to produce various transgenic plants. It is proved that glycine betaine is the popular osmolyte which can maintain cell membrane integrity and photosynthetic apparatus from osmotic stress (Tang et al. 2015). A study shows that in some cases, plants produce less glycine betaine. Transgenic expression of flavoprotein, choline oxidase (COX), and choline dehydrogenase (CDH) readily converts aldehyde to betaine (Huang et al. 2000). It is also reported that the transgenic wheat plant enhances salt tolerance by overexpression of GmDREB1 gene. Oxidation- and osmotic stress-related proteins are upregulated in transgenic plants (Jiang et al. 2014). The most promising approach that evolved in recent times is the application of plant growth-promoting bacteria (PGPR) in the rhizosphere of plants growing in saline soil through successful root colonization. PGPRs can ameliorate salt stress and improve plant growth and crop productivity by the production of many plant growth- and plant health-protecting factors (Ilangumaran and Smith 2017).

3.1 Plant Growth-Promoting Rhizobacteria

The soil associated with the close vicinity of the plants' root is often termed as rhizospheric soil (Noumavo et al. 2016). There are so many microorganisms found in soil. Among them, almost 95% are bacteria. The soil bacterial growth is highly influenced by different environmental factors like soil salinity, temperature, and moisture. Plant root leaches various types of amino acids, inorganic acids, soluble sugar, vitamins, and growth factors which are called chemical attractants. These chemical attractants help colonizing the diverse bacterial community. These groups of bacteria are collectively called plant growth-promoting rhizobacteria (PGPRs). The PGPRs are found in greater number in the rhizospheric region than non-rhizospheric region (Glick 2012; Nihorimbere et al. 2011; Hol et al. 2013). Plant growth-promoting rhizobacteria and root involve two main types of association; one is symbiotic, and other is nonsymbiotic. In symbiotic association, bacteria enter into the plant by root hair, and in non-symbiotic association, bacteria colonize freely at the close vicinity of plant roots (Agrawal et al. 2014). Some symbiotic PGPRs are *Rhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Mesorhizobium,* and *Sinorhizobium*. Some popular non-symbiotic strains are *Pseudomonas*, *Bacillus*, *Klebsiella,* and *Serratia* (Vijay et al. 2017; Sathya et al. 2017). PGPRs protect plants from diverse type of stresses of biotic and abiotic origin. Under salinity stress condition, the salt-sensitive plants totally lose their metabolic and physical health. At that time, PGPRs are the only eco-friendly solution to ameliorate the detrimental effects of environment (Albdaiwi et al. 2019). PGPRs employ direct and indirect mechanisms to fight against the hostile environment (Fig. 15.2). It plays a significant role in boosting up plant growth and plant immunity by producing growth hormones (IAA, gibberellin, and cytokinins), HCN, ACC deaminase; fixing atmospheric nitrogen; and solubilizing phosphate; it also produces various types of antimicrobial factors which trigger the induction of systemic resistance (ISR) (Jha and Saraf 2015; Mabood et al. 2014).

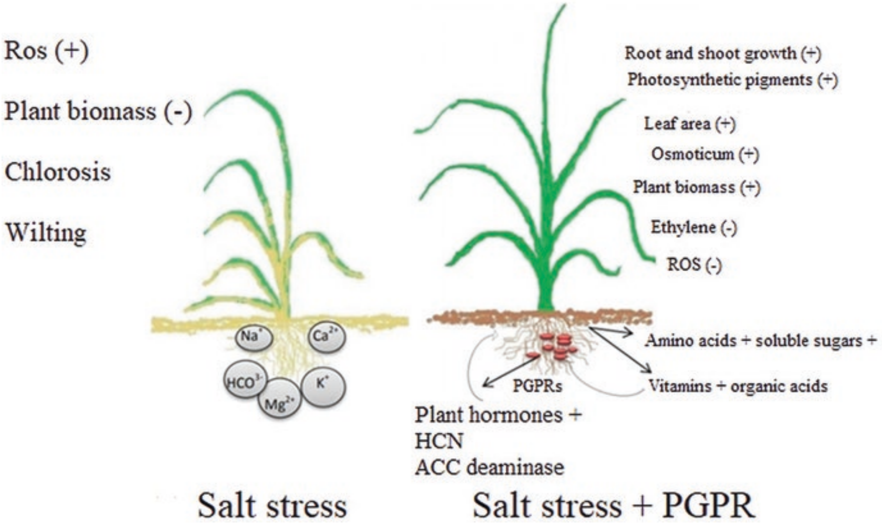

Fig. 15.2 Effects of PGPR on plant during salt stress conditions

3.1.1 Plant Growth Regulators (PGR)

Phytohormones, the plant growth regulators (PGRs), are the most precious factors for the plant physiology. In salinity stress conditions, plants cannot synthesize adequate amount of phytohormones. The PGPRs, which secret phytohormones, play an important role in ameliorating the stresses. Three main phytohormones such as auxin, gibberellins, and cytokinin are produced by the plant itself. PGPRs can also help in producing these phytohormones (Egamberdieva et al. 2017).

Auxin (IAA)

Auxin plays a key role in cell cycle promotion. It is the main signaling molecule to influence (i) cell division and enlargement, (ii) roots and shoots elongation, (iii) flower morphogenesis, (iv) phototropism, (v) geotropism, and (vi) apical dominance (Sharma and Kaur 2017; Verma et al. 2010). Plant root exudate contains L-tryptophan (amino acid), which is utilized by PGPRs to synthesize IAA. Tryptophan-independent IAA synthesis by PGPRs has also been reported (Gupta et al. 2015). It has been reported that PGPRs like *Pseudomonas, Azospirillum, Xanthomonas, Mycobacterium* sp., *Bacillus cereus,* and *Bradyrhizobium japonicum* can produce auxin hormone and promote plant growth (Kumar et al. 2015). It is reported that PGPRs like *Pseudomonas extremorientalis* TSAU 6 and TSAU 20 and *Pseudomonas aurantiaca* produce IAA and enhance wheat plant growth significantly in salt stress (Egamberdieva 2009).

Gibberellins or Gibberellic Acid and Cytokinin

Gibberellins are the most valuable group of hormones for the plant developments. It regulates cell division and elongation of stem, leaf, and meristem. It also plays a vital role in reproductive organ development (Tsukanova et al. 2017). The major roles of gibberellic acid (GA) are (i) seed germination, (ii) root hair production, (iii) inhibition of floral bud differentiation in angiosperm, (iv) relieve of heavy metal stresses, (v) fruit and flower development, and (vi) lateral root elongation (Bottini et al. 2004; Kang et al. 2017). Salinity stress has a brutal effect on seed germination. Salt can delay the germination process of soybean seed by downregulation of gibberellin production (Shu et al. 2017). Some PGPRs are readily involved with GA production such as *Bacillus cereus, Bacillus macroides, and Bacillus pumilus* (Joo et al. 2005).

The plant hormone cytokinin also plays a vital role for the plant growth. It can enhance plant growth by (i) seed germination, (ii) delay of leaf senescence, (iii) chloroplast synthesis, and (iv) stem differentiation (Kenneth et al. 2019). There is a clear evidence that cytokinin has a significant role to tolerate the abiotic stress interacting with other growth-promoting hormones. Cytokinin can show salt-induced response and enhance proline, osmotin, pinitol, PEPCase, and ononitol (Llanes et al. 2018). Some PGPRs are reported to produce cytokinin belonging to the genera such as *Bacillus, Pseudomonas,* and *Azospirillum* (Patel and Minocheherhomji 2018).

Nitrogen Fixation

Plant cannot fix the atmospheric nitrogen by its own. But nitrogen is the essential element for the plant. N_2 is one of the essential elements for the biosynthesis of nucleic acid, amino acids, and lipids. Some PGPRs can boost the plant to fix the atmospheric nitrogen into ammonia with the help of nitrogenase enzyme. PGPRs allow the whole process by both symbiotic and non-symbiotic mechanisms (Odoh 2017). About 70% of biological nitrogen is fixed by PGPRs. There are many genera which have been reported to fix atmospheric nitrogen like *Rhizobium*, *Azospirillum, Klebsiella, Pseudomonas, Cyanobacteria,* and *Enterobacter* (Sivasakti et al. 2017; Kuan et al. 2016). Excess salinity is one of the main barriers to nodule formation in nodulating plants. The overall process of root nodule formation is hampered. The number of root hair is the most important factor in producing root nodules, but salinity can reduce the number of root hair formation (Bruning and Rozema 2013). Gamalero and his group have (Gamalero et al. 2020) reported that PGPRs like *Pseudomonas stutzeri*, *Pseudomonas mendocina,* and *Bacillus subtilis* fix nitrogen successfully in salinity stress condition.

Phosphate Solubilization

Phosphorus is considered as a macroelement for plants. It plays a vital role in photosynthesis, nucleic acid biosynthesis, high-energy compound (e.g., ATP) synthesis, respiration, and abiotic stress mitigation. In spite of that, plant can't uptake phosphorus from the soil, and about 95% of inorganic and organic phosphorus remain in insoluble form in the soil (Gouda et al. 2018). Phosphate-solubilizing bacteria (PSB) is a special group of PGPRs that can transform insoluble phosphorus into soluble monobasic (HPO_4^{2-}) and dibasic ($H_2PO_4^-$) forms (Suleman et al. 2018). This reaction is catalyzed by phosphatase enzyme (Zandi and Chalaras 2014). Some studies revealed that in saline soil, the number of phosphate-solubilizing microorganisms are reduced (Jiang et al. 2018). However, halotolerant PGPR strains belonging to the genus *Pseudomonas* could solubilize phosphate in saline soil (Pirhadi et al. 2018).

Siderophore Production

Siderophore is a small peptide which has a ligand and high affinity to iron. Iron is an essential element, and it has different roles in plant's life. A huge number of proteins (e.g., hemoglobin), enzymes (e.g., carboxylase), and electron transporters are comprised of iron. Unlike phosphorus, iron resides in the soil in immobilized form (Beneduzi et al. 2012; Agrawal et al. 2017). In saline condition, the iron availability is decreased by some unknown reasons. The Fe^{2+} ions in soil can be in oxide, hydroxide, and other insoluble forms. The Fe^{2+} ions can be oxidized into Fe^{3+} ions with the help of oxygen and neutral pH. Various aerobic microorganisms are also responsible for the conversion of Fe^{2+} to Fe^{3+} ions. Fe^{3+} ions are the immobilized form and are inaccessible to the plants. Siderophore can chelate Fe^{3+} and facilitates uptake of iron-siderophore complex through roots (Ferreira et al. 2019; Perez-Montano et al. 2014). PGPRs belonging to genera like *Bacillus*, *Pseudomonas*, *Rhodococcus,* and *Enterobacter* strongly produce siderophore in stress condition (Singh 2018). Microbial siderophore production has been reported to alleviate heavy metal stress as well (Sinha and Mukherjee 2008).

Hydrogen Cyanide (HCN)

Hydrogen cyanide (HCN) is the secondary metabolite of some PGPRs. HCN is a potent antimicrobial agent. It is well established that plant secrets glycine (amino acid) which is the main carbon precursor of HCN. HCN inhibits the growth of various plant pathogens (Rathore 2014). HCN acts on diverse types of pathogenic bacteria and numerous fungal pathogens. Some studies claimed that HCN can solubilize elements from rock phosphate and increase their bioavailability in the soil (Rijavec and Lapanje 2016). Several genera like *Pseudomonas fluorescens*, *Pseudomonas aeruginosa,* and *Chromobacterium violaceum* have been reported to synthesize HCN (Soltani et al. 2010).

ACC Deaminase

Ethylene, a gaseous plant hormone, is responsible for the inhibition of plant growth. In stress condition, the level of ethylene is increased. The compound 1-aminocyclo propane-1-carboxylic acid (ACC) is the main precursor of ethylene. Methionine (amino acid) is converted into S-adenosyl methionine (SAM) by SAM synthase. Then SAM is converted into ACC, catalyzed by ACC synthase. ACC is then converted into ethylene by ACC oxidase (Nascimento et al. 2016; Eskandari Torbaghan et al. 2017). Scientist Abeles coined the name "stress ethylene." In salinity stress, the "stress ethylene" is increased in huge amount (Glick 2004). Elevation of ethylene indicates that the plant is susceptible with various abiotic stresses. The compound ethylene readily decreased the plant growth and led to plant death (Pandey and Gupta 2019).

PGPRs synthesize a unique enzyme ACC deaminase that hydrolyzes ACC into ammonia and alpha-ketobutyrate (Chen et al. 2013; Glick et al. 2007). According to Kang et al. (2017), *Leclercia adecarboxylata* was reported to be a potent ACC deaminase-producing PGPR. It has been reported by many scientists that ACC deaminase-synthesizing PGPR strains could alleviate salt stress (Pandey and Gupta 2019).

Reactive Oxygen Species (ROS)

Reactive oxygen species (ROS) has detrimental effects on plant growth and development. Generally, ROS may be free radicals (O_2^-, OH^-, HO_2, etc.) and nonradicals (H_2O_2 and $^1O_2$). ROS like H_2O_2 and superoxide (O_2^-) ions can disrupt cell constituents (DNA, protein, and lipid) and lead to plant death. In salt stress, stomatal conductance is reduced. This phenomenon decreases the amount of CO_2 intake and also produces oxidized $NADP^+$. $NADP^+$ is the terminal electron acceptor of the photophosphorylation process. Due to less amount of $NADP^+$, the excess electrons are accepted by O_2 and turned into O_2^- ions and then converted into various other ROS (Abogadallah 2010; Bi et al. 2009; Gill and Tuteja 2010). There are many antioxidants used as ROS scavenger. Nonenzymatic antioxidants such as flavonoids, carotenoids, betalains, and vitamin E and enzymatic antioxidants such as catalase (CAT), superoxide dismutase (SOD), peroxidases (POX), and ascorbate peroxidase (APX) are the essential antioxidant to ameliorate the adverse effect of ROS (He et al. 2018; Kazan 2015). Alexandra de Andrade Santos et al. showed that in salinity condition, co-inoculation of PGPRs like *Bradyrhizobium* and *Actinomadura* or *Bradyrhizobium* and *Paenibacillus graminis* in the cowpea increased the level of SOD, CAT, POX, and oxidized glutathione and decreased the level of H_2O_2 (Santos et al. 2018). Chandrasekaran and his group (Chandrasekaran et al. 2019) showed that in tomato plants, inoculation of *Bacillus subtilis* increases lycopene and various antioxidants. Ordookhani and his coworkers (Ordookhani et al. 2010) described that PGPRs like *Pseudomonas*, *Azotobacter,* and *Azospirillum* increased the lycopene synthesis and enhance antioxidant activity significantly. It has been reported that PGPRs like *Azotobacter chroococcum* and *Pseudomonas putida* reduced oxidative stress and increased antioxidant activity under salinity stress condition (Khalilzadeh et al. 2016).

4 Conclusion

Plant growth-promoting bacteria are the very important member of soil microbiome. Studies on halotolerant rhizosphere bacteria raised hope to confer adaptability to the plants growing under saline stress. Therefore, isolation and characterization of efficient salt-tolerant bacteria may be helpful for formulating successful biofertilizer. Consortium development by mixing potent PGPR strains may be tried to boost up plant health and productivity and could be exploited to combat saline stress and other associated abiotic stress in the agricultural fields. The scope of application of indigenous PGPR strains as biofertilizer has appeared to be very promising and ecologically acceptable without the question of horizontal gene transfer and other GMM-related environmental issues.

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Chapter 16
Improving Resilience Against Drought Stress Among Crop Plants Through Inoculation of Plant Growth-Promoting Rhizobacteria

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1 Introduction

Crop plants in arid and semiarid regions come across different abiotic stresses under field conditions such as water shortage, salinity problem, and high temperature (Tester and Bacic 2005; Liu et al. 2020). Along with all these types of stresses, the most severe and adverse factor in the whole world is the water-deficit conditions. It has been estimated that drought stress would result in about 50% loss in crop yield, specifically in the arid and semiarid areas of the world by 2050. Drought-stressed vegetation usually suffers water stress along with less nutrient uptake efficiency, less photosynthesis, disturbance in hormone balance, and enhanced production of reactive oxygen species (ROS) (Husen 2010; Husen et al. 2014; Getnet et al. 2015; Embiale et al. 2016; Siddiqi and Husen 2017, 2019). In response to drought stress, crop plants produce antioxidants and osmoprotectants that impede them in coping with stress conditions. Stress involves hormonal changes, and imbalance results in enhanced production of abscisic acid (ABA), minute reduction in indole acetic acid (IAA), and gibberellins (GA_3) concentration along with a rapid decrease in the zeatin level in plant leaves. The endogenous level of cytokines decreases with an increase in drought stress, resulting in triggered response in enhanced ABA level of shoots and increased ethylene contents of roots.

Numerous microbes exist in the region of the plant roots, that is, rhizosphere that forms a multifarious ecological population, impacting plant growth and productivity by their various metabolic activities and interactions with crop plants (Berg 2009; Lugtenberg and Kamilova 2009; Schmidt et al. 2014). In the vicinity of roots, structural changes occur in bacterial communities associated with the plant that select their assemblage as an adaptation toward abiotic stresses, help to improve resistance toward stress to endorse healthiness and tolerance from drought (Schmidt et al. 2014; Cherif et al. 2015; Naveed et al. 2020; Sabir et al. 2020). Presently, there are many techniques to lessen the drought stress/ water deficit and these are chemical, biological, and physical approaches. Several physicochemical strategies have been recommended by researchers to enhance water stress tolerance among crop plants. Furthermore, for soil water conservation and to make its efficient use, some agronomic practices such as bed planting, deep tillage, mulching, and the cover crops have been adopted. Likewise, foliar spray of glycine betaine osmolytes, proline, and phytohormones such as abscisic acid and cytokinins is found favorable to enhance plant enlargement and facilitate them for the recuperation in the stress, but all of these approaches are found to be costly, vigorous, as well as labor intensive. On the other hand, biological approaches could prove inexpensive and efficient. If we proceed toward the development of stress-tolerant varieties, it may take a long duration to develop a new variety, which will show adaptation to target; on the contrary, there is an alternative to all these time-consuming and expensive approaches that a tiny creature in the soil can do this in a short time and much more economically. Every technique is sound and has its good side along with consequences. However, the use of a biological approach that involves the inoculation of microbes has been found sustainable and environment-friendly. In this chapter, the main focus has been given to the rhizobacteria involved in improving drought tolerance in crop plants, their mechanisms of action, and prospects for sustainable agriculture under drought stress.

2 Effect of Drought Stress on Crop Plants

Drought stress has negative effects on crop plants, for example, on turgor pressure and plant–water potential, which is sufficient to obstruct regular functioning (Hsiao and Xu 2000), along with changes in the morphological as well as physiological characteristics of the crop plant (Rahdari and Hoseini 2012). Drought stress contributes to about 15–35% variation in the yield of wheat, grain crops, and oilseed crops. Furthermore, it also has an effect on growth stages like flowering and tillering, which need water critically. It is because many physiological and biochemical changes occur in the crops that affect the metabolic activities like reduced water-use efficiency, lessening of the leaf area, poor root growth, and less stem elongation (Farooq et al. 2009). The water-deficit condition also affects the opening and closure of the stomata that can reduce CO_2 levels drastically in the chloroplast (Farooq et al. 2009).

In addition to this, drought results in the reduced vacuole and cytosol volume. In the period of drought, reactive oxygen species have distorted protein and lipids composition results to adversely influence the plant's usual metabolism, ultimately harming plant's growth (Bartels and Sukar 2005). Ma et al. (2012) have practically proved that wheat crop development was adversely influenced by stress caused through drought by the shortage of water as all of the nutrients needed by plants for optimum growth are taken up by plants in dissolved form despite the fact that water is necessary to maintain the turgor pressure of the plant. Other abiotic stresses like salinity along with drought are the foundation for osmotic stress along with imbalance of ions which leads to dehydration, disintegration of the cellular membrane, and in the solute leakage, eventually affecting badly the growth of plant (Niamat et al. 2019; Rizwan et al. 2021). Gill and Tuteja (2010) also revealed that during stress conditions, reactive oxygen species like oxygen (O^-), superoxide (O_2-), hydrogen peroxide (H_2O_2), and the hydroxyl ion (OH-) production badly spoil the lipid-protein and the DNA through the oxidation process. The drought stress results in reduction in the seed number and seeds acquiesce at flowering, bud formation, and anthesis stage (Hadi et al. 2012). Yan and Shi (2013) also concluded that wheat fresh weight, dry mass, length of root, and plant height all decline drastically in the drought stress; furthermore, production loss is bloated up as the period of drought increases.

3 Strategies to Combat the Drought Stress in Plants

Presently, many approaches have been found successful under drought stress conditions, for example, application of genetic engineering including various biotechnological approaches and conservative breeding techniques, a combination of diverse strategies along with a selection of variety and microbial usage, especially rhizobacteria with drought stress tolerance.

Conventional breeding is thought to be a classical approach just to make crops tolerant to drought stress. In this technique, genetic variability under drought conditions is defined by testing the germplasm and after that, unlike mating design is followed to introduce beneficial traits in novel cultivars and lines. Thus, conventional breeding has been found useful in mitigating drought stress among crop plants (Howarth 2005). However, it is very costly and time consuming.

The biotechnological approach refers to the manipulation of crop genes into consideration to build up a better variety that could survive in an improved way under different climatic conditions or it could be said that the development of variety that will be better adoptive to climatic changes. Biotechnological approach and molecular breeding have been found better, as these give good results in a shorter period of instance than the other breeding techniques like conventional breeding. It has been chosen as the better technique than conventional breeding, as it lessens the breeding cycle of the plant and advances its selection competence genetically, and therefore boosts the potential of the crop to bear drought and the salinity stress as well (Ashraf 2010; Ditta 2013; Shahzad et al. 2019). At the same time, these techniques are time-taking, costly, and labor-intensive. Furthermore, another genetic method is the management of guard cells to reduce the water use of the product so as to enhance the tolerance against stress (Schroeder et al. 2001). Just to make plants tolerant of diverse abiotic stresses, most scientific research is concentrated on genetic engineering and further molecular techniques, but a combination of these techniques would be beneficial and these are most desirable (Varshney et al. 2011).

Different agronomic approaches are also being adopted to alleviate the negative impact of water-deficit condition on crops like customized irrigation methods as sprinkler and furrow and drip irrigation system. The purpose of these methods is to adopt good agronomic strategies to manage and preserve water from diverse sources like snow and rain. As in the growing season, upper layer residues are used to preserve the soil moisture (Nezhadahmadi et al. 2013). Todd et al. (1991) found that evaporation declines all through the season when residues of wheat are used as mulch just as it slows down the water movement and so reduces the evaporation, which ultimately decreases moisture loss. Crop rotation in addition to this is also a good technique to reduce drought effects such as wheat in winter which decrease the irrigation requirement, as it preserves water required by the plants. Among different approaches, the use of rhizobacteria is thought to be a cost-effective and environment-friendly solution to alleviate drought stress among crop plants.

4 Plant–Microbe Interaction

In agriculture, microbial use, for example, rhizobacteria, can prove a constructive approach to alleviate the undesirable effects of various abiotic stresses such as drought stress. Microbial usage for the alleviation of drought stress is an environment-friendly approach. Plant growth-promoting rhizobacteria (PGPR) take possession of plant roots and augment plant growth by straight and meandering mechanisms (Ditta et al. 2015, 2018a, b; Sarfraz et al. 2019; Ullah et al. 2020). The result of the inoculation of PGPR strains such as *Acinetobacter calcoaceticus* SE370 and *Burkholderia cepacia* SE4 @15% polyethylene glycol (PEG) level of drought showed significant increases in the relative water contents, protein level, and amino acids in cucumber plants (Kang et al. 2014).

Considerable upgradation was established in the potential of water and relative water contents once the seed of wheat crop was inoculated with *Azospirillum brasilense* (Creus et al. 2004). To alleviate water-deficit conditions by using PGPR, an experiment in the warehouse was carried out, and four pea seeds were sown in each pot coated with two selected strains of PGPR having a 1-aminocyclopropane-1-carboxylate (ACC)-deaminase enzyme. Results demonstrated a reduction in consequence of drought stress on the growth and capitulation of peas just because of inoculation with the PGPR accompanying ACC-deaminase (Zahir et al. 2008). Seedlings of maize inoculated with the *Azospirillum* resulted in additional stress tolerance, accumulation of proline than that of plants that are un-inoculated in the drought stress (Casanovas et al. 2002). In the same way, *Azospirillum lipoferum* strain secluded from the soil water deficit was inoculated on maize seeds and the rhizosphere application scheduled to two maize varieties headed for lessening the drought stress effects. Outcomes have shown that 54.54% amplification in the open amino acids and 63.15% inside the soluble sugar levels took place because of the inoculation of rhizobacteria (Bano et al. 2013). Along with the PGPR, the *Rhizobium* usage to allay stresses like drought stress in the cereals is thought to be a cost-effective and environmentally friendly resolution. Webster et al. (1997) have stated that the *Rhizobium* sp. colonize the rhizosphere of wheat crop and other cereals ultimately promoting the growth of the plant employing various straight and many tortuous mechanisms just as the creation of auxin, metabolites, ACC-deaminase, and siderophores by increasing the action of nitrogenase enzyme proficiently under different types of stress reminiscent of drought. Lettuce inoculated with the mycorrhizal arbuscular fungi (*Glomus mosseae*) along with *Pseudomonas mendocina* amplified the proline buildup, root phosphatase plus the antioxidants (catalase and the peroxidase) working in the stresses like drought (Kohler et al. 2008).

5 PGPR and Crop Plants Under Drought Stress

Rhizobium usage to diminish drought stress is an excellent strategy to improve crop productivity under changing climatic conditions (Saleh Al-Garni 2006). In the rhizosphere, the *Rhizobial* interface among crop plants is incredibly significant. Plants interact with *Rhizobia* in symbiotic or otherwise associative interaction. Usually, atmospheric nitrogen is fixed by *Rhizobia* in the nodules of legumes, which is very beneficial for legumes. However, rhizobacteria that reside in the root zone of non-legumes also have the potential to maintain plant growth and can be used as PGPR (Shakir et al. 2012; Noel et al. 1996; Hussain et al. 2019; Ullah et al. 2019).

Rhizobium belongs to family Rhizobiacea and is involved in the conversion of atmospheric-N, that is, N_2 into ammonia (NH_3), the process known as biological nitrogen fixation (BNF). On the other hand, apart from the atmospheric N fixation in the legumes, rhizobacteria also play an important role in enhancing the growth and productivity of the non-legumes (Hussain et al. 2009; Ullah et al. 2016). *Rhizobia* bring on forbearance and confrontation to stress among plants that are crucial for plant development under critical environmental conditions such as drought stress. Siderophores manufacturing, which is of low molecular weight and the organic compounds that chelates the iron (Fe) and Zn, production of phytochrome, enzymes biosynthesis to endorse plant development and perk up the nutrients uptake and their accessibility are important mechanisms behind improvement of growth and productivity of non-leguminous crop plants (Zahir et al. 2008; Zeb et al. 2018; Hussain et al. 2020). *Rhizobia* application to non-legumes plants such as maize, wheat, and rice can amplify the drought tolerance via improving the root morphology along with the rate of transpiration improvement that increases the uptake of nutrients under the drought stress conditions to benefit the plant growth.

Rhizobia also activate “Induced Systemic Resistance” (IST), which helps in provoking various biochemical and physiological transformations among crop plants to bear diverse abiotic stresses such as drought stress (Yang et al. 2009). Two main methods adopted by *Rhizobium* for movement of water in the membrane of cells under osmotic stress are as follows: (1) under the minute osmotic level, solute concentration is sustained by simple diffusion, whereas (2) speedy water movement is synchronized with aquaporin, known as water-specific channels (Bremer and Kramer 2000). *Rhizobium* possesses various mechanisms to enhance abiotic stress tolerance. Among them, primarily, the significant method is the secretion of low-molecular weight compounds for osmotic regulation in the cytoplasm. Further reaction of *Rhizobium* involves fluctuation in concentration of ions, provoking proteins produced under stress, and the osmolytes accumulation just as glycine betaine (Bano and Fatima 2009). Very normally, under drought stress, it is considered with the aim of investigating how *Rhizobium* or the further bacteria come across to conditions like hyper- and hypo-osmosis. In this condition, mechanosensitive channels are used by bacteria to sense the cell membrane tension that allows water and the solutes to break out even with a little difference (Poolman et al. 2002). Similar to legumes, *Rhizobia* also invade into roots of the cereals and act as natural endophyte where these produce vitamins, riboflavin, and phytohormones, namely auxin, gibberellins, cytokinins, and abscisic acid (ABA) that play a specific role in the maintenance of plant health and vigor under stress conditions (Dakora 2003). Furthermore, Nichols et al. (2005) reported the production of biopolymers just like exopolysaccharides (EPS) which boost the potential of *Rhizobia* to deal with drought stress conditions. These biopolymers help attach *Rhizobia* to the surfaces, give them protection against the antimicrobial agents released by the plants or animals and restrict the dehydration under drought stress. All of these features improve and amplify the capability of *Rhizobia* to live under water stress conditions that ultimately improves plant growth and development under the drought stress conditions.

Rhizobacteria linked with crop plants are categorized into two types, that is, endophytic and the rhizospheric. Endophytic bacteria are capable of living within the plant tissues, and these might inhabit different plant tissues like flowers and leaves along with stem and fruits (phyllosphere) (Naveed et al. 2014, 2020). On the other hand, rhizospheric bacteria are found on the surface of roots (Weyens et al. 2009). There are certain mechanisms through which these bacteria bring about useful effects on plant growth and yield (Yanni et al. 1997). The main mechanisms have been given in Fig. 16.1. The association of bacteria along plants could be helpful toward stimulating the plant strength or these could also be a restrictive aspect; it depends on the colonization of roots and the ability of rhizospheric bacteria (Antoun et al. 1998). Mehboob et al. (2011) have conducted various studies to elucidate the effect of these PGPR on the growth and productivity of cereals like wheat under drought stress. There was the isolation of different rapidly growing strains of *Rhizobia* from the rhizospheric soil of chickpea, nodules of lentils, and mung bean. Results showed that the isolated strains enhanced the growth, nodulation, and grain yield. Furthermore, a considerable rise in nutrient contents of straw and grain samples was also observed. Ultimately, it was recommended that the *Rhizobium* usage as PGPR can prove beneficial in progressing the development and efficiency of cereals under drought stress. Usually, the extended drought stress results in enhanced injuries (an ionic disorder of cell, denaturation of the proteins, and the alteration in the homeostasis of plants) to the crop plants (Manchanda and Garg 2008). Plant–microbe interactions result in enhanced tolerance against abiotic stresses such as drought stresses. Inoculation of cereals with microbes just like *Rhizobia* could prove environment-friendly and cost-effective approach to lessen the negative impact of the drought stress on plant growth; consequently, the use of microbes such as different *Rhizobia* is a beneficial method to reduce the severe effects of stresses via the augmentation of “induced systemic resistance” (ISR) and production of diverse bacterial compounds like osmolytes, antioxidants, enzymes, and phytohormones (Yang et al. 2009). Definite microbes can fight against abiotic stresses (salinity, drought, heavy metals, and nutrient deficiency). Particularly, the bacteria living in the rhizosphere can affect the tolerance of crops against the abiotic stresses more efficiently employing various direct and indirect mechanisms (Fig. 16.1). *Rhizobia* for non-legumes or cereals work as PGPR and reduce the impact of abiotic stresses through a process called induced systemic resistance (ISR) in the course of production of phytohormones such as auxins, gibberellin, cytokinin, and abscisic acid,

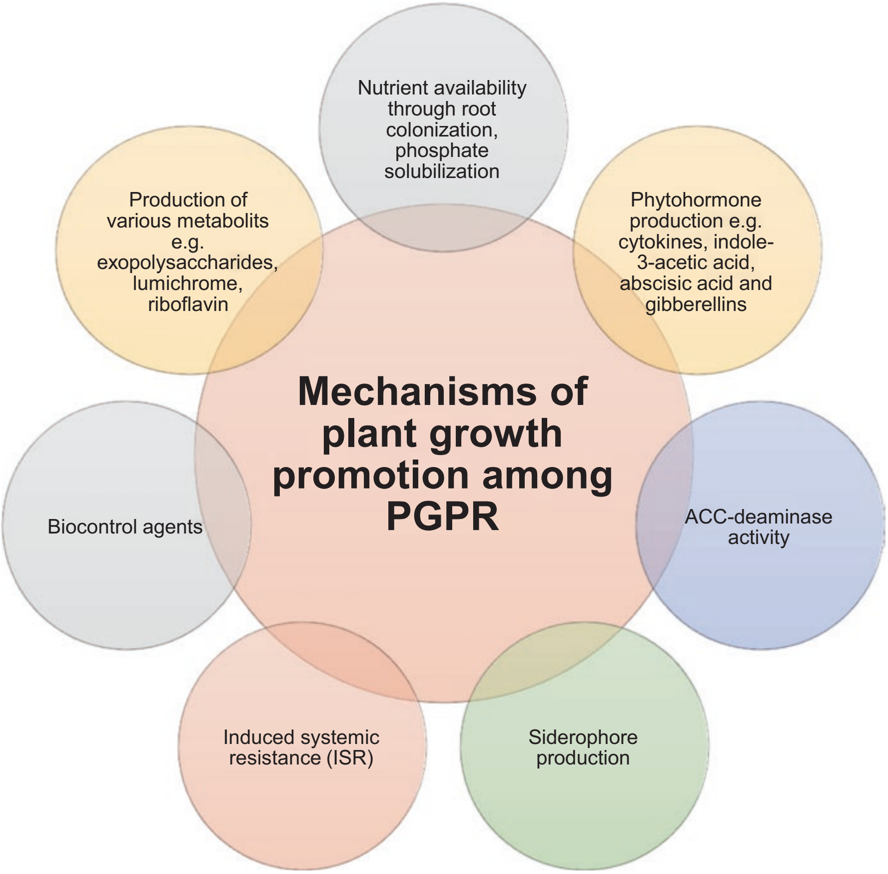

Fig. 16.1 Mechanisms of plant growth promotion among PGPR under drought stress

synthesis of antioxidants and reduction in ethylene levels by producing ACC-deaminase. This method causes a certain type of physical and chemical changes in the plant body that lead to increased tolerance against abiotic stresses (Dimkpa et al. 2009).

Rhizobia mitigate the undesirable impacts of abiotic stresses like salinity, drought, low temperature, high temperature, and the metal toxicity through the production of exopolysaccharides, inducing the resistant genes against stress, enhancing the water circulation and the formation of biofilms, particularly under drought. *Rhizobia* can also generate different osmoprotectants in the rhizosphere during abiotic stresses like drought stress. PGPR enhance plant growth by minimizing disease attack originated from pathogens like nematodes, fungi, viruses, and other types of bacteria (Grover et al. 2011). Literature established that *Bradyrhizobium* makes an association with cereals like wheat, rice, sorghum, barley, and the maize and promote growth through different mechanisms. In the phosphorus-deficient soils, the inoculation of *Rhizobium leguminosarum* makes it available from organic and inorganic compounds by producing an acid and phosphatase enzyme. *Bradyrhizobium* also increases phosphorus availability via the production of an enzyme named phosphatase (Abd-Alla 1994). Different species of the *Rhizobium* boost up the nutrient availability in the rice rhizosphere and improve the plant growth and productivity. Co-inoculation of the *Rhizobia* with other PGPR such as *Bacillus* also enhances the growth of the cereals like wheat by the making of phytohormones and the antioxidants under different abiotic stresses (Perveen et al. 2002).

Sinorhizobium meliloti is known to produce a variety of polysaccharides, for example, cyclic-glucans (unfettered through NdyB plus NdyA) that play an important role in the development of plant during the interaction of microbe and with the plant host. These PGPR are also known to sequester antibiotics and eliminate toxic rudiments in the rhizosphere (Brencic and Winans 2005). Matiru and Dakora (2004) affirmed that rhizobacteria possess the potential to generate vitamins, cytokinins, lumichrome, auxins, abscisic acid, riboflavin, and lipo-cheto-oligosaccharides under water-deficit conditions that increase the plant intensification, enlargement, and the grain output of cereals like wheat, maize, sorghum, and rice. Also, lipo-cheto-oligosaccharides help during germination of seeds, though lumichrome sustains the plant development, including characteristics, which also help in the uptake of nutrients under abiotic stress. Moreover, the nodule formation in the Parasponia by *Bradyrhizobium* and strains of *Rhizobium* are proof that *Rhizobium* could be a source for nodulation and infection in the cereals just like maize and wheat. The majority of PGPR associated with non-leguminous crop plants manufacture indole-3-acetic acid (IAA) that plays a vital role during root development under abiotic stress such as drought (Hayat et al. 2010). Hayat et al. (2010) revealed that *Rhizobia* can produce siderophore under abiotic stress conditions like pH stress, salinity stress, drought condition, and heavy metals. The siderophores produced confiscate the iron in addition to making Fe accessible for the plant uptake. Blend or consortium of *Rhizobia* with PGPR is also known to enhance plant resistance against drought stress. *Phaseolus vulgaris* L. inoculation with two strains of Paeni bacillus and the *Rhizobium tropici* CIAT 899 reduced the deteriorating impact of drought stress via improving nitrogen level via improved nodulation and growth and productivity in comparison to the un-inoculated control (Marcia et al. 2008).

Rhizobial adaptation toward abiotic stresses is multifaceted with rigid mechanisms because of the contribution of dissimilar genes, involving diverse mechanisms to stand against various stresses such as drought and salinity within the soil (rhizosphere). Bacteria bear the impacts of stress via manufacturing osmoprotectants like glycine, proline, trehalose, as well as the glutamate. Manufacturing these types of compounds provides a shield against stressful conditions (Tobor-Kapłon et al. 2008). Some *Rhizobial* isolates possessing saprophytic and competitive capability are competent to perform and survive well under abiotic stresses in the rhizosphere (Yap and Lim 1983). *Rhizobial* inoculation amplified the stress water resistance of the plant because of the manufacturing of exopolysaccharide (EPS). These EPS guard *Rhizobia* against drought, eventually increasing the tolerance of plants (Sandhya et al. 2009). Water-use efficiency was improved in cereals because of the increase in root length due to the inoculation of PGPR having the ability to produce ACC-deaminase (Zahir et al. 2008).

Development speed and wheat root colonization were enhanced when inoculated with the NAS206 *Rhizobial* strains, proficient in manufacturing exopolysaccharide. Those biopolymer compounds take part in biofilm formation, attachment of bacteria, and supply of nutrients under stress situations. Biofilms also assist *Rhizobial* colonization and perform like a channel for the water supply among colonies of microbes, genetic material, and transportation of nutrients (Amellal et al. 1998). Schembri et al. (2004) affirmed that beneath deficiency tension, *Rhizobia* make the polysaccharides smoothen the progress of their ordinary working, and therefore increase the development of cereal crops and growth such as wheat via alleviating the critical impact on wheat. Among the *Rhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Allorhizobium*, *Bradyrhizobium*, and *Mesorhizobium*, *Rhizobium* has been commonly used to enhance the growth and development of sunflower, wheat, maize, sorghum, and barley together beneath ordinary plus the stressed circumstances such as drought and salinity. In the same way, soil physical properties and wheat growth could be made better by the inoculation of exopolysaccharide producing PGPR under drought stress (Kaci et al. 2005). Alami et al. (2000) applied the strains of *Rhizobium* YAS34 possessing exopolysaccharide generating the capability in the rhizosphere of sunflower under drought stress. The results revealed increases in root dry biomass up to 70%, while the seeds of sunflower by 100% increase (soil adhering to the root) and enhanced exopolysaccharide manufacturing to increase the bacterial numbers in the rhizosphere. Grover et al. (2011) elaborated that *Rhizobium* sp. within the wheat enhanced nutrient uptake via the production of exopolysaccharide as soil formation is enhanced because of the creation of macro-aggregates in the dearth stresses and limit the uptake of sodium beneath the stress of salinity and, therefore, minimize the harmful effects of abiotic stresses. Plant development was enhanced via the chaperones in maize under water stress conditions as well as the harsh impact of stresses in maize was mitigated by the inoculation of bacteria, that is, *B. subtilis* due to the production of a protein known as CspB (Castiglioni et al. 2008).

PGPR have ACC-deaminase that decrease the intensity of ethylene generated under abiotic stress conditions (Mayak et al. 2004). Kang et al. (2010) found enzyme released from *Rhizobia* under stress and termed it 1-aminocyclopropane-1-carboxylate (ACC) deaminase that probably causes degradation of the ACC into ammonia and the α-ketobutarate, and so lowers the level of ethylene and ultimately reduces the impact of abiotic stress going on the crop plants. Phosphorus is an essential part of phosphor-lipids and phosphoproteins; its availability to the crop plants is enhanced by *Rhizobia*-possessing enzymes called phosphatase (Khan et al. 2012). Nutrient and water utilization for the effectiveness of the pants of sunflower was augmented due to its inoculation with *Rhizobia* YAS34 (Alami et al. 2000). In the sorghum, inoculation of *Rhizobia* amplified phosphorus uptake and growth of plants under variable environmental conditions. It was recommended that an appropriate mixture of cereals with *Rhizobium* would be able to improve the fodder production and grains under field conditions (Matiru and Dakora 2004). Similarly, Hafeez et al. (2004) observed a positive impact on the yield and growth of cotton when inoculated with *Rhizobium leguminosarum* under controlled conditions. The PGPR inoculation also amplified the uptake of nitrogen and biomass of the cotton. Naveed et al. (2014) found that strains of *Burkholderia phytofirmans* PsJN as well as *Enterobacter* sp. FD17 competently lessened the destructive effects of abiotic stress and enhanced photosynthesis, root biomass, shoot biomass, and the leaf area.

Ansary et al. (2012) affirmed that *Pseudomonas fluorescens* improved the prospective of maize against drought stress because of the joint relation among the rhizobacteria and the maize. For this reason, the yield of maize found under drought was increased. It was found that *R. leguminosarum* also augmented the rice biomass at the stage of vegetation under field conditions (Kennedy et al. 2004). Rashad et al. (2001) inoculated *Bradyrhizobium japonicum* and *Rhizobium leguminosarum* and estimated their perspectives for *Sorghum bicolor* L. under stress conditions. Outcome discovered that appreciably increased production of GA_3 (Gibberellin) and IAA (Indole acetic acid) in shoot and root with co-inoculation as compared to the treatment of control at field capacity level of 100% and 80%. Besides this, sugar contents in leaves, production of siderophore, and solubilization of phosphorus were also increased. Mia and Shamsuddin (2010) established that a few species of *Rhizobium* such as *Azorhizobium caulinodans* can enter the roots of cereals just as wheat, barley, maize, and rice. Their entry into the cortical cells enhances the development and growth of plants directly via hormonal production, that is, abscisic acid, cytokinins, gibberellins, and auxins in the dissimilar situation of surroundings. Abscisic acid plays an important role in the mitigation of various abiotic stresses, for example, temperature, drought, and salinity (Zhang et al. 2006). Also, Aziz et al. (1997) have declared that the plants which are water-stressed manufacture extra molecules like cadaverine that enhance the effectiveness of ABA to alleviate the impacts of drought on the cereal like sorghum, barley, and maize. Bacteria also produce cytokinins that alleviate the effect of dearth by the adjustment of osmotic on the plant.

Rhizobial inoculation proves advantageous for the development and growth of plants while the application of a mixture of dissimilar strains of *Rhizobia* and *Pseudomonas*, *Azospirillum,* and *Bacillus* further enhances this effect. The effectiveness of three strains of rhizobacteria (*Bacillus subtilis* SM21, *Serratia* sp. XY21, and *Bacillus cereus* AR156) inoculated in cucumber was observed under drought stress. The outcome revealed that inoculated plants had more chlorophyll contents and dark leaves than that of control or un-inoculated plants (Wang et al. 2012).

Likewise, an increased level of proline contents in the roots, superoxide dismutase, and enhanced photosynthesis was observed with the inoculation of PGPR (Wang et al. 2012). Akhtar et al. (2013) conducted a field experiment to evaluate the performance of *Rhizobium* and *Bacillus* sp. solely as well as in the combination of growth and yield of wheat crops. Results revealed that the co-inoculation of *Bacillus* sp. and *Rhizobium* appreciably improved grain yield by 17.5% extra compared to the un-inoculated control. Under separate inoculation, *Bacillus* showed the most efficient results as compared to *Rhizobium*. Also, grain proteins, grain numbers, number of tillers, and the biomass were found to be most within co-inoculation. In soil samples after harvesting, the available phosphorus was improved appreciably with the co-inoculation of both PGPR. Ilyas et al. (2012) took dissimilar type strain, that is, *Azospirillum* from the rhizosphere of maize roots and experimented on maize and wheat under normal and water stress conditions. Results showed that eight *Azospirillum* strains increased the level of zeatin, gibberellins, and auxin more under a well-watered situation compared to the water-stressed one.

In an experiment, strains of *Rhizobia* i.e. *Rhizobium phaseoli* MR-2, *Mesorhizobium ciceri* and *Rhizobium leguminosarum* (LR-30) were isolated from the rhizosphere of *Vigna radiata* L., *Lens culinaris* L. and *Cicer arietinum* L., grown in semiarid and arid regions of Pakistan and their potential to mitigate drought stress in wheat was tested. As a result, colonization of root by these strains, the water-holding capacity, and the nutrient-holding capacity were enhanced beneath the conditions of stress. Also, root length was enhanced because of the manufacturing of auxin via *Rhizobia* under the drought stress (imposed by PEG-6000). These also proved competent to produce plant hormones, and exopolysaccharides and catalase can prove helpful against drought stress in other cereals (Hussain et al. 2014). Colonization and growth promotion of roots of non-legume plants were observed many times via the inoculation of *Rhizobium leguminosarum*. The competent strains of *Rhizobia* should be screened for possible production of auxin as well as the seed of maize be drenched within separate or with the interaction of three *Rhizobia* isolate with L tryptophan. Results showed the inoculation increased the chlorophyll contents, photosynthesis, and transpiration rate greater than un-inoculated control. Also, L tryptophan adding up increased the fresh fodder of maize and dry matter (Qureshi et al. 2013).

A jar experiment was conducted under the axenic environment to find out the potential of chosen strains of *Rhizobia* on yield and growth parameters of the wheat. Results revealed that every strain of *Rhizobia* affected the growth of wheat positively and those strains of *Rhizobia* improved the length of the root by 51.72%, yield of straw by 35.14%, per-plant tiller numbers by 68.76%, the yield of grains by 30.29%, the height of the plant by 28.66%, yield of straw by 35.14%, the weight of the 1000 grains up to 28.40%, percentage of phosphorus within grain and straw up to 66.66% and 23.39, percentage of nitrogen within grain and straw up to 15.07% and 33.16, and potassium within grains and straw up to 51.72% and 21. In conclusion, it was suggested that *Rhizobia* isolated within wheat beneath conditions of axenic can prove effective as well as a useful strategy to improve the growth of wheat and the yield under field conditions both under normal and abiotic stress conditions like drought, salinity, and heavy metal (Mehboob et al. 2011).

A field experiment was performed to elucidate the endurance of *Pseudomonas fluorescens* PsIA12 and *Rhizobium trifolii* R39 within the cereal's rhizosphere (wheat, rape, maize) and the leguminous crop (pea and white lupins) on sandy soil which is loamy. Results confirmed undoubtedly that both of the strains colonize all crops' rhizospheres (non-legumes and legumes). The population of *Pseudomonas* declined with flowering as well as the maturity of the plant, but enlarged legumes during vegetative stages. Both of the strains were also able to survive within the weeds rhizosphere (log 3 CFU. g^{-1} root) as well as a non-inoculated crop (log

4.8 CFU/g root). Moreover, the space between non-inoculated and inoculated plants was about 0.6 m. Reason for that research was to approach continued existence of two bacteria under the moderate type of weather though taking into consideration the colonization of roots via both strains, their rearrangement from inoculated to non-inoculated plants, competency for inhabiting plants with the outcome of the bacterial survival and moisture on the plants (Wiehe and Hoflich 1995).

Weavert and Baldani (1992) revealed that the *Rhizobia* acquire cure derivatives to tolerate drought and heat stresses in an improved way than that of parent derivatives. Furthermore, the *Rhizobia* contain precise plasmid, which allows them to stay alive under high temperature as well as under the shortage of moisture content. Plasmid plays a crucial function via different protein syntheses that make *Rhizobia* physically powerful like manufacturing of succinate, catechol, the bacteriocin, lipopolysaccharides, thiamine, lactose, calystegine, melanin, and the succinate along with metabolism of transport of dicarboxylate in the cell of *Rhizobia* under moisture and heat stresses.

6 Multistrain Inoculation

Commercial inoculants of single strain are less effective as compared to multistrain/consortium inoculation. Plant growth with single strain inoculation becomes contradictory due to smaller amount of colonization and inability to bear attacks of pathogens on host plant besides different and variable conditions of environment and soil. Since it has been reported by Klopper and Raupach (1998), the performance of single PGPR strain might stay nonreliable continually under changing environmental conditions. In contrast, inoculation with a combination of PGPR could exert good results under different types of circumstances, as those require temperature settings, moisture, and diverse pH. Inoculants that are multistrain adjust best under changing environmental conditions existing all through the entire mounting season. Consistent colonization of root, defense against pathogens and the use of a wide range of plant growth enhancing mechanisms are a few prominent features of multistrain inoculants. Co-inoculation of *Bradyrhizobium* and *Rhizobia* operates like partners and has a symbiotic relationship with plants through the fixation of nitrogen within the nodule of the leguminous crop. These plant promoting rhizobacteria also work for non-legumes like sunflower, radish, barley, and wheat, through secretion of plant growth regulators, siderophores, biofilm formation, exopolysaccharides, as well as killing pathogens especially under drought stress. An experiment was conducted for checking the probability of two *Rhizobia* in the improvement of the yield of radish and growth. So, because of this, 266 strains were tested for their auxin potential, solubilization of phosphorus, siderophores, cyanide, and production of siderophores. Result revealed that all strains (83%) were competent to produce siderophores, and only 3% were able to produce cyanide, phosphorus solubilizing strains were 58%, and strains that were capable of producing auxin were 54%. The most distinct outcome found in the case of *Bradyrhizobium* *japonicum* strain Soy 213 inoculation was to improve dry biomass of radish by 60%, whereas radish was negatively affected by N44 strain arctic and also it decreased radish dry portion up to 44%. In the next experiment (growth cabinets), *B. japonicum* strain Tal 629 increased the dry stuff of plant by 15%. In the final experimentation, the researchers concluded that a precise *Bradyrhizobium* relation among cereals (maize, sorghum, sunflower, and wheat) has a prospect of improving yield and growth limitation of the plants (Antoun et al. 1998).

Microbes that possess a variety of metabolic activities like P-solubilization, N_2-fixation, antibiotic production, and phytohormone production could replace single-strain inoculation and it would lead to multistrain inoculation. In recent times, Adesemoye et al. (2008) reported that multistrain inoculation could increase the productivity and growth of plants wherever the inoculation of a single strain would be ineffective. Therefore, as compared to single-strain inoculation, plants get great benefits from mixed inoculation (Germida and Xavier 2002). Inoculation of the PGPR agents of multistrain contributes most toward the healthy growth and the high yield because of the wide variety spectrum of their actions, combination of dissimilar quality without linking greater reliability, and genetic engineering (Janisiewicz 1996). Despite ability in the development of multistrain inoculants, the compatibility of microbes is essential, as the microorganisms can have inhibitory effects for one another and can be potential antagonists to each other.

Rhizobial impending to get better non-legume crop growth could perk up by the multistrain inoculation. Berg (2009) has reported that use of inoculation mixture of *Rhizobia* is a hopeful approach. Also, Gunasekaran et al. (2004) confirmed that uptake of plant nutrient was enhanced under nutrient degrading and limiting soil environment through a *Rhizobia*-compatible inoculation in combination with arbuscular mycorrhizal (AM) fungi over inoculation of single microbe. Likewise, enhanced phosphorus uptake, spike length, plant biomass, height of the plant, the yield of grain, leaf sugar and the leaf protein was noted via mixed inoculation of *Rhizobia* (Afzal and Bano 2008). In the same way, Sahin et al. (2004) reported substantial increases within the sugar content plants by the co-inoculation for fixing of N2 or the P-solubilizing bacteria. In the same way, Sheikh et al. (2006) also confirmed that the seed dressing of *Bacillus thuringiensis* (Bt-10), *Rhizobium meliloti* (R5), and drenching of soil were found to increase the seed germination, height of the plant, plant biomass in okra and length of the root. Furthermore, the health of the plant was found to be enhanced because of the protection which is provided against fungi infections, that is, bioprotection. In addition, beneath the stress of salinity, performance of lettuce was found to be relatively inspiring because its dry and fresh biomass increased by 7.86% and 12.87%, respectively, via joint inoculation of the strain of PGPR of *Serratia* sp. and *Rhizobium* (Han and Lee 2005). Despite the single-strain inoculation of the PGPR, its mixture by the *Rhizobium* and mycorrhizal fungus creates lenience within the plants with limited water conditions (Wang et al. 2012). Besides this, co-inoculation of wheat with *Azotobacter chrocoocum* and *Pseudomonas* sp. (E2) releived water stress by altering the anatomy of plants i.e. by increasing phloem and epidermis thickness, diameter of xylem vessel and root system dimensions under different levels of field capacity (50, 75 and 25% FC) (El-Afry et al. 2012).

Microbial consortium usage was found to be a proficient plan to improve the wheat crop dearth stresses (Asghar et al. 2015). By the consortium of PGPR, rice growth improved under water stress due to enhanced production of proline contents which lessened oxidative injury (Gusain et al. 2015). Inoculation of the microbial consortium of *P. aeruginosa* (Pa2) and *P. penneri* (Ppl) with EPS production had superior perspectives to enhance tolerance among crop plants under drought stress as compared to the sole strain inoculation of PGPR within the maize (Naseem and Bano 2014).

On the joint beneficial interaction of *Rhizobia*, a few studies have reported the improvement in non-leguminous plants under abiotic stresses. That is why there is a dire need to investigate the prospects of the poly-*Rhizobial* inoculants for improving the productivity and growth of non-leguminous plants under water shortage stress. Various mechanisms of the plant microorganism connections in the rhizosphere are necessary to be elucidated. Complexity pertains to numerous range of processes that are associated with different communities of microbes. Mitigation of stress in crop plants by means of knowing the crosstalk of microorganism's microbes could be optimized and under stress conditions, their capability to stay alive could be enhanced. An abundance of the techniques which are molecular needs to be accessible and will be applied to describe the interaction of the plant microorganisms (Barea 2015).

7 Conclusions

Drought stress has been the foremost threat to food security and sustainable agriculture. Approximately, 38% of agricultural land is currently at the risk of drought stress, and this proportion is being increased because of climate change. Drought stress imposes oxidative stress on the plants by producing the ROS in high amounts that ultimately upset the photosynthetic process of the flora. Conventional methods to develop the drought-tolerant crops are very time consuming, while on other side, total implementation with the latest biotechnology for the product improvement is at a standstill considered by caution. Future climate situation predicts that increased inconsistency in the rainfalls is heading toward more extreme drought actions that would extend faster with the severe intensity. Restricted water accessibility hinders plant growth, resulting in considerable losses in agricultural productivity. Plant growth-promoting rhizobacteria (PGPR) might be used as an economical and environmentally friendly technique to improve crop growth under abiotic stress. PGPR play a significant role in generating rigidity and adjustment in plants toward water-deficit condition and has the capacity to solve the future food security problem. There should be the usage of wide range of methods for leguminous as well as non-leguminous crops growth improvement. For example, PGPR by the production of 1-aminocyclopropane–1-carboxylate (ACC) deaminase amplify the nutrient uptake of plants by breaking the ACC, thereby stopping ethylene accumulation, and by the production of lumichrome, and riboflavin as indirect mechanisms for non-legumes to tolerate drought stress. Exopolysaccharides formed are another strategy adopted by bacteria that perk up the capacity of soil to retain water. Interaction among the plants and PGPR in drought circumstances influences not only the plants but at the same time also changes the characteristics of the soil. The valuable PGPR improve the construction of the defense system of antioxidant and the osmolytes that lessen the unfavorable ROS impact on the crops. Multistrains inoculation of PGPR is thus important for the improved yield as well as for food security, chiefly in an unfriendly ecological situation. PGPR augment the osmolytes manufacturing that is supportive in reducing the harmful effects of ROS. Multistrain PGPR are potentially competent contenders to reduce the negative impact of the drought on crops, especially in the arid regions. Utilization of plant growth-promoting rhizobacteria as bio-inoculants to maintain vigorous growth of plants is essential in supporting food security, especially in hostile ecological circumstances. The above-highlighted studies provide us better understanding of the relationships among the plants plus useful soil microorganisms that symbolize the forward step to take best out of these dealings. However, the existing information is at the evolution process and for that reason, there is a dire necessity for further research paying attention to plant–microbe interactions at the molecular level to have a mechanism for pathways exploited by microorganisms living in the rhizosphere for the plant development and for the infection inhibition to sustain agricultural productivity. Knowing all that PGPR manufacture the osmolytes such as proline, and glycine-betaine that decrease ROS negative impacts on the plants under drought stress but overexpression of genes responsible for the production of these osmolytes can improve the resistance capability in bacteria and ultimately would enhance stress tolerance capacity of plants. Despite this, the useful activities of the PGPR can be frequently affected by abiotic stresses. The effectiveness of multiple strains can be improved for the better performance by the use of *Rhizobia* as bioinoculants under field conditions employing new tools like nanoencapsulation that advances the colonization to the root hairs by favorable bacterial strains. Even after that, the genes responsible for drought tolerance are multifarious in the plants and require further elucidation through better understanding of their genomics, proteomics, metabolomics, and transcript-omics. Hence, the present studied research can take to an advanced notion to use above-mentioned prospects by using genetic, molecular level strategies, using multistrain PGPR to develop ecologically acceptable biofertilizers to enhance the development and the quality of the harvest grown under drought stress.

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Chapter 17
Trends in Biosensors and Current Detection Methods for Stress Monitoring of Plants Growing in Adverse Environmental Conditions

Vasileios Tsekouras, Sofia Mavrikou, and Spyridon Kintzios

Contents

Abbreviation

2D-DIGE	two-dimensional differential gel electrophoresis
2-DE	two-dimensional gel electrophoresis
BAW	bulk acoustic wave
CP	conducting polymers

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ELISA	enzyme-linked immunosorbent assay
LOD	limit of detection
MOS	metal oxide semiconductors
NMR	nuclear magnetic resonance
NPs	nanoparticles
QCM	quartz crystal microbalance
SPCE	screen printed carbon electrode
VOCs	volatile organic compounds

1 Introduction

Climate change is defined as the modification of climate patterns caused by anthropogenic activities. During the last years, significant changes in climate indicators are observed due to gas emissions, mainly recorded as fluctuations in temperature, annual and seasonal precipitation, seasonal patterns, and the emerging of extreme weather conditions (Fawzy et al. 2020).

These phenomena have been related with fundamental alterations on ecosystem functions and services. Biophysical environment shapes species distribution, phenology, and community composition, therefore shifts in key bioclimate variables and extreme climatic events are linked with modifications in ecosystem functioning and dynamics (Brown 2018). Against this background individual species, communities and ecosystems are able to cope with abiotic stress factors. Ecological community capacity to respond and adapt to natural disturbances is attributed to resistance and resilience, fundamental components of ecosystems stability tendency to preserve structure and functions (López et al. 2013; Sánchez-Pinillos et al. 2019). Resistance is considered as the ability of an ecosystem, community, or species to remain at a stable condition despite disturbance, while resilience is accredited as post-disturbance responses of a particular ecosystem, community, or species to recover and maintain a reference condition (Falk et al. 2019).

Plant morphology and physiology are influenced by abiotic stresses to a great extent. Large-scale shifts in weather pattern and the increase frequency of extreme climate events may cause physiological stress affecting plant growth, development, and yield. Nevertheless, plants have evolved tactics to avoid or tolerate these environmental challenges so as to survive and reproduce. In accordance, a number of defense mechanisms have been developed at cellular, physiological, and morphological levels to surpass hostile environment and facilitate species conservation (He et al. 2018; Pareek et al. 2020). The estimation of stress levels is critical, and to date, a number of morphological, physiological, biochemical, and molecular traits are employed to outline plants ability to adapt under harsh conditions. This highlights the necessity for conducting a vast number of phenotypic and intracellular component measurements, often for long time periods and on a large number of individual plants. The fabrication of low-cost and quick detection methods for the assessment of abiotic stress responses are key factors for species preservation and the reduction of losses in crop yield. Standard analytical methods of detection such as gas chromatography–mass spectrometry (GC/MS), the polymerase chain reaction (PCR), and enzyme-linked immunosorbent assays (ELISA) are invasive, expensive, time-consuming, labor-intensive, and require detailed data sampling and processing time (Kumar and Arora 2020; Piasecka et al. 2019; Waliullah et al. 2019). Image analysis techniques present advantages since represent rapid and nondestructive approaches but numerous variables influence spectral records downregulating methods accuracy, while statistical estimation models are needed for data processing (Li et al. 2014). Novel monitoring techniques involve biosensors, portable devices presenting significant advantages such as ease of use, high sensitivity, real-time detection, and low cost. A biosensor is considered as an analytical device that contains a biologically active material and a transducer in order to produce qualitative and/or quantitative sensing of chemical or biochemical phenomena taking place at sensor's surrounding environment (Fang and Ramasamy 2015; Kumar and Arora 2020). This chapter focuses on the monitoring techniques applied for the identification of traits indicating resilience, emphasizing on bio-recognition technologies.

2 Monitoring of Plant Species Physiological and Morphological Traits to Identify Resilience

Nowadays, climate changes force plant species to grow and develop under adverse environmental conditions. Abiotic stress occurrence triggers intrinsic regulatory mechanisms that initiate morphological, physiological, and biochemical responses altering species phenotype and physiological processes. The identification and estimation of the interactions between climate conditions and physiological stage are essential for the evaluation of resilience across species and the management of vulnerable populations (Gray and Brady 2016). In this context, a number of invasive and noninvasive methods have been applied in order to assess species ecophysiology performance and adaptation to novel environmental conditions.

2.1 Assessment of Plant Traits for Resilience Evaluation

Physiological and morphological traits have been thoroughly used to evaluate species resilience at novel environmental conditions. Therefore, the recording and analysis of quantitative and qualitative data from different developmental stages is a necessity for portraying climate change correspondence to plants resilience (de la Riva et al. 2017; Kohler et al. 2017). Raw measurements of phenotypic traits are the most profound processes to evaluate the potentiality of plant species to adjust and recover from disturbances and abiotic stresses (Baath et al. 2020; Tzuk et al. 2020; Wang et al. 2017). Above ground biomass characteristics such as plant height, leaf area, and stem dry mass are highly linked to important physiological functions indicating growth rate, light capture ability, physical resistance to natural hazards, stress tolerance, and species competition. Respectively, the knowledge of plants below ground morphology is a prerequisite to identify species adaptation in adverse conditions. Records regarding root architect and dry mass are valuable for the estimation of plants' ability to uptake minerals and water from the rhizosphere, as well as to evaluate mechanical resistance to natural hazards (de la Riva et al. 2016).

Novel imaging technologies provide high-level visualization and resolution abilities. Consequently, these techniques are widely applied for the quantitative estimation of complex and multidimensional traits regarding growth dynamics and plant morphology (Li et al. 2014). Plant height, fresh and dry matter yield have been estimated to evaluate cocksfoot (*Dactylis glomerata L.*) population productivity and behavior under intense drought (Zhouri et al. 2019). In another study, image analysis systems have been applied for the evaluation of Black spruce (*Picea mariana*) above ground and root biomass as both measurements are indicators of species adaptation to extreme climatic conditions (Sniderhan et al. 2018). In accordance, plant resilience have been estimated by calculating total leaf area and the number of leaves with scanning techniques and remote sensing data obtained from satellite (Gebauer et al. 2020; Wu and Liang 2020). Optical tools are also applicable for monitoring species developmental stage. Several qualitative data regarding species dormancy break (Footitt et al. 2018; Tixier et al. 2020), senescence (Berger et al. 2010), flowering and fruit bearing (Tchokponhoué et al. 2019), and seed germination (Yi et al. 2019) are valuable for understanding modifications in plants' life cycle.

Environmental disturbances are linked with alterations in cellular processes and regulation. Abiotic stress occurrence reflects on intrinsic regulatory networks and adjusts metabolic functions such as carbon storage, nutritional status, biochemical profile, redox status, and reactive oxygen species (ROS) signaling (Dusenge et al. 2019; Raza et al. 2019). The identification and quantification of intracellular alterations is essential for understanding abiotic stress perception and recovery mechanisms (Lamers et al. 2020). Plants' physiological operations depend on nutrient availability to a great extent, since vital metabolic processes require sufficient quantities of inorganic components in order to be performed. Consequently, the monitoring of essential elements uptake is very important to understand species growth and development, distribution, community structure, and biomass production (Guignard et al. 2017; Mueller and Vyn 2016). Nutrient analysis have been performed by both analytical methods (i.e., Kjeldahl method, elemental analyzers) and noninvasing imaging technologies that estimate chemical components concentrations throughout the assessment of phenotypical traits (Bartholomew et al. 2020; Dahl et al. 2020; Li et al. 2020; Read et al. 2017). In addition, chromatography-based analytical methods have been utilized to identify potential stress indicators operating in signal regulation and metabolic pathways such as heat shock proteins (Xu et al. 2011), proline (Abrahám et al. 2010), soluble sugars (Rosa et al. 2009), abscisic acid (Kempa et al. 2008), and phytohormones (Kasote et al. 2016).

Photosynthesis is the most important physiological activity controlling energy use, growth, and metabolite synthesis. Temperature, gas emissions, and water availability regulate photosynthetic performance and species have developed photoprotective and antioxidative mechanisms to moderate photosynthetic fluctuations (Kirschbaum 2004; Manabe 2019). These physiological responses are associated with stomatal closure, adjusting transpiration rate in order to facilitate the reduction of water loss and intracellular CO_2 levels, as well as biochemical alterations reflecting in chlorophyll concentration, pigment synthesis, and the activity RuBisCO and other key enzymes (Chaves and Oliveira 2004; Martin-StPaul et al. 2017). Ecophysiological studies focus on chlorophyll and photosynthetic pigment levels estimation (Begam et al. 2020; Melo et al. 2017; Sánchez-Reinoso et al. 2019), particularly in real time determination of photosynthetic rates incorporating sophisticated portable devices (Santos et al. 2018; Tombesi et al. 2015; Wang et al. 2018). Cellular levels of specific proteins, metabolites and enzymes are associated with photoprotective mechanisms and several assays involve analytical techniques in order to identify and estimate them (Dubberstein et al. 2020; Zhu et al. 2009).

Adverse conditions challenge gene function and regulation, shaping the reconstruction of genetic or biochemical pathways (Garg et al. 2014). Recent advances investigate genome structure, as well as transcriptional, translational, and posttranslational modifications of defense-related genes to elucidate molecular mechanisms indicating resilience (Jiang et al. 2020; Mostert-O'Neill et al. 2020; Nagaraju et al. 2020). High-throughput DNA and RNA sequence, microarray-based gene expression analysis, and bioinformatic tools enabled the acquisition of large-scale genomics data to a more comprehensive understanding of diversity and resilience (Janni et al. 2020; Scheben et al. 2016). Genome sequencing of wheat identifies heat shock factors and elucidates their functions and signal transduction pathways (Duan et al. 2019), while in the case of *Themeda triandra*, a widespread grassland species of Australia, genomic variation indicates species adaptation to hotter and drier climates (Ahrens et al. 2020). RNA transcripts can unveil the expression of the genome under abiotic stresses, which can be a valuable tool to assess transcriptional and translational regulations modulating stress implications (Wang et al. 2020). Transcription factors detection are associated with *Arabidopsis thaliana* stress responses (Ng et al. 2018), and thus they can be a valuable tool for genetic engineering and marker-assisted selection of cultivating plants (Zaikina et al. 2019).

2.2 Noninvasive Methods to Monitor Plants Traits Indicating Resilience

Several optical tools and sensors have been developed during the last decades to observe and quantify plant traits in a reliable and accurate manner. There are clear advantages of nondestructive detection methods, as plants can be subjected to several measurements delivering multiple data of various traits simultaneously. In addition, nondestructive methods allow the monitoring of plants' life cycle enabling the monitoring of temporal variations in vegetation dynamics (Tardieu et al. 2017).

These techniques can be classified in two major categories, high-throughput phenotyping and volatile organic compound monitoring.

2.2.1 High-Throughput Phenotyping with Imaging Techniques

High-throughput phenotyping is plant's trait data acquisition in a noninvasive manner with high-throughput approaches using remote sensing and data analysis. These technologies rely on diverse imaging techniques and deliver morphological and physiological information by high spatial and temporal resolution (Yang et al. 2020). Digital red, green, and blue (RGB) imaging is the most common image processing technique, applied for studying plant characteristics. In RGB imaging, every pixel is the combination of images taken through red (600 nm), green (550 nm), and blue (450 nm) spectral bands of visible light (Li et al. 2014). These image-derived data are particularly advantageous for performing morphological analysis of various plant features such as biomass, height, color, chlorophyll content, number of leaves, and roots in order to estimate physiological parameters like plant growth rate, drought stress, and early vigor (Chen et al. 2014; Hu et al. 2013; Kim et al. 2020; Kipp et al. 2014). Spectroscopic imaging is another technique applied for the assessment of vegetative functions. This method yields spectra derived by applying numerous, narrow, and increasing wavelengths to an image point and gathering all the reflectance values. The radiation emitted vary from visible spectrum (400–700 nm) up to 2500 nm and the quantification of the reflectance pattern enables the measurement of morphological characteristics and metabolite concentrations in plant tissues (Li et al. 2014; Raychaudhuri 2016; Skoch et al. 2008). Several spectral reflectance indices have been used for fast, nondestructive measurements of morphological traits and biochemical traits such as leaf morphology, water, nutrient (Ge et al. 2019) carbon and fiber content (Serbin et al. 2014), and pigment analysis (Matsuda et al. 2012).

Fluorescence imaging delivers in vivo measurements of plant-specific fluorescence signals with high precision and sensitivity. The method relies on the detection and visualization of fluorescence, emitted by organic molecules when exposed on UV or visible light in appropriate wavelength (Chaerle and Van Der Straeten 2001). Plant illumination with UV waves generates fluorescence signals permitting the capture of four spectral bands at blue (440 nm), green (520 nm), red (690 nm), and far-red (740 nm) wavelength. Chlorophyll complex is the main fluorescing component of the plants accompanied by secondary metabolites such as ferulic acid, flavonoids, and cinnamic acids (Buschmann and Lichtenthaler 1998). Fluorescence emissions have been used to calculate the direct responses of harsh environmental conditions on photosynthetic performance, and the consequent indirect effects on physiological processes (Kalaji et al. 2018b). A number of assays have been conducted to assess the effect of abiotic stress factors such as heat (Willits and Peet 2001), low temperatures (Ehlert and Hincha 2008), and drought (Yao et al. 2018) against plant species by using chlorophyll measurements as diagnostic tool (Pérez-Bueno et al. 2019).

Thermal imaging has been successfully applied for monitoring temperature distribution on plant level. The technique relies on scanning systems imaging thermal radiation emitted by plants representing spatial distribution of temperature differences (Costa et al. 2013). Leaf temperature can be an indicator of water content, stomata conductance, and transpiration rate (Still et al. 2019). As a result, thermography can be applied for monitoring the physiological activity of vegetation (Jones and Schofield 2008; Still et al. 2019), plant–environment interactions regarding water availability and evapotranspiration (Brenner et al. 2018; Gutiérrez et al. 2018), genotypic variation (Prashar et al. 2013; Wang et al. 2004) and analyzing circadian rhythms in plants (Dakhiya and Green 2019).

Plant growth performances are critical for predicting plant adaptation in changeable natural environments. The 3D imaging systems offer robust and reliable spatial vision to analyze and quantify the structure of the plants (Smith et al. 2018). The visualization of the third dimension is necessary to achieve sequential plant growth quantification at high precision and several time-points. Two major groups of methodologies have been applied to determine cues for 3D information recovery, the active approaches using artificial light emissions, and the passive approaches, which are based on naturally depicted information such as color and texture (Bernotas et al. 2019; Li et al. 2017). Active 3D imaging technologies include laser scanning and structured light imaging techniques both relying on triangulations for the 3D reconstruction. The most frequently applied passive 3D imaging techniques are multiview stereo vision, shape from shading, focus or texture, and structure from motion (Li et al. 2017; Yu et al. 2018). Three-dimensional imaging techniques provide valuable information regarding plant growth and functioning (Omasa et al. 2006) such as biomass accumulation, vigor traits (Armoniené et al. 2018), chlorophyll content (Hosoi et al. 2019), root growth (Lockhart 2019), and drought responses (Zhao et al. 2012).

2.2.2 Monitoring of Volatile Organic Compounds

Plants release to the atmosphere a great diversity of secondary metabolites known as biogenic volatile organic compounds (VOCs). Terpenoids, alkanes, alkenes, phenylpropanoids, alcohols, and fatty-acid-derived molecules are the most common volatile compounds released by plant species (Bouwmeester et al. 2019). These compounds are involved in a wide class of ecological functions mediating plant signaling, communication with surrounding organisms, and abiotic stress adaptation (Effah et al. 2019). The chemical synthesis of gas emissions varies among different species, plants, even organs within the same individual entity, and it is highly affected by environmental conditions (Vivaldo et al. 2017).

Traditionally plant volatile compounds research relies on analytical procedures based on gas chromatography and soft chemical ionization mass spectrometry. Prior to chemical analysis, whole plants or tissues are fitted in enclosing chambers to gather gas emissions (Materic et al. 2015; Niederbacher et al. 2015). These methods may allow the identification of plants' volatile signature in vivo under laboratory conditions or small-scale applications but is difficult to apply them for generating data on field. On the contrary, sensor-based techniques are more suitable for open field or large-scale observations regarding volatile emissions. The electronic nose technology is a novel, electronic and nondestructive sensor-based method for testing VOCs. E-nose instruments are capable of detecting changing VOC profiles released by plants with gas-sensor arrays. These devices operate using different sensor types based on different gas-sensing principles including conducting polymer sensors (CP), metal oxide semiconductors (MOS), bulk acoustic wave (BAW), optical fluorescence, quartz crystal microbalance (QCM), and amperometric gas sensors (Saeed et al. 2009; Wilson 2013). The signals from the sensor devices generate a pattern analogous to the volatile content of the sample, illustrating plant VOC profiles in a noninvasive and real-time matter. Electronic nose signals have been used for species identification (Zou et al. 2015), forest structural stability evaluation (Baietto et al. 2010), drought stress assessment (Abbey et al. 2003), physiological phase identification (Hawari et al. 2013), and phytopathological diagnosis (Cellini et al. 2017; Ghaffari et al. 2012).

2.3 Invasive Methods to Monitor Plants Traits Indicating Resilience

Appropriate identification and characterization of molecules involved in plant metabolism is significant for understanding stress-induced responses. A number of invasive techniques have been developed to assess modifications occurred at biochemical and molecular level in a direct and accurate and way (Pérez-Clemente et al. 2013; Sharma et al. 2019). Spectrophotometric analysis and omics technologies have been ubiquitously employed in modern biosciences enabling the analysis and identification of biomolecules in order to investigate the complex interplay between species, abiotic stress, and metabolic functions (Ambrosino et al. 2020; Trumbo et al. 2013).

2.3.1 Spectrophotometric Analysis

Spectrophotometry applications are thoroughly applied for quantitative analysis of various biomolecules in biochemistry. The basic principle of the method is that every chemical compound absorbs or reflects light in a specific way after the interaction with a wavelength of a certain range. Analytical instruments have been fabricated to measure the light spectra transmission, absorption, and reflection by matter, allowing the examination of a substance (Samokhvalov 2020; Trumbo et al. 2013). There are different types of spectrophotometric methods distinguished by the type of light involved in the interaction and the interaction with the material.

The ultraviolet-visible spectroscopy (UV-vis) is an analytical laboratory method, essential for the qualitative and quantitative determination of many organic and inorganic compounds suitable for biochemical and environmental assays (Ojeda and Rojas 2009). The UV-vis spectroscopy use light in the visible, ultraviolet, and near-infrared range (200–750 nm) passing through a medium to measure the absorbance or transmittance as a function of the wavelength (Rocha et al. 2018). Measurements using UV-vis spectroscopy have been applied to determine the biosynthesis of several molecules under stress conditions such as lipid hydroperoxides (Lodeyro et al. 2016), chaperones (Seo et al. 2019), total protein content (Azri et al. 2020), chlorophyll, and pigments (Scheel et al. 2019).

Fluorescence spectroscopy or spectrofluorometry is an investigation method for analyzing fluorescence from a sample. When a molecule absorbs energy, after the explosion in ultraviolet or visible light at a specific wavelength, it undergoes a transition to a high-energy electronic state. Then, within a few seconds, it returns to the initial stable state, liberating energy in the form of light emission. Spectrofluorometry measures the absorbed and emission spectra describing the fluorescence characteristics of specific molecules (Karoui and Blecker 2011), for example, to detect changes in chlorophyll content (Kalaji et al. 2018a), for the assessment of total RNA integrity under drought stress (Liu et al. 2017b) and the quantification of the oxidative stress biomarker malondialdehyde (Hu et al. 2018).

Atomic emission and absorption spectrometry is another type of spectroscopic technique applied for quantitative and qualitative analysis of metal elements in a sample. Metal elements have a specific atomic structure, and their electrons can move between energy levels when they receive appropriate energy. Atoms can absorb energy from light projection, and electrons of the outer shell can be excited in a higher energy state. Atomic emission occurs during the falling of an excited electron in a stable position (Potts 2014). Metal elements play a significant role in plant physiology and atomic spectrometry are accurate, rapid, and reliable tools for plant analysis (Smith and Schrenk 2020). A variation of atomic spectroscopy is flame emission spectroscopy, a method that use flame as a source of energy to achieve atom excitation. It is a rapid method, suitable for the determination of element concentration in plant tissues (Janusa and Beck 2002). These techniques have been used to assess abiotic stress responses in various species such as mineral uptake in sugar cane (Silva et al. 2017), phosphorus, and potassium accumulation patterns in an evergreen Mediterranean forest (Sardans and Penuelas 2007), total phosphorus, aluminum, iron, and manganese content in mixed species plantations (Koutika et al. 2018), as well as the determination of macro and micronutrient status in *Bryonia Alba* (Karpiuk et al. 2016).

2.3.2 Omics Technologies

Omics technologies integrate approaches applied for the better understanding of plants' physiological adaptations on environmental disturbances. Proteomic, genomic, transcriptomic, and metabolomic profiling of plant tissues can be performed to elucidate and monitor valuable biological processes determining species fate (Mehta et al. 2019).

Proteome is a set of expressed proteins within an organism, and protein profiling by proteomic analysis elucidates protein's gene-driven production and function under stress mechanisms. Proteomic approaches assist in the identification of stress-induced protein synthesis, as well as the understanding of their physiological role (Aslam et al. 2017; Priya et al. 2019). Protein purification have been achieved with chromatography-based techniques, especially ion exchange, size exclusion, and affinity chromatography, as well as electrophoretic procedures such as sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE), two-dimensional gel electrophoresis (2-DE), and two-dimensional differential gel electrophoresis (2D-DIGE) to achieve complex mixture separation (Coskun 2016; Magdeldin et al. 2014).

Selective proteins analysis can be achieved by enzyme-linked immunosorbent assay (ELISA) and Western blotting. ELISA is a sensitive immunoassay that utilizes antigen or antibodies absorbed on a solid surface and enzymes conjugated to antibodies. Measurements of enzyme activities correspond to antibody and antigen concentration in the biological sample (Lequin 2005). Western blotting is a widely applied method to detect low abundance proteins by linking them with specific antibodies. Gel electrophoresis for protein mixture separation by size is a prerequisite for this method followed by antibody detection (Mahmood and Yang 2012).

Mass spectrometry (MS)-based methodologies coupled with chromatographic techniques are the most widely used analytical approaches for simultaneous analysis of biomolecules. Nowadays, mass spectrometry approaches have been thoroughly developed to analyze the proteome on a large scale. MS techniques present analytical advantages for distinguishing differences in complex mixtures and provide the ability to generate detailed data for portraying protein expression, modification, and interactions (Han et al. 2008). MS-based proteomics is the output of the amino-acid sequences spectra resulting from protein digestion. The molecules are transformed to gas-phase ions, then separated, and analyzed in an electric or magnetic field according to mass-to-charge ratio. Proteins and their modifications are identified from the peptide spectra using computational methods (Wang and Wilson 2013).

Genomics is the analytic study of the genetic information existing in an organism. The characterization of gene sequences, expression, and regulation is a valuable tool for understanding genetic functions in climate change (Horgan and Kenny 2011; Varshney et al. 2018). Gene transcription is defined as the process where genetic information encoded in DNA are transcribed to RNA molecules. Consequently, transcriptomics are the scientific tools applied for studying RNA transcripts, to record gene expression and posttranslational modulations (Lowe et al. 2017). Different techniques, incorporating hybridization or sequence approaches, have been developed for conducting nucleic acid analyzes to unravel gene expression and understand plant responses to environmental stresses (Moustafa and Cross 2016). The identification of nucleotides order in polynucleotide chains generates fundamental knowledge regarding genome and genetic information, elucidating hereditary and biochemical functions (Heather and Chain 2016).

Polymerase chain reaction (PCR) is a fundamental tool for the detection of targeted DNA sequences, as well as the production of several copies of specific regions. It is a sensitive assay as rare amounts of DNA are needed to be placed in a thermal cylinder within a reaction solution composed by appropriate buffer, template DNA, primers corresponding to the DNA region that undergoes amplification, nucleotides, and the enzyme DNA polymerase. Agarose gel electrophoresis can be performed for partitioning PCR products according to size, prior to visualization (Garibyan and Avashia 2013). Several modifications of the standard PCR technique have emerged such as real-time PCR, a quantitative approach employing complementary DNA (cDNA) molecules derived from RNA sequences (Xu et al. 2020), in situ PCR, which is used for amplifying nucleic acid sequences within plant tissues (Athman et al. 2014), and reverse transcriptase PCR (RT–PCR) for measuring RNA expression levels (Niu et al. 2017). Sanger sequencing is a traditional, well-established PCR-based method, applied for determining DNA nucleotide sequence of genomic regions. Fluorescence-labeled dideoxynucleotides are incorporated as DNA chain terminators, during PCR cycles for chain elongation. The various length fragments of nucleotides produced can be visualized after gel electrophoresis-based separation and UV/VIS spectrophotometry (Heather and Chain 2016; Karger and Guttman 2009). Nowadays, novel, high throughput sequencing tools are available for the simultaneously sequencing of multiple DNA and RNA regions. These next-generation sequencing platforms are based on the incorporation of luminescent signals and sensitive monitoring systems that can detect fluorescent from single nucleotides (Almeida and De Martinis 2019; Qiang-long et al. 2014).

Hybridization of nucleic acid is the matching of complementary nucleotide strands, DNA or RNA, to specific target nucleotide sequences. The nucleic acid hybridization is the starting point of several diagnostic approaches relying on the incorporation of a labeled probe, a fragment of DNA or RNA radioactively or fluorescently labeled (Kolpashchikov 2019). Hybridization of nucleic acids on blots, solid nitrocellulose or nylon membranes, is one of the most important techniques used for DNA and RNA detection. Total DNAs of RNAs are extracted, separated according to size on agarose gels, and then are placed onto blots. Then, hybridization occurs with a complementary to the targeted sequence probe, synthesized of DNA or cDNA when applied for RNA detection. The technique is distinguished as Northern blotting when applied for RNA detection and Southern blotting for DNA sequence analysis (He and Green 2013; Southern 2006). Fluorescence in situ hybridization (FISH) is a recognition technique using fluorescence microscope or imaging systems to visualize the hybridization of DNA fragments incorporated with fluorophore-coupled nucleotides to its complementary sequence (Cui et al. 2016). This detection tool has proven to be very sensitive and precise for the mapping of genes and specific genomic sequences on targeted chromosomes in many plant species, especially through the propagation and application of probes based on synthetic oligonucleotides (Jiang 2019). DNA microarray is a very significant technique that enables the large-scale detection and sequencing of specific DNA sections.

Microarray technology has been broadly used to assess functional analysis ranging from single gene expression to whole genome, in order to elucidate plants' molecular mechanisms (Shiu and Borevitz 2008). The principle of the technique relies on the attachment of different nucleotides on small, solid surfaces, to probe an investigated sequence within a solution of labeled nucleic acids. The specific binding of targets and probes via hybridization can be identified by their fluorescence emission (Bumgarner 2013).

Metabolomics is a branch of omics technologies applied for the identification and characterization of the metabolic profile, the metabolome, within a single cell, tissue, or organism. Therefore, metabolomics can be used to assess the biochemical organization of a biological entity under certain environmental circumstances (Piasecka et al. 2019). Plant metabolite examination is primarily performed by mass spectrometry, coupled with gas or liquid chromatographic separation of the compounds (Nakabayashi and Saito 2013). Mass spectrometry is a widely applied technique in omics research, especially for proteins and metabolite analysis. A suitable technique for the elucidation of chemical molecule structure, often involved in metabolome studies, is nuclear magnetic resonance (NMR). NMR is considered as a quantitative technique with no need for particular sample preparation and frequently it is performed in parallel to mass spectrometry for the better resolution of metabolite profiling (Emwas et al. 2019; Zhao et al. 2016). Nuclear magnetic resonance spectroscopy utilizes the presence of an external magnetic field to transmit elements' nuclei isotopes spin from a lower to higher energy state. Excitation pulse at radiofrequency range interacts with nuclear spins generating NMR spectra (Deleanu and Jocelyn Paré 1997; Tesiram and Separovic 2005).

3 Biosensors

Biosensors are generally defined as analytical devices for biomolecule detection that modify a biological response into an electrical signal. In principle, biosensors should provide high sensitivity and specificity regardless of physical constraints such as pH and temperature (Mehrotra 2016). In order to develop a biosensor assembly in practice, several steps of multidisciplinary research such as immobilization of biorecognition element, fabrication, transducing devices should be considered (Bhalla et al. 2016). Biosensor devices integrate three indispensable parts: (a) the biorecognition element, (b) the transducer, and (c) the signal processor. After the application of an unknown sample to the device, the sensor identifies the target analytes, and afterward, the transducer transforms the output into measurable signals for the detector (Turner et al. 1987).

The vast variability in biosensor types allows the detection of pesticides, hormones, toxins, drugs, pollutants, heavy metals, etc., with significant precision. The main biosensors features are:

(a) Selectivity that depends on the affinity of the bioreceptor for a specific analyte in a sample containing several contaminants
(b) Reproducibility that indicates whether the biosensor is able to provide an identical output after repetition of the experimental setup
(c) Stability that reveals the biosensor's ability not to be influenced by ambient conditions in and around the device. (Bhalla et al. 2016). Potential perturbations may alter the biosensor's output signals leading to errors and negative effects on the biosensor's efficiency. Moreover, the transducer, as well as the electronics, can be susceptive to temperature alternations, causing variations in the biosensor's performance. Another element that could affect the biosensor's performance is the binding affinity between the analyte and the bioreceptor (Fu et al. 2019)
(d) Sensitivity that is based on the limit of detection (LOD). In several applications, biosensors have to detect analytes in concentrations at the ranges of fg/mL – ng/mL, in order to confirm traces of the analyte in the sample
(e) Linearity that associates with the accuracy of the obtained measurements. A small change in the analyte's concentration may have a significant impact on the biosensor's yield (Bhalla et al. 2016)

3.1 DNA-Based Biosensors

DNA biosensors depend on the complementary sequence hybridization of the immobilized probe with the target DNA sequence. The DNA probe is an artificially synthesized sequence designed to bind the target sequence. RNA targets can also be identified via the conversion of RNA into cDNA prior to hybridization by utilizing the enzyme reverse transcriptase (RTase). Afterward, specific transducers convert the response into signals that are further expanded by an amplifier (Sánchez-Paniagua López et al. 2018). The signals can be generated by several types of reactions (electrochemical, magnetoelectric, optical, colorimetric, and piezoelectric), depending on the type of transducer used (Manzanares-Palenzuela et al. 2016; Moura-Melo et al. 2015). Labeling can be performed by the use of redox, fluorescent, enzymes, chemiluminescence or nanoparticles (Asefpour Vakilian 2019).

Drought stress is a factor that could significantly reduce the yield and quality of agricultural plant production. Thus, the development of a selective method for the determination of drought stress is rather difficult since plant common morphophysiological and biochemical characteristics are not generally specific to biotic and abiotic stresses. The micro-RNA concentration in plant tissues could provide a selective and specific indicator of plant stress. Hence, an optical biosensor based on gold nanoparticles fabricated for the determination of sly-miRNA-1886in tomato plant roots was able to discriminate mild, moderate, and severe drought stress in tomato plants with quite good performance characteristics (Asefpour Vakilian 2019).

DNA-based electrochemical biosensors usually demand a redox reaction and transfer of electrons between electrodes to take place after hybridization of the target to an immobilized capture probe. On the contrary, electrochemical label-free biosensors depend on the change in current, impedance, or conductivity (Huang et al. 2019; Liu et al. 2017a). Tristeza is considered as one of the destructive diseases of citrus. A label-free impedimetric biosensor for the detection of nucleic acid of citrus Tristeza virus has been developed based on immobilization of thiolated ssDNA probes onto a screen-printed carbon electrode (SPCE) by electrodeposition of gold nanoparticles (AuNPs), for the enhancement of the electrode's conductivity. The sensor was able to selectively detect CTV nucleic acids in the presence of other nonspecific DNAs with good performance even in a real plant samples matrix.

Nevertheless, DNA sensors also present considerable pitfalls. One of the most important drawbacks is that nucleic acid extracts are susceptible to degradation and contamination. Moreover, false positive or negative results are also possible to occur, as well as the inefficiency of the biosensor to assess live and dead pathogens or toxins. In addition, some types of DNA based biosensors (i.e., enzymatic, piezoelectric) are quite sensitive to pH alterations (Fu et al. 2019). On the other hand, transducers such as nanoparticles in combination with an isothermal amplification technique could provide a promising potential for the effective on-site detection of plant stress biomarkers (Lau et al. 2017).

3.2 Antibody-Based Biosensors

Antibody-based sensors follow the principles of ELISA technique for the production of signals after binding of the target antigen (Ag) to antibodies (Abs) immobilized onto a solid supporting surface made up of glass, polystyrene, or a paper (Barbosa et al. 2017; Küchler et al. 2015; Lim and Ahmed 2019). The generation of the signal relies upon several transducers utilized such as electrochemical, piezoelectric, optical, and surface plasma resonance (SPR) (Amiri et al. 2018; Kumar and Arora 2020). The detection can be direct or label based (Pilolli et al. 2013); however, this technique is expensive, and the synthesis of antibodies can take a long time (Lim and Ahmed 2019). In addition, the Ag-Ab binding reaction is also influenced by alterations in the physiological or biochemical conditions. Furthermore, cross-reactivity and false-positive readings could potentially occur. Moreover, immunosensors present a short-term storage stability creating the need to maintain them at a low temperature conditions (Lau and Botella 2017; Lim and Ahmed 2019).

Regardless of the abovementioned limitations, these immunosensors are widely applied in several diagnostic fields as they do not necessitate the extraction of the purified analyte. Hong and Lee (2018) highlight the development of thirteen immunosensors for plant viruses and utilizing several transducers and signal generation methodologies ranging from quantum dots and magnetic nanoparticles through immunomagnetic separation, optical measurements, and FRET (fluorescence resonance energy transfer) phenomena through surface plasmon resonance. It should be annotated that the majority of the immunosensors reported make use of optical modes of detection rather than electrochemical detection with detection limits down to ng mL^{-1}. Fluorescence resonance energy transfer immunosensors that utilize graphene oxide as a label have been fabricated for the detection of rotavirus. When the target Ag linked to GO arrays binds to the Ab-DNA-AuNP complex, photoluminescence quenching between GO and AuNPs was induced resulting in a reduction of fluorescence, indicating the presence of the pathogen (Liu et al. 2011).

Indole-3-acetic acid is a phytohormone with a vital role in the plant growth and development. A label-free electrochemical impedance immunosensor for indole-3-acetic acid determination extracted from the stems of sunflowers under different salt stress conditions has been developed by the application of a three-dimensional PAMAM dendrimer in order to increase the antibodies immobilization capacity onto a gold electrode. The immunosensor's sensitivity was also enhanced by the use of gold nanoparticles that formed complexes with the antibodies for indole-3-acetic acid. The sensor performance was validated by UPLC-MS with quite good results.

For plant pathogen diagnostics, an electrochemical immunosensor integrated with metallic nanoparticles and the enzyme horseradish peroxidase (for the signal generation) has also been fabricated where the enzymatic catalytic reaction with H_2O_2 is followed by either an amperometric or a voltammetric redox reaction. This methodology was 20–50 fold more sensitive than conventional ELISA assay for the detection of the pathogens *Pantoea stewartii* (Zhao et al. 2014), and Citrus tristeza virus (Shojaei et al. 2016).

3.3 Aptamer-Based Biosensors

Aptamers are single-stranded DNA/RNA polymers (30–32 bp) that display high affinity for the target analyte (i.e., whole cell or cell component such as proteins, enzymes, toxins). The selected aptamer sequence is enriched by many continuous rounds of systematic evolution of ligands by exponential enrichment (SELEX) from an aptamer combinatorial library (containing approximately 1015 different sequences). This approach has several significant advantages in comparison with the antibodies due to their low cost and rapid synthesis (aptamers: 2 days, Ab synthesis: 3–4 months). Furthermore, aptamers are highly flexible and stable, as well as have versatile binding capacities (Pleshakova et al. 2017).

Aptasensors development requires the selected aptamer's immobilization onto a solid surface to bind the target molecule, leading to the conversion of the resultant signal into a readout by the transducer (Khedri et al. 2018). They can be integrated with several detection systems such as colorimetric, optical, chemiluminescent, electrochemical, fluorometric, surface plasma resonance (SPR), and magnetic. Numerous nanomaterials have been proposed for use in aptasensors in order to augment sensitivity and specificity (Yan et al. 2020). Unfortunately, some commonly observed pitfalls include the inefficiency to target small molecules and to detect slight differences between the large molecules, as well as their limited applicability toward a diverse range of pathogens (Rozenblum et al. 2019). Additionally, the commonly used SELEX process is labor-intensive, expensive, time-consuming, and sometimes inefficient (Zhuo et al. 2017).

Aptasensors are not widely used in agriculture. The first aptamer against a plant viral coat protein of the apple stem pitting virus has been developed in 2010 (Balogh et al. 2010). The proposed method, double oligonucleotide sandwich–enzyme-linked oligonucleotide assay (DOSELONA), was further investigated through Western blots and SPR. The aptasensors' flexibility and portability make them very promising tools for use in plant pathogen diagnostics (Kim et al. 2016).

3.4 Phage-Based Biosensors

Bacteriophages are DNA/RNA viral genomes encapsulated by a protein coat that lack their own metabolic machinery and multiply in their host's cells. Initially, phages were utilized as treatments to bacterial plant infections. Since they have a natural binding affinity to bacterial cells, proteins, or carbohydrates, phages have been used for bacteria detection (Aliakbar Ahovan et al. 2020). When the bacteriophage binds to the targeted bacterial component, an alteration in the reaction is triggered that is subsequently converted to measurable signals by the transducer. The phage-based biosensors are specific, cost-effective, very sensitive, and quick methodologies. Additionally, they are stabile at high temperatures providing a long shelf life to the biorecognition element (Janczuk-Richter et al. 2019).

The most significant drawbacks are the extensive sample preparation required and their inefficiency to the detection of fungal and unculturable bacterial pathogens in combination with the general lack of knowledge on phage-based biosensors (Singh et al. 2013).

Very few aptasensors have been developed for plant stress responses detection. A phage magnetoelastic (ME) biosensor platform was fabricated for the detection of *S. typhimurium* on the surface of spinach and tomato leaves. The biosensor exhibited a good limit of detection (1.94 CFU/leaf) (Park et al. 2013a). In spite of the narrow number of research investigations in this area for detection of plant stress responses, these phage-based biosensors have shown higher sensitivity and stability than real-time PCR (Park et al. 2013b), implying their future use in plant diagnostics.

3.5 Volatile Compounds Sensors

Plants demonstrate phenotypes considerable phenotype alterations in response to stress. Not only they exhibit visual differences to color and shape from unstressed plants (Mahlein 2016; Potters et al. 2007) but also they emit volatile organic compounds in adverse condition, that is, when they are exposed to drought or herbivores (Holopainen and Gershenzon 2010; Paré and Tumlinson 1999). VOCs can potentially be transferred to 50 neighboring plants, inducing resistance in these plants (Heil and Karban 2010).

In a recent study, the authors have developed a smartphone-integrated plant volatile organic compound sensing assembly utilizing a paper-based colorimetric sensor array that integrated cysteine-functionalized gold nanomaterials and chemoresponsive organic dyes for accurate and early detection of late blight in tomato leaves (Li et al. 2019). In order to obtain specific recognition of the organic compound (E)-2-hexenal, one of the main volatile organic compound markers released when the plant is infected by *Phytophthora infestans*, gold nanoparticles were used as plasmonic aggregative colorants. Ten common plant volatiles were identified including green leaf volatiles and phytohormones (i.e., methyl jasmonate and methyl salicylate) within 1 min of reaction with a handheld device. A three-dimensional (3D)-printed smartphone reader scanned the multiplexed sensor array in real time, and by an unsupervised pattern-recognition method, the sensing platform was able to detect (E)-2-hexenal and a range of disease-related organic compounds. In conclusion, this biosensor platform could be a cost-effective, portable method that will allow for in situ measurements on the field.

4 Conclusion

Dealing with the impending universal challenge of this century, the global food demand due to adverse environmental conditions, complementary, and multidisciplinary approaches integrating plant sciences and engineering are required. Several destructive and nondestructive methods have been developed during the last decades, enabling the monitoring of temporal variations. These conventional diagnostic methodologies have proven sensitive, specific, and reliable to some extent, but have significant shortcomings. However, they are time consuming, require sophisticated, high-cost equipment, and demand experienced/highly trained users. To surpass these difficulties, recent research advances have enabled for developing biosensors for the determination of chemical signals released from plants under stress conditions. The translation of chemical signals related to adverse environments into optical, electrical, and wireless signals makes biosensors powerful tools for plant growth and yield improvement. Moreover, biosensors could ease the rapid identification of desired crop traits due to the capability for high-throughput screening of chemical phenotypes. Numerous sensors already exist for plant signaling molecules associated with abiotic and biotic stresses, as well as for sensing plant nutrient deficiencies. What is more, remote sensing technologies can be extremely helpful tool diagnostic results spatializing. Finally, these innovative techniques could create new perspectives for unravelling plant interactions with the environment and offer prominent effects on plant protection and agriculture.

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Chapter 18
Secondary Metabolites for Sustainable Plant Growth and Production Under Adverse Environment Conditions

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Abbreviations

$^1O_2$	Singlet oxygen
ABA	Abscisic acid
AFP	Antifreeze proteins
APX	Ascorbate peroxidase
CAT	Catalase
DMAPP	Dimethylallyl pyrophosphate
H_2O_2	Hydrogen peroxide
HSP	Heat shock proteins
IPP	Isopentenyl pyrophosphate
MEP	2-C-methyl-D-erythritol 4-phosphate
MVA	Mevalonic acid
MVAPP	Mevalonate 5-diphosphate
NO	Nitric oxide
$O_2^{\bullet}$	Superoxide
–OH	Hydroxyl
ROS	Reactive oxygen species
SMs	Secondary metabolites
SOD	Superoxide dismutase

1 Introduction

Plants are known to produce numerous compounds for growth, support, structure, and metabolic functions. They have been classified as primary metabolites and include small and large molecules such as sugars, amino acids, tricarboxylic acids, or Krebs cycle intermediates, proteins, nucleic acids, and polysaccharides. These are the essential compounds and are not exclusive to plants (Hussein and El-Anssary 2018). Apart from these compounds, plants are known to synthesize several nonessential compounds which perform several functions which indirectly help in plant growth and/or survival, these compounds are called secondary metabolites (SMs) (Thirumurugan et al. 2018). Secondary metabolites in plants can be classified in several ways. The most common way is based on their biosynthetic origin, which divides SMs into three major groups, namely, alkaloids, flavonoids and phenolic acids, and terpenoids. Each group is further subdivided into subclasses on the basics of their structure. Some of the common examples of SMs are phenolic acids, chalcones, tannins, terpenes, caffeine, nicotines, etc. These secondary metabolites along with primary metabolites perform different functions during the various stages of plant's growth and development (Hussein and El-Anssary 2018).

Plants are sessile in nature and thus to protect themselves from the harsh environmental conditions they produce a range of metabolites. Such metabolites may work synergistically with each other to provide protection and/or help in survival and growth of plants. Abiotic and biotic stresses are the broad classes of stresses which plants get exposed to during their life cycle and adapt and protect themselves using secondary metabolites. There are three major pathways in the plants, which produce majority of the secondary metabolites. These pathways are shikimate, mevalonate, and nonmevalonate pathways, named on the basis of the precursor molecule. The regulation of these pathways is facilitated by the presence of a range of signaling molecules, including phytohormones, brassinosteroids, jasmonates, and nitric oxide. These signaling pathways respond to different types of stresses and lead to generation of specific secondary metabolites meant for protecting the plants from that particular stress (Mandal et al. 2010; Rudin and Choi 2013; Siddiqi and Husen 2017, 2019). This chapter aims at giving a generic overview of the production of different types of SMs in the plants with respect to resilient environmental conditions, especially under abiotic stresses and the major signaling molecules involved in their production.

2 Major Secondary Metabolites

Briefly the type and nature of some main types of secondary metabolites has been discussed, namely, flavonoids and phenolic acids, terpenoids, alkaloids containing nitrogen and sulfur elements.

2.1 Flavonoids and Phenolic Acids

The most abundant group of aromatic compounds of secondary metabolites is the polyphenols. These compounds contain the aromatic hydrogen group attached to a hydroxyl group (–OH). Polyphenols are a diverse class of polyhydroxylated phytochemicals based on the same common structure (Khatri et al. 2019). Phenol (C_6H_5OH or carbolic acid) is the simplest member of the group. Polyphenols have further been branched into three classes—the flavonoids, the phenolic acids, and the tannins.

Flavonoids are found in several parts of the plants, predominantly in fruits. These are compounds containing two or more carbon ring structures each linked to phenolic hydroxyl groups. Panche et al. (2016) state the function of flavonoids is spread over a wide range of biotic and abiotic stresses. They have been known to act as signaling molecules, UV filters, and also provide plants resistance against microbial activities. Flavonoids are also temperature sensitive and help the plant adjust to changing temperature by providing freezing tolerance (Samanta et al. 2011). Flavonoids have been further divided into seven subclasses: anthocyanidins, chalcones, dihydrochalcones, flavones, flavanones, flavanols, isoflavones, and isoflavonoids.

Phenolic acids are the second class of abundant polyphenols. Their structure is based on a phenolic ring being bound to a carboxylic functional group, thereby forming a C6–C1 skeleton. Hydroxybenzoic acid and hydroxycinnamic acids are the two important naturally occurring phenolic acids derived from benzoic acid and cinnamic acid, respectively (Heleno et al. 2015). Phenolic acids act as key signaling molecules in induced resistance of plants at the site of reaction (hypersensitive response) by induction of signal transduction pathways. Certain phenolic acids (methyl salicylate) have been discovered to provide induced resistance at a distance to prevent the spread of infection among different parts of the plant (Mandal et al. 2010; Białecka-Florjańczyk et al. 2018).

Tannins are the third type of polyphenols. They undergo modification and destruction during the ripening of fruits indicating its harvest time. Tannins are also well known for protecting the plants from predators. These molecules consist of the largest and complex polyphenols and can bind and precipitate other metabolites (Olivas-Aguirre et al. 2014). Hättenschwiler and Vitousek (2000) describe tannins as regulators of carbon cycling owing to their role in decomposition and nitrogen cycle.

2.2 Terpenoids

Terpenoids constitute the largest group of secondary metabolites in plants. As of 2015, 40,000 terpenoids have been isolated and identified (Tholl 2015). The diversity of terpenoids has been observed due to modifications in their basic structure. Once the backbone of terpenoids is synthesized by terpene synthase enzyme, they undergo dehydration, glycosylation, hydroxylation, etc., to form a stable compound (Dudareva et al. 2004). The basic structure of terpenes follows the isoprene rule as proposed by Otto Wallach (1869). Thus, the terpenes are multiples of $(C_5H_8)_n$ where n = linked isoprene units.

Production of terpenoids in plants takes place via two independent pathways, namely, the mevalonate pathway and the nonmevalonate pathway (Rudin and Choi 2013). Both the pathways form the same final products which further form a precursor for a wide array of terpenoids.

2.3 Alkaloids

A large group containing nitrogen atoms in their structural backbone has been collectively termed as alkaloids. In some cases, these N might be associated with amino or amido groups and usually are placed in a cyclic arrangement. To exemplify, indole alkaloids contain N in indole rings while quinolone alkaloids have N in the quinolone backbone. Alkaloids have been discovered majorly in flowering plants and certain species of animals.

The presence of N imparts alkalinity to the metabolites and thus they readily react with acids to form salts. About 3000 alkaloids have been discovered from 4000 plant species. Previously deemed as plant waste products, alkaloids have recently been proven to be essential in plant growth and sustainability. Most alkaloids are bitter and thus help in deterring herbivores away from the plant. The most common alkaloids include caffeine, morphine, nicotine, etc. (Khatri et al. 2019).

3 Pathways Involved in SM Production

3.1 Shikimate Pathway

Shikimate Pathway has been described as a linkage between the production of primary and secondary metabolites. This pathway has been studied in microorganisms and plants. The only difference in both systems is that in the microbial systems, the final product is primarily utilized in aromatic acid production, whereas in plants, chorismate forms a precursor for several secondary metabolites along with amino acid production (Weaver and Hermann 1997).

Shikimate or shikimic acid derives its name from the flowers of Japanese poisonous plant *Illicium amisatum* or shikimi from which it was first discovered (Santos-Sánchez et al. 2018). The pathway is also called the chorismic acid pathway as the chorismate formation step is the key intermediate step of the pathway and forms a precursor to several secondary metabolites (Seigler 1998). This is a seven-step pathway (Fig. 18.1) that branches out to form a wide array of metabolites including amino acids such as L-phenylalanine and L-tryptophan. A novel variation, the amino shikimate pathway, has been discovered in certain plant and microbial species (Floss 1997). Several secondary metabolites (especially antibiotics) such as ansamycins are a product of this pathway.

3.2 Mevalonic Acid Pathway

Reductive polymerization of acetyl-CoA from glycolysis further undergoes ramification to form the mevalonic acid (MVA) pathway (Bellés et al. 2005). The MVA pathway has been known to regulate the biosynthesis of isoprenoids in plants which contribute to the development and integrity of membranes. Thus, it is sometimes denoted as isopentenyl pathway (Buhaescu and Izzedine 2007).

The MVA pathway is a six-step pathway producing isopentenyl pyrophosphate (IPP) that undergoes isomerization to further form dimethylallyl pyrophosphate (DMAPP) (Fig. 18.2). IPP and DMAPP as precursors together contribute to make a diverse class of over 30,000 isoprenoids including coenzyme Q_{10}, vitamin K, and all steroid hormones (Holstein and Hohl 2004). Venkateshwaran et al. (2015) report

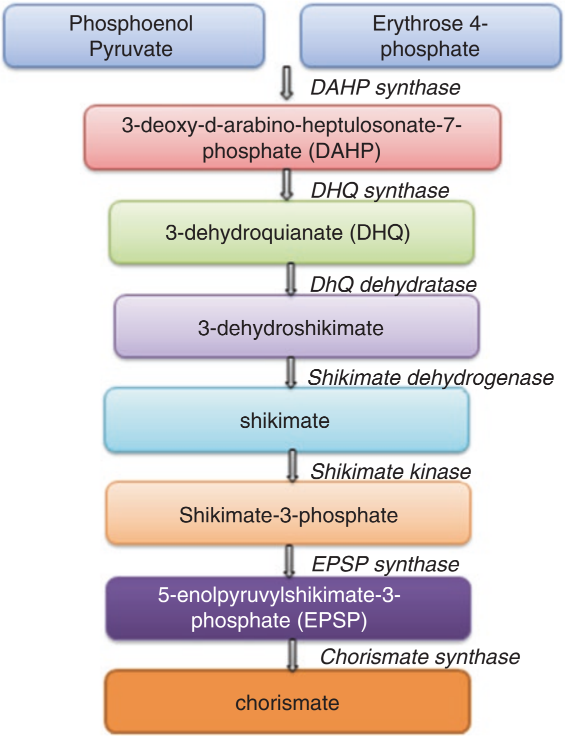

Fig. 18.1 The shikimate biosynthesis pathway

that the earliest plant response for symbiosis is mediated via this pathway wherein the host plant responds to arbuscular mycorrhizal fungi and rhizobia. Phytoalexins and cytokinins such as hormone messengers are some of the major end products resulting from this pathway (Bellés et al. 2005).

3.3 *Nonmevalonate Pathway*

The nonmevalonate pathway is an alternative pathway adapted by several higher eukaryotes and is not readily observed in bacteria. The outcome or final product of this pathway is the same as the MVA pathway resulting in the formation of isoprenoid precursors, that is, IPP and MVAPP. This biosynthesis occurs in the chloroplasts of the plant while the MVA pathway takes place in the cytoplasm (Dubey et al. 2003). The pathway is also called the MEP pathway as 2-C-methyl-D-erythritol 4-phosphate (MEP) is an initial step in IPP and MVAPP production (Fig. 18.2).

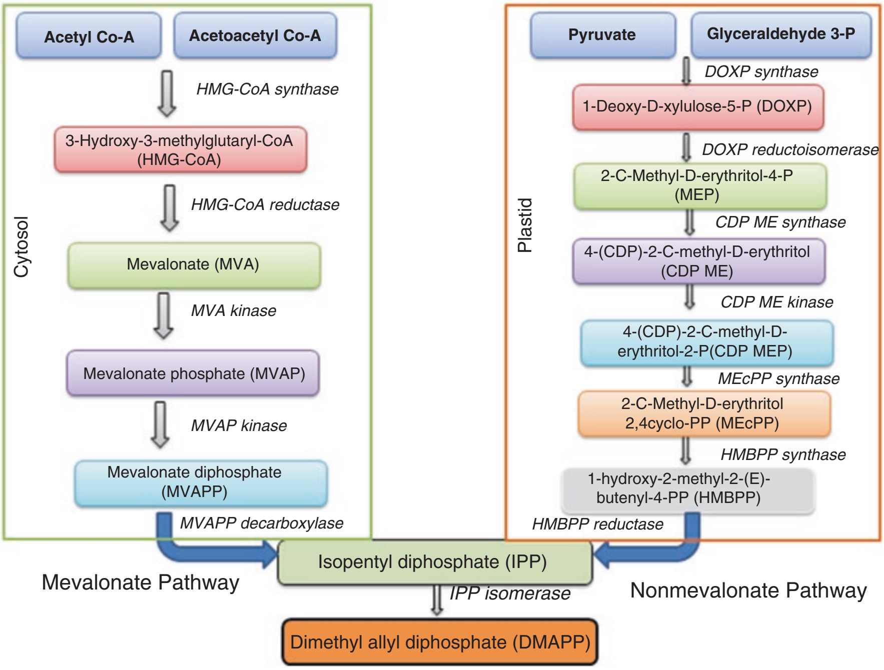

Fig. 18.2 Overview of mevalonate and nonmevalonate pathway

Table 18.1 Effects of stress in plants

Effect on growth	Effect on physiology	Effect on the molecular level
Inhibition in germination that results in growth reduction Productivity reduction Premature senescence	Water uptake decreases Reduction in photosynthesis Altered respiration Altered transpiration rate A decrease in nitrogen assimilation	Enzyme activity decreases Protein synthesis decreases Disorganization of membrane systems

4 Secondary Plant Metabolites and Adaptation to Extreme Environmental Conditions

During the course of development, plants get exposed to several environmental stress conditions and get affected at morphological, physiological, as well as at molecular level as shown in Table 1. There are two major groups of environmental stresses: (a) Abiotic stresses which include potentially adverse effects of drought, salinity, heat, high light, cold, heavy metals, water excess, and air pollutants (Gall et al. 2015); and (b) Biotic stresses which include various pathogenic microorganisms, fungi, weeds, and a number of other predators (Mazid et al. 2011).

Secondary metabolites are the trademark highlight of plants against both abiotic and biotic stress conditions. To manage abiotic stress conditions, plants acquire various protective mechanisms such as stabilization of biological membranes, ROS scavenging, and expression of stress proteins. To cope with climate change factors, plants produce various SMs, for example, phenolic compounds, carotenoids, polyamines, and antioxidants, and a number of signaling molecules, for example, nitric oxide (NO), jasmonic acid, methyl-jasmonate, salicylic acid, glycine betaine, and calcium (Ramakrishna et al. 2011).

Phenols help the plants during pigmentation, as well as defense. Flavones and flavonols, which are considered to be two major flavonoid groups, protect the cells from UV-B radiation (Panche et al. 2016). Carotenoids have a huge number of metabolic functions in plants such as protection against over excitation in strong light, protect cellular structures of various species of plants oxidative stress tolerance, helps in scavenging ROS formed during photo-oxidative stress, and also moderate the impact of extreme temperatures (Tapiero et al. 2004).

Polyamines, small aliphatic molecules, also play an important role in modulating plants' defense responses to various environmental stresses such as salinity, drought, chilling stress, and heavy metal stress (Gill and Tuteja 2010). Soluble sugars, which are primary compounds, are highly reactive to environmental stress conditions. Sugars such as sucrose and glucose helps in the osmoregulation of cells. Fructan, because of its high solubility and resistance to ice crystallization, also contribute during drought or low-temperature stress (Lintunen et al. 2016).

Plants have evolved antioxidant defense mechanisms to maintain homeostasis and protect macromolecules from the negative impacts of free radicals under stress conditions. Researchers have shown that ROS-scavenging enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), and glutathione peroxidase are involved in tolerance to abiotic stress in plants (Sarker and Oba 2018).

5 Role of Secondary Metabolites Under Stress Conditions

5.1 Abiotic Stress

Abiotic stress adversely influences various biochemical, molecular, and physiological processes of plants such as photosynthesis, respiration, and transpiration, which leads to the reduction in plant growth, development, and ultimately productivity. Abiotic stress such as drought, salinity, heavy metals, UV light, and temperature appear to have adverse effects on plant metabolism as shown in Table 18.2. These abiotic factors induce the oxidative and osmotic stresses in which reactive oxygen species (ROS) are formed that results in proteins, RNA, DNA damage, also

Table 18.2 Different abiotic factors, their effects on plants, and plants responses to those abiotic stress factors

Abiotic stress factors	Impact on plants	Secondary metabolites, signaling molecules, and phytohormones produced under stress
Drought	Stomata closure, rolling of leaves, stress-responsive enzymes, osmolyte synthesis	Compatible solutes—proline, glycine betaine, polyols, sugar alcohols, and soluble sugars Phytohormones—salicylic acid, auxins, gibberellins, cytokinin, and ABA, NO, JA Antioxidants—polyamines, citrulline, salicylic acid, and other enzymes such as APX
Salinity	Osmolyte synthesis, stress-responsive enzymes detoxification, ion transporters	Osmolytes—polyols, proline, sugar alcohols, pinitol, glucosinolates, and glycine betaine Soluble sugars—glutamate, sorbitol, mannitol, oligosaccharides, fructans, sucrose, etc. Antioxidants—ascorbic acid, glutathione, vitamin E, flavonoids, carotenoids ABA, cytokinin, gibberellic acid, NO, JA Antioxidants – salicylic acid, SOD, CAT, guaiacol peroxidase, APX, monodehydroascorbate peroxidase, and dehydroascorbate peroxidase Proline is considered to act as an osmolyte, a ROS scavenger, and a molecular chaperone
Heat	Heat shock protein synthesis, induction of protein repair mechanism	Compatible solutes—GABA, glycine betaine Phenolic compounds such as flavonoids and phenylpropanoids Antioxidants—polyamines, glutathione, salicylic acid NO, cytokinin
High light	ROs production increase	Antioxidants—APX, SOD
Cold	Osmolyte synthesis and acclimation increase	Antioxidants—salicylic acid, CAT, SOD, glutathione, glutathione reductase Phenolic compounds (suberin or lignin) Accumulation of sucrose and other simple sugars, fructans Phytohormones—ABA, JA Polyamines
Heavy metals	Generation of reactive oxygen radicals, deposit excess metal in vacuoles	NO, isoprene, salicylic acid

promotes lipid peroxidation and ultimately causes the cell death (Sharma et al. 2012). In the presence of any environmental stress, the products of secondary metabolites synthesis from primary metabolites (carbohydrates, lipid, and amino acids) increases, which is often low in case of normal metabolic conditions (Ramakrishna and Ravishankar 2011). For the maintenance of their physiology under stress, plants accumulate phenylpropenoids and phenolic compound in higher amount. To assist the plants in combating various stress conditions, the expression levels of certain genes governing the production of these compounds have also been shown to be increased (Sharma et al. 2019).

5.1.1 Drought

On a global basis, water is a paramount factor for plant existence, as it is needed for nutrients transportation. Drought stress is a result of water shortage. Drought stress may occur due to constant loss of water through transpiration or evaporation, high alkaline conditions, high or low temperature, etc., and further leads to the efflux of cellular water, leading to plasmolysis and thus causing cell death. Under drought stress, the accumulation of ROS species such as singlet oxygen ($^1O_2$), hydroxyl (–OH), superoxide ($O_2^{\bullet}$), and hydrogen peroxide (H_2O_2) may occur that negatively alters the antioxidant metabolism, and consequently results in cell peroxidation (Gill and Tuteja 2010). Under physiological conditions, coordination of secondary plant metabolites and scavenging enzymes keep the level of ROS low. In various in vitro studies, it has been found that phenolic acids, flavonoids, sesquiterpenes, and coumarins have significant antioxidant activity (Kaurinovic and Vastag 2018).

Drought stress influenced changes in anthocyanin concentration although plants containing this pigment are resistant to drought but at cold temperature, there is an increase in concentration of anthocyanin (Chalker-Scott 1999). Reduction in photosynthesis rate because of drought as reported in *Catharanthus roseus* (Garcia and Lamattina 2002). As reported by de Matos-Nunes et al. (2014), the production of SMs such as phenols, terpenes, and alkaloids during in vitro and in vivo growth increases through ionic and osmotic stress induction as plants get exposed to drought. Previously in 2010, Nowak et al. also saw same reports in case of *Pisum sativum* where after getting exposure to drought stress, plants drastically enhanced the phenolic compounds synthesis in comparison to control (Nowak et al. 2010).

5.1.2 Salinity

Similar to drought, salinity also acts as an important abiotic factor, which reduces the production in various arid and semi-arid regions (Msanne et al. 2011). Plants respond to salt stress through various biochemical and physiological processes, which are mentioned in Table 18.2.

Salinity stress leads to ionic stress, as well as osmotic stress. To cope with osmotic stress imposed by salt stress, a significant number of SMs such as phenolics, flavonoids, alkaloids, terpenoids, and steroids have been produced in plants. Osmotic adjustment also includes production and accumulation of cellular osmolytes (polyols, proline, sugar alcohols, pinitol, glucosinolates, glycine betaine, etc.) and soluble sugars (glutamate, sorbitol, mannitol, oligosaccharides, fructans, sucrose, etc.) (Sharma et al. 2019).

5.1.3 Temperature

Temperature strongly influences the metabolic activity, as well as the ontology of plants. Increase and decrease in temperature both are considered the abiotic factors accountable for the production of SMs in plants. High temperature (heat) results in low transpiration and photosynthetic rate, denaturation of proteins, reduction in biomass production, and premature leaf senescence. Against heat stress, plants increase the production of heat shock proteins (HSPs/Chaperons). Along with these HSPS, the expression of other proteins such as ubiquitin, cytosolic Cu/Zn-SOD, and Mn-peroxidase also get enhanced (Khan and Shahwar 2020). In 2010, Chan et al. reported that the incubation of *Melastoma malabathricum* cell cultures at a lower temperature gives better growth and a high amount of anthocyanin compared to those, which were grown, at high temperature (Chan et al. 2010). In the case of *Stevia rebaudiana,* it has been shown that increase in incubation temperature affects the growth of their hairy root cultures but the accumulation of glycoside stevioside is up to a certain level only (Kumari and Chandra 2016).

Likewise, lower temperature, that is, chilling stress or freezing stress have severe impacts on the production of SMs. During cold stress, photoinhibition of Photosystem I and increased H_2O_2 accumulation in chilled leaves occurs. In response to this, plants produce phenolics such as suberin or lignin, antioxidants such as polyamines, and endogenous phytohormones such as abscisic acid (ABA) (Ramakrishna and Ravishankar 2011). Concentrations of total ascorbic acid, glutathione, and β-carotene are found to be increased in chilling sensitive maize lines (Hodges et al. 1996). In response to chilling stress, antifreeze proteins (AFPs) help the plants to survive under freezing conditions by inhibiting the growth and ice recrystallization formed in intercellular spaces (Bredow and Walker 2017).

5.1.4 Heavy Metals

Metal ions such as silver, cadmium, europium, and lanthanum are also responsible for the production of SMs (Marschner 1995). It is well known that nickel, which is a vital component of urease enzyme, is required for the development of plants. Nevertheless, elevation in the concentration of this trace metal is directly proportional to the reduction of plant growth. According to Hawrylak et al. (2007), it has been revealed that nickel stress leads to decrease in anthocyanin levels by inhibiting activity of l-phenylalanine ammonia-lyase enzyme. In *Lithospermum callus* cultures, it has been described that copper and cadmium metal ions induce higher amounts of SMs such as shikonin (Mizukami et al. 1977).

5.1.5 Light

Light is considered as one of the most important limiting factors among all that affect plant growth and development during both in vivo and in vitro conditions. Therefore, it can affect the production of SMs depending on species/genotype, development stage, light type, and duration of exposure. For example, in *Catharanthus roseus*, UV-B light exposure significantly influenced the biosynthesis of vinblastine and vincristine, which are leukemia and antilymphoma drugs. Thoma et al. (2020) describe the production and accumulation of SMs in consumable leafy vegetables. Biosynthesis of a wide range of SMs is regulated by photoreceptors, which get activated by photons, thereby activating signaling pathways. This leads to gene expression changes of photoreceptor proteins and chromophores (Tilbrook et al. 2013; Folta and Carvalho 2015). Contrary to the amount of light received for photosynthesis, only a small amount of a particular fraction of light is required for activation of these photoreceptors inducing SM production (Schopfer and Brennicke 2010).

5.2 *Biotic Stress*

Plants and animals/insects may share symbiotic or parasitic interactions. Plants require them for pollination or seed dispersal and thus attract them by producing SMs with colors or fragrance. On the contrary, herbivores maybe attracted to plants, which produce flavorful and therapeutic SMs along with high nutritive value. Insects feeding on only one particular plant species (moths, butterflies, etc.) have been suggested to be addicted to a particular SM (Isah 2019).

5.2.1 Attraction

Majority of angiosperms depend on pollinators for their asexual reproduction. Thus, these plants produce colorful flowers, which release aroma when they are ready for pollination. A cascade of SMs acts during this process to attract the pollinators and no other insects.

Colors are the most important aspect to attract pollinators and/or other animals. The plant/part of the plant needs to stand out from the environment and thus the plant produces a varied range of colored SMs. The most important are the flavonoids contributing to cyanic colors (red-blue), yellow, and white, while carotenoids give shades of red-yellow. Every pollinator is attracted to a different set of colors. For example, nocturnal animals such as bats are attracted to white color, as they are easily detectable at night, while butterflies are attracted to cyanic colors (Harborne 2001). The flavorful or fragrant odor is the second important factor to be considered in attraction toward plants. Mono and sesquiterpenoids act synergistically with other SMs to liberate pleasant odors (Limonene in citrus fruits/flowers), while volatile aromatic substances (vanillin) liberate flavorful odor. Unlike colorful SMs, these types of SMs are produced in a lower amount by the plants (Wink 2018).

Nectar and pollens act as rewards for these pollinators/herbivores. Thus, SMs are specific to certain species. *Catalpa speciosa* produce iridoids such as catalpols to protect its nectar from ants (Harborne 2001).

5.2.2 Repulsion

Anthocyanin production have been known to be stimulated by pathogen attack along with other abiotic stress factors such as high light intensity, sugar, and nutrient deficiency (Winkel-Shirley 2001). Leaves of poisonous plants have been known to produce tannins in their vacuoles for bittering their taste wherein strong essential oils are produced in the trichome to deter herbivores/insects from their consumption. Pathogen invasions have been known to be prevented by the plants through production of serotonin (Ramakrishna et al. 2011). Furthermore, this serotonin induces production of other SMs with antioxidant properties when subjected to cold temperature in plants such as *Datura metel.* In a comprehensive study of *Camptotheca acuminata,* exposure to biotic and abiotic factors stimulated the camptothecin biosynthesis (Isah 2019).

Chitin, a primary component of cell wall in fungi, is identified by *Hypericum perforatum* during a fungal infection which stimulates the plant to synthesize antibiotic compounds such as phenylpropanoid, naphtodianthrone, hypericin, and pseudohypericin (Naik and Al-Khayri 2016). Attack by one species of microorganism can induce synthesis of different type of antibiotics in different plants. For example, *Escherichia coli* leads to synthesis of gymnemic acid and atropine in *Gymnema sylvestre* (Chodisetti et al. 2012) and *Datura metel* (Zahra et al. 2015), respectively.

5.3 Elicitors

Biotic and abiotic elicitors are used by researchers for eliciting production of SMs from a desired plant in in vitro and in vivo conditions. Since several SMs have been known to be therapeutic in nature, stress conditions are introduced to the plant in order to trigger and expedite their production. Being known to have lesser side effects, these SMs have gained popularity in the past few decades. Combination of stress factors are subjected to the plant, which along with careful regulation of biosynthetic pathways have given rise to new and novel SMs in plants (Naik and Al-Khayri 2016).

6 Role of Signaling Molecules under Stress Conditions

6.1 Phytohormones

Phytohormones have a vital role in adaptation to various environments by regulating their growth, development, nutrient absorption, germination, senescence, transduction, and various other metabolic processes. Traditional well-known phytohormones are—auxin, cytokinin, gibberellin, ethylene, and abscisic acid.

Auxin plays an important role in plants adaptation to drought, salinity, and cold stress (Bielach et al. 2017). Cytokinin enhances resistance to salinity, as well as heat stress in plants (Barciszewski et al. 2000). It has been reported that gibberellin is useful in enhancing plant growth under saline and cold-stress conditions (Prakash and Prathapasenan 1990). Ethylene (stress hormone) concentration increases several times under saline, drought, and mechanical stress (Cheng et al. 2013). Abscisic acid (ABA) acts as an endogenous messenger and plant adaptive process is controlled mainly by this phytohormone (Sah et al. 2016). Zhu et al. (2009) reported that in case of rice, ABA accumulates in response to water stress. Plants exposure to salinity induces a relative increment in ABA concentration. In sorghum, ABA improves plants tolerance to ionic stress by delaying the harmful effect of NaCl. Moreover, ABA also contributes during salt stress by increasing the water potential of xylem and plant water uptake (Amzallag et al. 1990).

6.2 Brassinosteroids

Brassinosteroids are polyhydroxy steroids, a relatively recent group of plant hormones involved in significant growth-promoting activities. These hormones can now be synthesized in vitro. Brassinolide, 24-epibrassinolide, and castasterone are chosen to be the most important ones that occur naturally due to their wide distribution and potent biological activity (Kaur et al. 2020). They can induce resistance to abiotic (drought, heavy metals, salinity, extreme temperature), as well as biotic stresses (herbicide injury). During abiotic stress, it enhances the photosynthetic rate, bioavailability of antioxidants such as ascorbate, carotenoids, glutathione, and enhances activity of antioxidant enzymes such as SOD, CAT, and APX. During biotic stress, it enhances the activity of peroxidases and polyphenols involved in polyphenol metabolism, stimulates the synthesis of ABA and ethylene, as well as pathogenesis related proteins synthesis by increasing salicylic acid level (Bartwal et al. 2013).

6.3 Salicylic Acid

Salicylic acid has been reported to induce tolerance to several abiotic stresses, for example, drought, heavy metals, variation in temperature, salinity, and other oxidative conditions (Szepesi et al. 2009; Afzal et al. 2006; Hussein et al. 2007). Various studies on tomato (Tari et al. 2002), maize (Gunes et al. 2007), and bean (Azooz et al. 2009) revealed the beneficial nature of salicylic acid during salinity stress conditions. In case of *Arabidopsis*, salicylic acid also triggers the NO production by regulating NO-dependent pathways (Zottini et al. 2007).

6.4 Jasmonates

There are many reports demonstrating the participation of jasmonates by activating the defense mechanisms in plants under environmental stress conditions such as drought, salinity, and low temperature (Cheong and Choi 2003; Siddiqi and Husen 2017). Due to their well-known elicitation activity, plants produce jasmonate and methyl-jasmonate under abiotic and biotic stresses. Jasmonate activate plant defense system in response to various pathogens, insect-driven wounding, and environmental stress conditions, such as drought, salinity, and low temperature (van der Fits and Memelink 2000). The application of jasmonate results in the aggregation of phenolics compounds and alkaloids in plants (Lee et al. 1997; Zabetakis et al. 1999).

6.5 Nitric Oxide

Nitric oxide (NO) is implicated in the signaling cascade upstream of H_2O_2 synthesis and downstream of jasmonate synthesis. The implementation of exogenous NO to plants seems to activate different biochemical pathways that provide some resistance against several stress conditions (salinity, heavy metal, ozone, etc.) by regulating the expression of some genes involved in abiotic stress tolerance (Isah 2019). Various studies described the role of NO in photosynthetic or oxidative characteristics in different plants exposed to high temperature combined with different abiotic stresses (Chen et al. 2013). The participation of NO in moderating physiological, chemical, and metabolic functions are also observed in soybean plants at high temperature (Vital et al. 2019).

7 Conclusion

Primary metabolites contribute directly to the development, growth, and reproduction of plants. In addition to primary metabolites, plants synthesize a wide array of SMs, which play quintessential role in interaction of plants with its environment and is mainly produced in unfavorable conditions. Production of SMs get triggered by signaling molecules resulting from the biotic and abiotic stress. Stress may induce SM production locally restricted to the part of plant under stress. Usually, a number of SMs act synergistically to enhance their activity. SMs range in their functionality from being pungent to avoid attack of pests during biotic stress to controlling of stomatal closure during abiotic stress conditions such as droughts and high salinity. Three pathways are linked to the production of SMs, and the enzymes involved in the pathways get triggered in accordance to the plant's environment. SMs not only have been proven beneficial to plants but have been found to have innumerable therapeutic properties for plants, animals, and human beings. Though the immobility of plants renders it to be subjected to numerous resilient conditions, SMs assist primary metabolites to maintain the cellular integrity, thereby contributing to growth and development of the plants.

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Chapter 19
Medicinal Plants and Their Pharmaceutical Properties Under Adverse Environmental Conditions

Archana Bachheti, Deepti, R. K. Bachheti, and Azamal Husen

Contents

1 Introduction

Health is wealth. In consonance with this proverb, human beings have always been in search of various types of medicine to eliminate their illnesses. Plants are the natural source of these medicines mainly due to the presence of secondary metabolites and have been used as medicine in crude extract form. They have been also used to isolate the bioactive compounds in modern medicine and herbal medicine systems (Parveen et al. 2020a). Thus, they play an important role in the development, synthesis, and formulation of new drugs. Right now, numerous plant-based drugs are available in the market, and they have shown a remarkable contribution in disease management. In fact, from the ancient times, several herbal plants have been used as medicine or a source of medicines. For instance, in 2600 BC, the medicinal system in Mesopotamia had thousands of plant-derived medicines. Also, the

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Egyptian medicine system "Ebers Papyrus" has the written records of 700 drugs obtained from plants (Borchardt 2002; Cragg and Newman 2013; Sneader 2005). Traditional Chinese medicine and Indian Ayurveda and Unani medicine systems also documented evidence for the use of plant-derived medicine over thousands of years (Parveen et al. 2020b; Patwardhan 2005; Unschuld 1986).

A literature survey has shown that several families of plants have been used for medicinal purposes and in the development of new drugs. Some of the important medicinal plants are frequently obtained from Rutaceae, Asteraceae, Apocynaceae, Solanaceae, Caesalpiniaceae, Liliaceae, Piperaceae, Ranunculaceae, Apiaceae, Sapotaceae, Orchidaceae, and many more (Nautiyal et al. 2002; Husen and Rahman 2003; Husen and Faisal 2005; Aftab 2019). Aspirin, atropine, artemisinin, colchicine, digoxin, ephedrine, morphine, physostigmine, pilocarpine, quinine, quinidine, reserpine, taxol, tubocurarine, vincristine, vinblastine, etc., are important drugs obtained from the various medicinal/herbal plants. These drugs are obtained from the whole plant, leaves, roots, shoots, flower, or bark, etc. (Parveen et al. 2020a). For example, the root of *Rauvolfia serpentina* (Apocynaceae) is used to isolate serpentine, which is useful in the treatment of hypertension. Similarly, *Catharanthus roseus* is a source of vinblastine used in the treatment of different types of cancer (Iqbal and Srivastava 1997).

Numerous medicinal plants and their parts are a good source of bioactive compounds and/or secondary metabolites (terpenoids, phenolics, and nitrogen-based compounds) and have made a lot of contributions in drug formulation for the treatment of chronic diseases, such as heart disease, cancer, and diabetes (Iqbal 2013). Additionally, many other bioactive compounds obtained from herbal plants and combined with other compounds have shown to enhance the biological activity and are used in drug formulation (Kennedy and Wightman 2011; Shariff 2001). Generally, the significance of medicinal plants depends on the content and production of secondary metabolites. Swift et al. (2004) have reported over 100,000 known secondary metabolites with diverse chemical structures and function. Several factors such as harvest time, seasons, soil type, nutrient supply, altitude, geographical location, stage of plant (juvenile or mature stage), genotypes or cultivars, biotic stress, and abiotic stress (such as temperature variation, drought, salinity, and light intensity) extensively affect various plant processes including plant growth and development, and synthesis, accumulation, and production of secondary metabolites (Arshi et al. 2006a, b; Berini et al. 2018; Chetri et al. 2013; Falk et al. 2007; Iqbal et al. 2018; Ramakrishna and Ravishankar 2011; Zykin et al. 2018). Extraction process may also influence the chemical composition of natural products (Bucar et al. 2013; Jones and Kinghorn 2012). Like food crops and other higher plants, the medicinal plants also cope up with the surrounding adverse environment by producing secondary metabolites which help them to adopt and/or tolerate the stress situations (Berini et al. 2018; Isah 2019; Kroymann 2011). Several secondary metabolites have shown a specific role in defense against herbivores, pests, and pathogens (Bennett and Wallsgrove 1994; Zaynab et al. 2018) (Fig. 19.1). Accordingly, this chapter aims at reviewing the information about the secondary metabolites obtained from medicinal plants, their variation at different developmental stages, and the overall impact of adverse environmental conditions on their production.

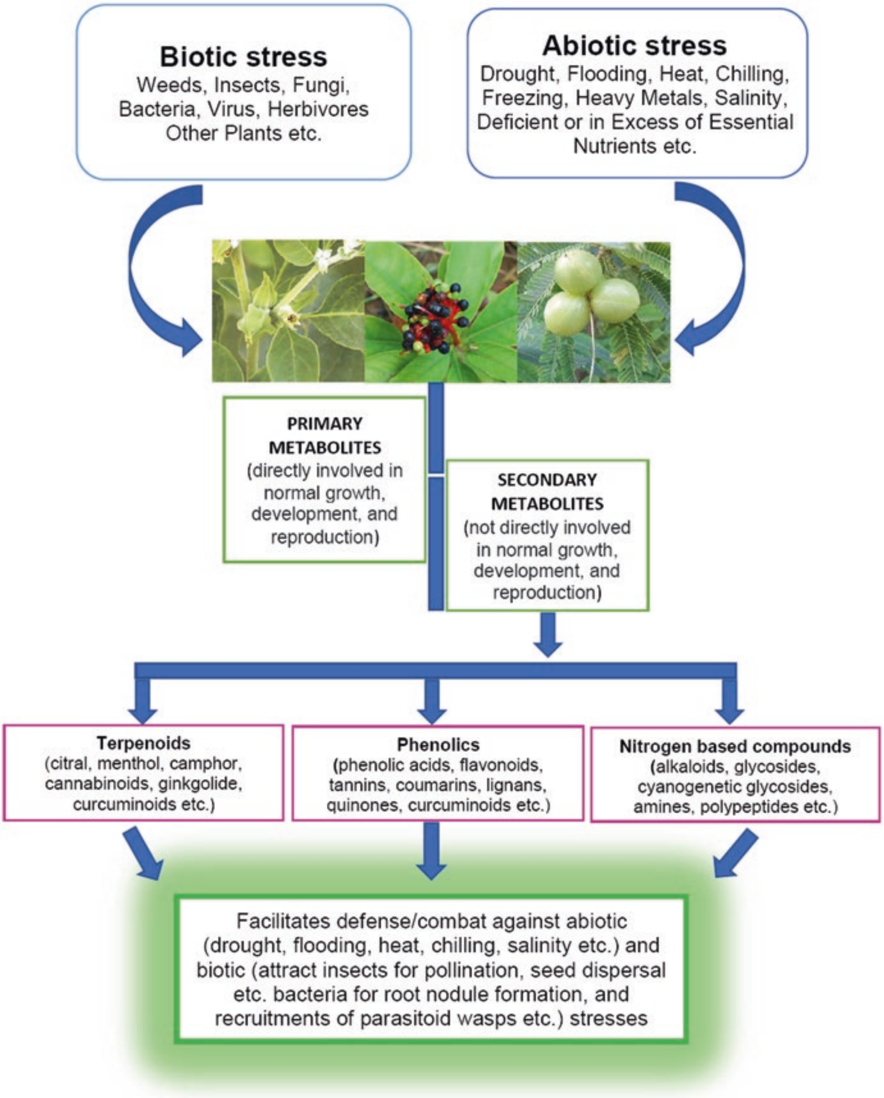


Fig. 19.1 Secondary metabolites under adverse environmental conditions and their role in plant defense

2 Secondary Metabolites and Their Production Sites

Herbal medicine is receiving attention in both developed and developing countries because of its natural origin and minimal adverse effects (Lawal and Yunusa 2013; Parveen et al. 2020b). The World Health Organization (WHO) report revealed that over nearly 80% of the global population uses herbal plants to cure human ailments (WHO 2019). Phytochemicals (natural products) are produced by plants via primary and/or secondary metabolism (Huang et al. 2016). They have shown various biological activities and play a key role in plant communication, growth, or defense against competitors, pathogens, or predators (Bachheti et al. 2019; Molyneux et al. 2007). Based on their biosynthetic pathway, secondary metabolites can be categorized into three major groups – phenolic compounds, terpenes, and nitrogen-containing compounds (Fang et al. 2011; Parveen et al. 2020b).

The flavonoids constitute one of the most widespread groups of natural products and are important to humans because they contribute color to plants and many of them, namely, coumestrol, phloridzin, rotenone, rutin, and artemetin. Flavonoids that occur as aglycones, glycosides (O-glycosides and C-glycosides), dimers, and methylated derivatives are physiologically active (Jay et al. 1975; Swain 1976). Glucose is the common sugar present in the flavonoids glycoside although the presence of galactose, rhamnose, xylose, arabinose, mannose, fructose, and apiose is also reported in mono-, di-, or tri-flavonoid glycosides (Harbone and Mabry 1975; Markham 1982). Structurally, flavonoids are benzo-y-pyrone derivatives that resemble coumarin. All the flavonoid aglycones consist of a benzene ring (A) condensed with a six-membered heterocyclic ring (C), which is either a γ-pyrone (chromone) or its dihydro derivative (4-chromone). The 4-chromone substituted by an aryl ring (B) at 2-position gives flavones and dihydroflavonols, and a similar substitution of chromone by aryl ring divides the flavonoids class into flavonoids (2-position) and isoflavonoids (3-position). Flavonols differ from flavanones by OH-group in the 3-position and a double bond at C2–C3 (Fig. 19.2). The common substituents such as free OH and OMe (methoxy group) are reported in flavonoids. In the case of O-glycosides, the C1 of sugar moiety is linked to flavonoid unit through O-atom. A free ortho position to phenolic hydroxyl groups appears to be a common feature that is a prerequisite for the formation of a C-glycosidic linkage in flavonoid (Markham 1982). In different classes of flavonoid C-glycosides (Fig. 19.1), the sugar moiety is attached directly to the ring A by C–C bond and is resistant to acid and enzymatic hydrolysis even after prolonged acid treatment, although partial isomerization often takes place under these conditions.

Terpenoids cover the major and most extensive group of natural plant products, and over 20,000 such structures have been described from plant sources. Isoprene a five-carbon unit, that is, isoprene, is the precursor of all terpenoids. Biosynthetically, they are formed in vivo by the condensation of two C_5 precursors, that is, dimethylallyl pyrophosphate and isopentenyl pyrophosphate (IPP), which give rise to C_{10}-intermediate, geranyl pyrophosphate (GPP). This is the immediate precursor of the monoterpenoids and the related monoterpene, and lactones are known as iridoids. GPP can be condensed in turn with another C_5 unit of IPP to produce the C_{15} intermediate, farnesyl pyrophosphate (FPP). This compound is the starting point for the synthesis of sesquiterpenoids. FPP can undergo further extension by linking with another IPP residue to produce the C_{20} intermediate, geranyl-geranyl pyrophosphate (GGPP). This is the general precursor of all the plant diterpenoids with their C_{20} base structures. Two molecules of the intermediate FPP can condense together in a further step in terpenoid biosynthesis with the formation of squalene, the C_{30} precursor of the largest group of isoprenoids, the triterpenoids. Two molecules of GGPP may condense together tail to tail to form a C_{40} intermediate called phytene, which

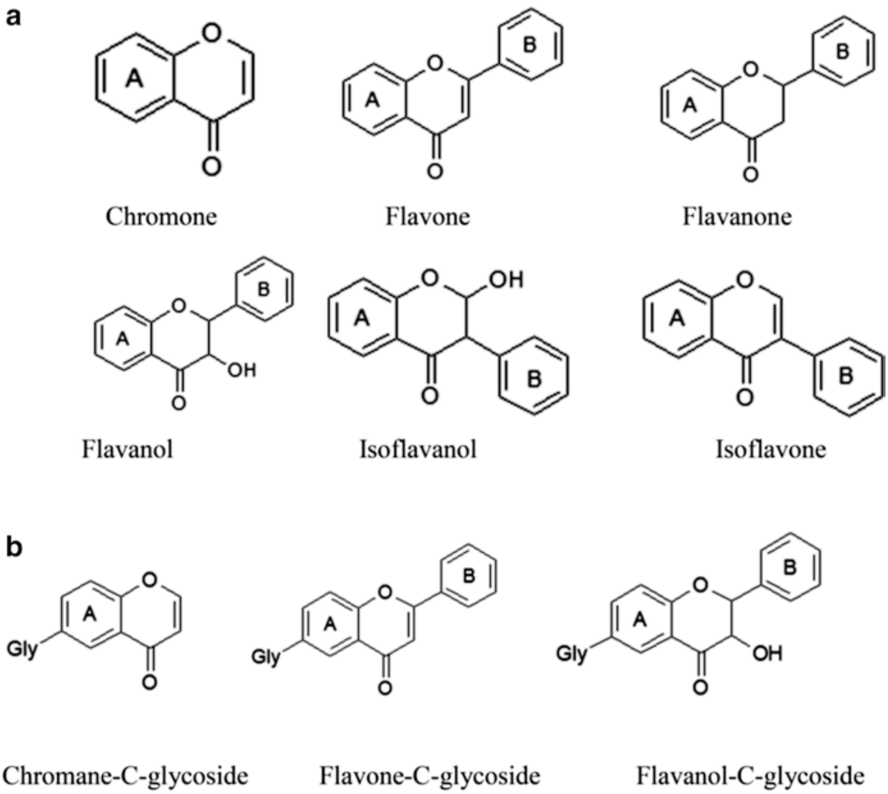


Fig. 19.2 Basic skeleton of natural occurring (**a**) flavonoid glycosides and (**b**) C-glycoside

is the immediate precursor of the yellow carotenoid pigments. The whole class of terpenoids is thus structurally very complex. Polymerization of IPP can occur in plants leading to polymer, which is commonly secreted in special cells as milky latex. Terpenoids have been classified into different classes such as monoterpenoids, sesquiterpenoids, diterpenoids, sesterterpene, and triterpenoids (Fig. 19.3) (Harborne 1998; Nakanishi et al. 1974).

Nitrogen-containing secondary metabolites contain alkaloids, cyanogenic glycosides, and glucosinolates. Alkaloids contain more than 12,000 nitrogen-containing low-molecular-weight compounds family (Facchini 2001; Khan and Rahman 2017) and are known for their biological activities. Examples of alkaloids are quinine, antineoplastic agents (camptothecin and vinblastine), and strychnine (poison for rats). Precursors for the biosynthesis of alkaloids include tyrosine, lysine, and tryptophan (Khalil 2017; Taiz and Zeiger 2006).

The growth and developmental stage (juvenile or mature phase) of medicinal plants, harvest times, etc. affect the production of secondary metabolites (Table 19.1). The major production sites of secondary metabolites are leaves, flowers, fruits and seeds, roots, and stem. Leaves produce food for plants by the process of photosynthesis. Also, it is used for synthesis and storage site for secondary metabolites. The

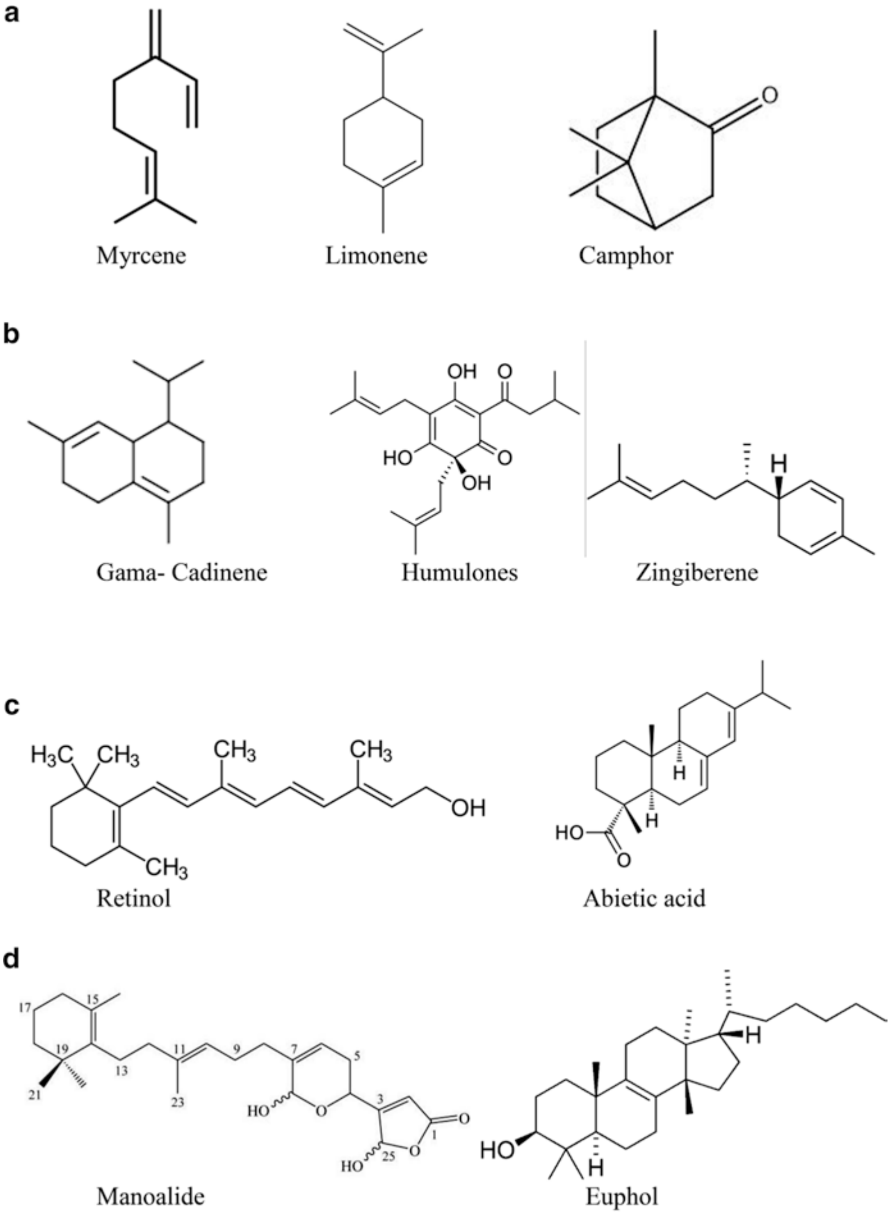
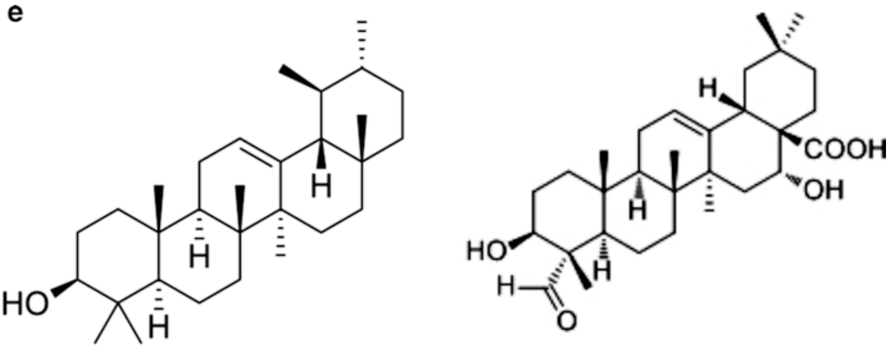


Fig. 19.3 Structures of naturally occurring terpenoids. (**a**) Monoterpenoids, (**b**) sesquiterpenoids, (**c**) diterpenoids, (**d**) sesterterpenoids, (**e**) triterpenoids



Beta Amyrin

Quillaic acid

Fig. 19.3 (continued)

amount and/or concentration of secondary metabolites in plant leaves are usually affected by harvesting season, leafage, growth stage, etc. (Gomes et al. 2019; Li et al. 2016b; Vazquez-Leon et al. 2017). For instance, it was found that biosynthesis of terpenes (monoterpenes and sesquiterpenoids) starts at cotyledon stage of *Melaleuca alternifolia* (Southwell and Russell 2002). The highest content of essential oil (eugenol) in *Cinnamomum verum* was present in a 1-year-old leaf (Li et al. 2016b). However, in some plants, synthesis of compounds starts in the mature leaves. For instance, compounds associated with the sabinene hydrate–terpinen-4-ol–γ-terpinene pathways seem to be formed at later stages of development (Southwell and Russell 2002).

Normally, flowers have a good smell due to the presence of terpenes and aromatic compounds in them; their synthesis and storage are also affected by different developmental stages (Srivastava and Iqbal 1994). A study on volatile oils content of flower buds of *Magnolia zenii* at different growth stages found a remarkable difference in oil content at different growth stages (Hu et al. 2015). Volatile oil yield first increases and then decreases with the growth of flower buds, while maximum oil yield was obtained in October (Hu et al. 2015). Figueiredo et al. (2008) reported that the content of 1,8-cineole and camphor increases with the development stage of the flowers of *Achillea millefolium,* while the content of azulene decreases. In the case of *Antirrhinum majus,* contents of ocimene and elemene quickly increased on the second day after flowering and decreased after attaining peak on the sixth day (Dudareva et al. 2003). The developmental stages of fruit and seed also have a remarkable influence on the secondary metabolites content and composition. A study by Liang et al. (2006) has shown that the highest amount of essential oils (volatile oil) is present in citrus fruit when it is light yellow. Wu et al. (2013) also reported that the yield of essential oil increased the maturation process and the contents of β-pinene, α-thujone, carene, and γ-terpinene in *Citrus medica* change significantly during the maturation stage. Also, the maximum content of morphine was reported at the maturity of *Papaver somniferum* roots (Shukla and Singh 2001). The content of dicoffee quinic acids decreases with the developmental stage, while the content of quinic acid was the highest in the early developmental stage in coffee seeds (Lepelley et al. 2007). The highest saponins content in the root of *Panax notoginseng* was found when the plant was 3-year-old (Hong et al. 2005). Further details are presented in Table 19.1.

3 Role of Secondary Metabolites Under Adverse Environment

During the entire life span, plants come across both abiotic and biotic stresses. Secondary metabolites exhibit a significant role in tolerance and adaptation of plants to adverse environmental conditions (Anjum et al. 2014). Additionally, the biosynthesis of secondary metabolites is also influenced under various environmental conditions (Iqbal et al. 2011). Further details of different types of stresses encountered by the plant are shown in Fig. 19.1.

3.1 Biotic Stress

Like crop plants, medicinal plant growth and production are also affected by potential biotic enemies, such as bacteria, viruses, fungi, nematodes, mites, insects, mammals, and other herbivorous animals. Due to sessile nature, plants are unable to change their position to get rid of such enemies. In this negative situation, they protect themselves by producing secondary metabolites. For instance, phytoalexins having antimicrobial activity are produced by plants on attack of pathogen (Taiz and Zeiger 2006). Similarly, Verma and Shukla (2015) have reported that when a plant undergoes fungal infections, significant variation occurs in phenolics content. Kim et al. (2008) have reported that among the various secondary metabolites, the phenolic compounds play a vital role in plant defense against pathogens and insects attack. Alkaloids are also involved in plant defense and are produced in response to attacks by a microorganism (Joosten and van Veen 2011). It has been also reported that the content of trigonelline, camptothecin, and castanospermine increased due to reactions with fungus inoculum (Jia et al. 2016). Some specific enzymes are capable of avoiding the attack of any unsuitable organisms. For instance, the activity of polyphenol oxidase increases in wounded plants attacked by pests or infected by pathogens (Vanitha et al. 2009). Some plants also produce o-quinones, which act as antimicrobial agents and protect plants (Constabel et al. 2000).

Table 19.1 Secondary metabolites changes at various developmental stages in some medicinal plants

Medicinal plant (family)	Plant part	Developmental stage	Major class of secondary metabolite/ bioactive compounds	Name of metabolite	Concentration variation	Key references
Mentha × piperita (Lamiaceae)	Plants	Matured plant	Terpenoids	Menthofuran, limonene, and pulegone	Decreased as plant matured	Abdi et al. (2019)
Mentha × piperita (Lamiaceae)	Plants	Matured plant	Terpenoids	Menthol, cineole, and neomenthol	Increased as plant matured	Abdi et al. (2019)
Lonicera japonica (Caprifoliaceae)	Flower	Whole growth stage	Phenols	Chlorogenic acid	Increasing first and then decreasing	Li et al. (2019); Kong et al. (2017)
Scutellaria baicalensis (Fabaceae)	Root	Before the full-bloom stage	Flavonoids	Flavonoids	Strong increase	Xu et al. 2018
Cinnamomum verum (Lauraceae)	Leaf	1-year-old	Phenols	Eugenol	Highest	Li et al. (2016b)
Magnolia zenii (Magnoliaceae)	Flower bud	October	Terpenoids	Essential oils	Highest	Hu et al. (2015)
Codonopsis pilosula (Campanulaceae)	Root	Older tree	Terpenoids	Triterpene	Low	Zhu et al. (2014)
Cinnamomum cassia (Lauraceae); *Cinnamomum verum* (Lauraceae)	Leaf	2-year-old branch	Terpenoids	Essential oils	Highest	Li et al. (2013)
Citrus medica (Rutaceae)	Fruit	Maturation process	Terpenoids	Essential oils	Significant increase	Wu et al. (2013)
Magnolia officinalis (Magnoliaceae)	Bark	13-year-old	Flavonoids	Hyperin and quercetin	Highest	Yang et al. (2012)
Magnolia officinalis (Magnoliaceae)	Bark	7-year-old	Flavonoids	Rutin and quercitrin	Highest	Yang et al. (2012)

(continued)

Table 19.1 (continued)

Medicinal plant (family)	Plant part	Developmental stage	Major class of secondary metabolite/ bioactive compounds	Name of metabolite	Concentration variation	Key references
Scutellaria baicalensis (Lamiaceae)	Root	Whole growth stage	Flavonoids	Baicalin	Increases and then gradually decreases	Hu et al. (2012)
Magnolia officinalis (Magnoliaceae)	Bark	13-year-old	Phenols	Chlorogenic acid	Highest	Yang et al. (2012)
Cinnamomum cassia (Lauraceae)	Stem and bark	Increased years	Terpenoids	Essential oils	Increase	Geng et al. (2011)
Allium sativum (Alliaceae)	Bulb	Late planting during December	Organosulfur compound	Alliin, allicin, allyl sulfide, (E)-ajoene, and (Z)-ajoene	Higher	Montaño et al. (2011)
Allium sativum (Alliaceae)	Bulb	Late harvesting	Organosulfur compound	Alliin	Higher	Belguith et al. (2010)
Rosa × *hybrid* (Rosaceae)	Flower	Fully open flowers	Flavonoid	Anthocyanin	Increased from bud stage to fully open flowers, and decreased in senescent ones	Schmitzer et al. (2010)
Rosa × *hybrid* (Rosaceae)	Flower	Fully open flowers	Flavonoid	Quercetin	Increased from bud stage to fully open flowers, and decreased in senescent ones	Schmitzer et al. (2010)
Rosa × *hybrid* (Rosaceae)	Flower	In buds or partially open flower stage	Total phenolics	Phenolics	Highest content	Schmitzer et al. (2010)
Achillea millefolium (Asteraceae)	Flower	With the development of the flowers	Terpenoids	Camphor and 1,8-cineole	Increase	Figueiredo et al. (2008)
Citrus medica (Rutaceae)	Fruit	Fruit is light yellow	Terpenoids	Essential oils	Highest	Liang et al. (2006)

3.2 Abiotic Stress

Climate change and an environmental variation, such as temperature, drought, salinity, solar radiation, and air pollution, have been reported to affect the production of secondary metabolites (De Castro et al. 2020; Ferreira et al. 2016; Iqbal et al. 2018; Kulak et al. 2020; Nascimento et al. 2015; Qureshi et al. 2013; Sampaio et al. 2016; Sharma et al. 2019; Zhou et al. 2017). Some of the major abiotic stress conditions and plant response in terms of secondary metabolite production are discussed in the following.

3.2.1 Temperature Stress

Change in temperature affects plant growth and secondary metabolite content due to changes in the metabolic pathways that control physiology, signaling, and defense mechanisms. Studies have shown that the production of secondary metabolites increases in response to elevated temperatures in *Pringlea antiscorbutica* (Hummel et al. 2004) and *Panax quinquefolius* (Jochum et al. 2007). However, in the case of *Pseudotsuga menziesii*, high temperature has reduced the content of monoterpene (Snow et al. 2003). Some studies such as Ruelland et al. (2009) and Sevillano et al. (2009) have suggested that low temperature generates reactive oxygen species (ROS), and to neutralize their effect, the plant generates antioxidative enzymes. However, almost all the abiotic stresses, including high- and low-temperature stresses, cause oxidative damage and generate ROS in plants (Aref et al. 2016; Siddiqi and Husen 2017, 2019). Thus, plants evolved a range of tolerance mechanisms to manage the damage produced by these stresses, such as activation of antioxidative enzymes, and the accumulation of compatible solutes that effectively scavenge ROS. The chemical composition of essential oil has also been affected due to changes in temperature conditions. For instance, the effect of cold temperature on essential oil composition *Origanum dictamnus* was examined by Lianopoulou and Bosabalidis (2014). This investigation has shown that the main components of essential oil of *Origanum dictamnus* were p-cymene, carvacrol, γ-terpinene, and borneol; however, in winter, content of p-cymene was 59.2%, whereas in summer, carvacrol content was 42%. Low temperature increases the accumulation of withanolides (steroids) in the leaves of *Withania somnifera* (Khan et al. 2015; Kumar et al. 2012). Also, in transgenic plants of this species, the same trend was noticed when exposed to low temperature, that is, increase in withanolide content when plant exposed to low temperature (Saema et al. 2016). Rivero et al. (2001) studied the effect of high temperature on tomato plants and found that high temperature causes accumulation of phenolic contents. Wu et al. (2016) studied polyphenols in different sorghum genotypes under high-temperature stress. They have suggested that the brown sorghum was rich in phenolic profile, and thus exhibited a greater temperature tolerance. Further details associated with medicinal plants and their response under temperature stress are given in Table 19.2.

Table 19.2 Medicinal plants and their response under temperature stress

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Temperature stress	Concentration variation	Key references
Mentha piperita (Lamiaceae)	Leaves	To treat flatulence, menstrual pains, depression-related anxiety, muscle, nerve pain, etc.	Total phenol, flavonoid, and saponin	–	Heat stress	Decrease	Haifa et al. (2019)
Catharanthus roseus (Apocynaceae)	Leaves	Used for relieving muscle pain, depression of CNS, also for applying to wasp stings and in wound healing	Total phenol, flavonoid, and saponin	–	Heat stress	Decrease	Haifa et al. (2019)
Camellia japonica (Theaceae)	Leaves	Used as astringent, antihemorrhagic, hemostatic, salve, tonic, etc.	Tannins, terpenoids, and alkaloids	–	Low temperature	Increase	Li et al. (2016a)
Aquilaria sinensis (Thymelaeaceae)	Plant cells	Used against cancer, abdominal pains, asthma, colic, and diarrhea	Terpenes	Sesquiterpene-α-humulene, α-guaiene, and δ-guaiene	Heat shock	Increase	Xu et al. (2016)
Camellia japonica (Theaceae)*Astragalus compactus* (Fabaceae)	Leaves, roots, and flowers	Used as astringent, antihemorrhagic, hemostatic, salve, tonic, etc. Used as anti-inflammatory, immunostimulant, antioxidative, anticancer, antidiabetic, cardioprotective, hepatoprotective, and antiviral	Fatty acids	α-Linolenic acid and jasmonic acid	Low temperature and high temperature	Increase	Li et al. (2016a); Naghiloo et al. (2012)
			Phenols	Phenolics		Increase	

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Temperature stress	Concentration variation	Key references
Astragalus compactus (Fabaceae)	Roots, leaf, and flowers	Used as anti-inflammatory, immunostimulant, antioxidative, anticancer, antidiabetic, cardioprotective, hepatoprotective, antiviral, etc.	Tannins, terpenoids, and alkaloids	–	High temperature	Increase	Naghiloo et al. (2012)
Artemisia annua (Asteraceae)	Whole plant	Used in fever, liver disease, depression, muscle pain, and memory loss	Sesquiterpene lactone	Artemisinin	A transient prechilling treatment	Increase	Yin et al. (2008)
Panax quinquefolius (Araliaceae)	Roots	Used to boost energy, lower BP and cholesterol levels, reduce stress, promote relaxation, treat diabetes, manage sexual dysfunction in men, etc.	Saponins	Ginsenoside	Heat stress	Increase	Jochum et al. 2007
Beta vulgaris (Amaranthaceae)	Root	Improve blood flow, lower blood pressure, etc.	Flavonoid	Anthocyanin	50 °C temperature	Decreases	Thimmaraju et al. (2003)
Perilla frutescens (Lamiaceae)	Cultured cells	Used for cure of asthma and cough, etc.	Flavonoid	Anthocyanins	Heat stress	Decrease	Zhong and Yoshida (1993)
Chrysanthemum (Asteraceae)	Whole plant	Used to treat chest pain (angina), high blood pressure, type 2 diabetes, fever, cold, headache, dizziness, swelling, etc.	Phenols	Anthocyanins	High temperature	Decrease	Shibata et al. (1988)

3.2.2 Drought Stress

Global climate change is increasing the frequency of severe drought conditions. Drought stress conditions affect adversely growth, development, and the overall physiological and biochemical status of plants (Embiale et al. 2016; Getnet et al. 2015; Husen 2010; Husen et al. 2014). Similarly, drought stress affects the production of secondary metabolite contents (Caser et al. 2019; Podda et al. 2019). Plants accumulate more secondary metabolites in water-stressed conditions and a decrease in biomass production (Kleinwächter and Selmar 2014). A study was performed on *Adonis amurensis* and *A. pseudoamurensis* to check the effect of drought on secondary metabolites and changes in growth and physiology. In the early stage, both the perennial plants showed an adaptive change to drought stress and a significant increase in flavonoids and total phenols content in response to drought stress (Gao et al. 2020). In another study, García-Caparrós et al. (2019) observed the impact of drought stress on the essential oil content of *Lavandula latifolia*, *Mentha piperita*, *Salvia sclarea*, *S. lavandulifolia*, *Thymus mastichina*, and *T. capitatus*. The essential oil content of *Lavandula latifolia* and *Salvia sclarea* plants showed a reduction under drought stress conditions. Chavoushi et al. (2020) examined *Carthamus tinctorius* and found that secondary metabolites (flavonoids, anthocyanin, phenol, and phenylalanine ammonia-lyase activity) increased under drought stress conditions. Drought stress also increased the concentration of monoterpene in *Salvia officinalis* (Nowak et al. 2010), and its concentration was more than the reduction in biomass as compared to control plants. A similar type of result (increases in monoterpenes concentration and biomass reduction) was observed in another experiment conducted on *Petroselinum crispum* under drought stress condition (Petropoulos et al. 2008). An increase in secondary metabolites content of total anthocyanins, phenolics, and total flavonoids was also observed in *Labisia pumila* when it was kept under high water stress conditions (50% evapotranspiration) (Jaafar et al. 2012). Further details associated with medicinal plants and their responses to drought stress are given in Table 19.3.

3.2.3 Salinity Stress

Salinity stress is another important global problem that negatively affects plant growth and production (Husen et al. 2016, 2018, 2019; Hussein et al. 2017; Isayenkov and Maathuis 2019). It also affects the accumulation of secondary metabolites in plant tissues (Arshi et al. 2002; Cui et al. 2019; Hakeem et al. 2013; Ibrahim et al. 2019; Wang et al. 2015). In *Gossypium hirsutum*, salinity stress enhanced the secondary metabolism as indicated by the increased accumulation of gossypol, flavonoids, and tannin (Wang et al. 2015). Germination of *Prosopis strombulifera* seed was severely affected by increased salinity (Sosa et al. 2005). Further, seed germination of some other medicinal plants decreases under salt stress, as in *Ocimum basilicum* (Miceli et al. 2003), *Petroselinum hortense* (Ramin 2005), and *Thymus maroccanus* (Belaqziz et al. 2009). Seedling growth is also negatively affected by

Table 19.3 Medicinal plants and their response under drought stress

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Hordeum vulgare (Poaceae)	Leaves	Used in the treatment of dyspepsia caused by cereals, infantile lacto-dyspepsia, regurgitation of milk and breast distension	Terpenes	Carotenoids	Severe drought condition	Decreases	Ghorbanpour et al. (2020)
Salvia dolomítica (Lamiaceae)	Leaves	Used in seizure, ulcers, gout, rheumatism, tremor, paralysis, and hyperglycemia	Phenols and total flavonoids	Sesquiterpene and terpenoids	Irrigation	Increases	Caser et al. (2019)
Achillea pachycephala (Asteraceae)	Leaves	Treatment of wounds, bleedings, headache, inflammation, pains, spasmodic diseases, flatulence, and dyspepsia	Flavonoids and phenolic compound	Luteolin and apigenin, chlorogenic acid, and caffeic acid	Irrigation	Increases	Gharibi et al. (2019)
Dracocephalum moldavica (Lamiaceae)	Shoot	Antioxidation and antiaging	Phenolic acids, ellagitannins, and flavonoids	Rosmarinic acid, chlorogenic acid, p-coumaric acid, caffeic acid, ferulic acid, apigenin, acacetin 7-O-glycoside, gentisic acid, apigenin-7-O-glycoside, luteolin-7-O-glycoside, and quercetin	Irrigation	Increase	Kamalizadeh et al. (2019)

(continued)

Table 19.3 (continued)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Datura stramonium (Solanaceae)	Whole plant	Used as analgesic, anthelmintic, anti-inflammatory, to treat toothache, dandruff, and hair fall	Alkaloids	Atropine and scopolamine	Severe water deficit stress	Increases	Alinejad et al. (2020)
Mentha piperita (Lamiaceae)	Leaves	To treat flatulence, menstrual pains, depression-related anxiety, muscle, and nerve pain	(i) Total phenol, flavonoid, and saponin (ii) Tannins, terpenoids, and alkaloids	– –	Drought	Decreases Increases	Haifa et al. (2019)
Catharanthus roseus (Apocynaceae)	Leaves	Used for relieving muscle pain, depression of CNS, also for applying to wasp stings and to heal wounds	(i) Total phenol, flavonoid, and saponin (ii) Tannins, terpenoids, and alkaloids	– –	Drought	Decreases Increases	Haifa et al. (2019)
Thymus kotschyanus (Lamiaceae)	Seedling	Used as antibacterial, antifungal, antiviral, antihelminthic, antioxidative, antispasmodic, and sedative	Phenols and monoterpenoids	Thymol, carvacrol, linalool, p-cymene, and γ-terpinene	Water stress	Increases	Mohammadi et al. (2018)
Scutellaria baicalensis (Lamiaceae)	Whole plant	Used in epilepsy, hepatitis, infections, and cancer	Phenols	Baicalin	Severe drought condition	Increases	Cheng et al. (2018)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Salvia sinaloensis (Lamiaceae)	Leaves	Digestive problems	Phenols and total flavonoids	–	Irrigation	Increase	Caser et al. (2018)
Ocimum basilicum (Lamiaceae)	Shoot	Used as antioxidant antimicrobial, antiviral, cytoprotective, anticonvulsant, hypoglycemic, hypolipidemic, hepatoprotective, renoprotective, neuroprotective, spermicidal, dermatologic, and insecticidal	Total phenols	–	Irrigation	Increases	Pirbalouti et al. (2017)
Stellaria dichotoma (Caryophyllaceae)	Roots	Used in fever and malaria, night sweats, and infantile malnutrition	Total flavonoids	–	(i) Moderate drought stress (ii) Severe drought stress	(i) Increases (ii) Decreases	Zhang et al. (2017)
Melissa officinalis (Lamiaceae)	Shoot	Used in gastrointestinal disorders and as sedative	Phenolic compounds	Hydroxycinnamic acid	Irrigation	Decreases	Szabo et al. (2017)
	Leaves		Total flavonoids and phenolic compound	Rosmarinic acid			Radacsi et al. (2016)

(continued)

Table 19.3 (continued)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Mikania glomerata (Asteraceae)	Leaves	For respiratory illness	Phenolic acids	Chlorogenic acid and dicaffeoylquinic acid	Water deficiency	Increases	Almeida et al. (2016)
Cuminum cyminum (Apiaceae)	Leaves	For chronic diarrhea and dyspepsia, acute gastritis, diabetes, and cancer	Flavonoids and phenolics	–	150 mm irrigation regime	Increases	Alinian et al. (2016)
			Flavonoid	Anthocyanins	200 mm irrigation regime	Increases	
	Seeds		Flavonoids and phenolics	–	200 mm irrigation regime	Increases	
Helichrysum petiolare (Asteraceae)	Leaves	Used for respiratory infections, diabetes, fever, headache, heart problem, high blood pressure, pain, and reproductive problems	Flavonoids and polyphenol	Anthocyanins	Moderate drought stress	Increases	Caser et al. (2016)
Anadenanthera colubrina (Fabaceae)	Bark	Used for respiratory problems and inflammation	Phenolic compounds	–	Precipitation	No effect	Araujo et al. (2015)
Gethyllis multifolia (Amaryllidaceae)	Leaves	For wound healing	Tannin, flavonoids, phenolics, saponins, and terpenoid	Flavonol and flavanone	Drought stress	Present	Daniels et al. (2015)
	Roots		Polyphenol			Increases	

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Hypericum brasiliense (Hypericaceae)	Whole plant	Used as astringent, antimicrobial, wound-healing, anticancer, anti-inflammatory, antispasmodic, and antidepressant	Phenols and pentacyclic triterpenoid	Rutin, quercetin and betulinic acid	Severe drought condition	Increases	Verma and Shukla (2015)
Artemisia spp. (Asteraceae)	Whole plant	Used in fever, liver disease, depression, muscle pain, and memory loss	Sesquiterpene lactone	Artemisinin	Severe drought condition	Increases	Verma and Shukla (2015)
Achillea millefolium (Asteraceae)	Leaves	For treating wounds, stopping the flow of blood, treating colds, fevers, kidney diseases, and menstrual pain	Total phenolic and total flavonoid	–	Moderate drought stress	Increases	Gharibi et al. (2015)
Astragalus propinquus (Fabaceae)	Roots	Used for immune-boosting, antiaging, and anti-inflammatory, used to treat fatigue, allergies, heart disease, and diabetes	Flavonoids	Calicosin-7-O-b-D-glycoside, ononine, calicosin, and formononetine	Drought stress	Increases	Jia et al. (2015)

(continued)

Table 19.3 (continued)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Petroselinum crispum (Apiaceae)	Shoots	Used as a diuretic, antimicrobial, antiseptic, antispasmodic, and for kidney stone	Flavones	Malonylapiin, diosmetin apiosylmglucoside, and diosmetin malonyl-apiosyl-glucoside	Moderate drought stress	Decreases	Kleinwächter et al. (2015)
			Essential oil			Increases	
Hypericum polyanthemum (Hypericaceae)	Leaves and reproductive parts	Used as antidepressant, antiviral, antinociceptive, antimicrobial, antipyretic, and anti-inflammatory	Phenolic compounds	Uliginosin B (phloroglucinol), 6-isobutyryl-5,7-dimethoxy-2,2-dimethylbenzopyran and 5-hydroxy-6-isobutyryl-7--methoxy-2,2-dimethylbenzopyran (benzopyran) and total phenols	Drought stress	Increases	Nunes et al. (2014)
Eucalyptus globulus (Myrtaceae)	Leaves	Used as expectorant, febrifuge, tonic, astringent, antiseptic, hemostatic, and vermifugal	Total phenols	–	Moderate or severe drought stress	Decreases	McKiernan et al. (2014)
			All plant SMs	Total condensed tannins and two floroglucinols and terpenes		No effect	
Labisia pumila (Primulaceae)	–	Used for cardiovascular protection and osteoporosis	Phenols flavonoids	Total phenolics and anthocyanins	Severe drought condition	Increased	Jaafar et al. (2012)
Thymus vulgaris (Lamiaceae)	Shoot	Used for diarrhea, stomach ache, arthritis, and sore throat	Phenolic compounds	–	Long-term drought stress	Decreases	Khosh-Khui et al. (2012)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Trachyspermum ammi (Apiaceae)	Leaves	Used as atonic dyspepsia, diarrhea, fominal tumors, abdominal pains, piles, and bronchial problems, asthma, antispasmodic, and carminative	Phenols	Total phenolics	Severe drought condition	Increases	Azhar et al. (2011)
Lippia sidoides (Verbenaceae)	Leaves	Used for cough, bronchitis, indigestion, liver, hypertension, dysentery, worms, and skin diseases	Total flavonoids and essential oil	–	Water stress	Decreases	Alvarenga et al. (2011)
Salvia miltiorrhiza (Lamiaceae)	Root	Used for coronary heart diseases and cerebrovascular diseases	Polyphenol	Rosmarinic acid	Drought stress	Decreases	Liu et al. (2011)
			Phenolic acid	Salvianolic acid B		Increases	
Nepeta cataria (Lamiaceae)	Whole plant	Used to treat intestinal cramps, indigestion and to induce menstruation	Essential oil	–	Drought stress	Increases	Manukyan (2011)
			Polyphenols	Caffeic acid, rosmarinic acid, and p-coumaric acid		Decreases	
Calendula officinalis (Asteraceae)	Leaves	Used to heal wounds, burns, and rashes	Flavonoids	–	Water deficiency	Decreases	Pacheco et al. (2011)

(continued)

Table 19.3 (continued)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Salvia officinalis (Lamiaceae)	Whole plant	Used for seizure, ulcers, rheumatism, tremor, and paralysis	Terpenes	Monoterpenes	Severe drought condition	Increases	Nowak et al. (2010)
Petroselinum Crispum (Apiaceae)	Leaves	Plague and malaria	Terpenes	Monoterpenes	Severe drought condition	Increases	Petropoulos et al. (2008)
Rehmannia glutinosa (Orobanchaceae)	Roots	Used for diabetes, metabolic syndrome, obesity, kidney disease, chronic obstructive pulmonary disease (COPD), "tired blood" (anemia), fever, weakened bones (osteoporosis), rheumatoid arthritis (RA), and allergies	Phenolic compounds	Resveratrol, gentisic acid, catechin, p-hydroxybenzoic acid, chlorogenic acid, caffeic acid, syringic acid, coumaric acid, ferulic acid, hesperidin, narigin, salicylic acid, hyricetin, quercetin, t-cinnamic acid, and naringenin	Water deficiency	Increases	Chung et al. (2006)
Camellia sinensis (Theaceae)	Leaves	Used for cancer prevention, to lower cholesterol, and to prevent/delay Parkinson's disease, etc.	Phenols and polyphenols	Flavan-3-ols (epicatechin, epigallocatechin-3-gallate) and their quinones	Water stress	Increases	Hernández et al. (2006)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Drought stress	Concentration variation	Key references
Myracrodruon urundeuva (Anacardiaceae or Fabaceae)	Leaves	Used for kidney problems, hemoptysis, metrorrhagia, for postnatal vaginal washes, stomach ulcers, and colitis	Tannins	–	Precipitation	No effect	Monteiro et al. (2006)
	Bark					Negative correlation	
Hypericum brasiliense (Hypericaceae)	Roots and shoot	Used as anti-inflammatory, antibacterial, and antidepressant	Phenolic compound and betulinic acid	Isouliginosin B; 1,5-dihydroxyxanthone, quercetin, and rutin	Water stress	Increases	Abreu and Mazzafera (2005)
Crataegus laevigata (Rosaceae)	Leaves	Used for congestive heart failure, chest pain, irregular heartbeat, low BP, high BP, and high cholesterol	Polyphenolic compounds	Chlorogenic acid, catechin, and epicatechin	Water deficiency	Increases	Kirakosyan et al. (2004)
			Flavonoid	Vitexin, hyperoside, and rutin		Increases	
				Acetylvitexin-2″-O-rhamnoside		Decreases	
				Vitexin-2″-O-rhamnosid and quercetin		No effect	

salinity, as in basil (Ramin 2005), chamomile, and marjoram (Ali et al. 2007) and *Thymus maroccanus* (Belaqziz et al. 2009). There are inconsistent reports on the effect of salt stress on essential oil content. In some studies, a negative effect of salt stress in essential oil yield is noticed, as in *Trachyspermum ammi* (Ashraf and Orooj 2006), *Mentha piperita* (Tabatabaie and Nazari 2007), *Thymus maroccanus* (Belaqziz et al. 2009), and basil (Said-Al Ahi et al. 2010). In these cases, oil content decreased under salt stress conditions. Nonetheless, in *Matricaria recutita*, the main chemical constituents of essential oil such as α-bisabololoxide B, α-bisabolonoxide A, chamazulene, and α-bisabolol oxide A increased under salt stress conditions (Baghalian et al. 2008). In *Origanum vulgare,* the main chemical constituents of essential oil carvacrol were found to decrease in salt stress, whereas p-cymene and γ-terpinene content increase under normal condition (Said-Al Ahl and Hussein 2010). De Castro et al. (2020) observed the effect of salinity on essential oil profile, growth, and morphology in *Lippia alba* and found that increase in linalool and decrease in eucalyptol levels at higher salt stress conditions. Further details associated with medicinal plants and their response to salinity stress are given in Table 19.4.

3.2.4 Light Intensity

Light intensity determines the concentration of plant secondary metabolites (Jurić et al. 2020; Pedroso et al. 2017; Tavakoli et al. 2020; Thoma et al. 2020). Light may suppress or stimulate the production of various secondary metabolites depending on its quantity (intensity) or duration (photoperiod). Production of flavonoid, phenolic compound, and terpenoids in root and shoots of *Hordeum vulgare* got stimulated in the presence of full sunlight as well as in monochromatic light, that is, blue light (Klem et al. 2019). Similarly, the concentration of scutellarin (phenols) in leaves of *Erigeron breviscapus* increased in full sunlight (Zhou et al. 2016). Li et al. (2018) have also reported that the alkaloids concentration in root, shoots, and essential oils in leaves of *Mahonia breviracema* increases in the presence of full sunlight. This study also found that hexadecanoic acid in leaves increases when *Mahonia bodinieri* was grown under 50% stress of light availability. Also, Kong et al. (2016) examined some other parts of *Mahonia bodinieri* and concluded that under 30–50% stress, the alkaloid content get enhanced, and in the case of *Flourensia cernua*, the alkaloids content of leaves such as sabinene, β-pinene, borneol, bornyl acetate, and Z-jasmone was increased when half of the regular sunlight available for plants was provided, that is, in 50% light stress. Further details associated with medicinal plants and their response to light are given in Table 19.5.

3.2.5 Heavy Metal Stress

The secondary metabolites production in plants also gets affected by the presence of heavy metals (Iqbal et al. 2015; Jabeen et al. 2009). Various researchers have claimed this, such as Manquian-Cerda et al. (2016) reported that in the presence of

Table 19.4 Medicinal plants and their response under salinity stress

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Salinity	Concentration variation	Key references
Salvia officinalis L. (Lamiaceae)	Seeds	Used for secondary memory improvement, improve alertness, neurotoxic	Niacin, nicotinamide, and flavonoid glycosides	α-thujone, α-pinene, camphor, camphene, β-thujone, and 1,8-Cineole	Salt concentration increases	Essential oil composition get affected	Kulak et al. (2020)
Thymus maroccanus (Lamiaceae)	Whole plant	Used as antioxidant, antimicrobial, antitumor, and cytotoxic	Essential oil	Carvacrol, p-cymene, α-pinene, α-terpineol, and p-cymene	Salt stress	Decreases	Belaqziz et al. (2009)
Thymus vulgaris (Lamiaceae)	Shoot and leaves	Used for gastroenteric and bronchopulmonary disorders	Phenolic acids	Syringic, gallic, vanillic, caffeic, chlorogenic, rosmarinic, cinnamic, and trans-2-hydroxycinnamic acids	Salinity increases	Increase	Bistgani et al. (2019)
					Severe salinity	Not found	
Thymus daenensis (Lamiaceae)	Shoot and leaves	Used as anti-inflammatory, antimicrobial, and antioxidant	Flavonoid	Quercitrin, apigenin, luteolin, naringenin, and rutin	Salinity increases	Increase	Bistgani et al. (2019)
Mentha piperita L. (Lamiaceae)	Leaves	Used as carminative, spasmolytic, antitumor, antidiabetes, and antinociceptive	Flavonoids and phenols	Hesperidin, rosmarinic acid, didymin, buddleoside, and diosmin	Less salinity	SMs concentration increased	Çoban and Göktürk Baydar (2016)
Trigonella foenum graecum L. (Fabaceae)	Leaves	Used as aphrodisiac, carminative, astringent, demulcent, suppurative, aperients, diuretic, emollient, anti-inflammatory, etc.	Total phenolic content and flavonoids	Phenols and diosgenin	Salinity increases	Increases	Baatour et al. (2018)

(continued)

Table 19.4 (continued)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Salinity	Concentration variation	Key references
Catharanthus roseus (Apocynaceae)	Leaves	Used to treat cancer	Vinca alkaloid	(i) Vinblastine (ii) Vincristine	(i) Salinity increases (ii) Salinity increases	(i) Increases (ii) Decreases	Fatima et al. (2015)
Stevia rebaudiana (Asteraceae)	Leaves (dried)	Used as antiproliferative/ antimutagenic/antioxidant and natural sweetener	Flavonoids	Stevioside and proline	Salinity increases	Increase	Zeng et al. (2013)
Foeniculum vulgare Mill. (Apiaceae)	Seed	Used as diaphoretic, diuretic, carminative, expectorant, febrifuge, stomachic, stimulant, appetizer, cardiac stimulant, and vermifuge	Phenols, monoterpenoid glycosides	Furocoumarins imperatorin, psoralen, bergapten, xanthotoxin, isopimpinellin, quercetin, and kaempferol	Salinity increases	SMs concentration decreased	Nassar et al. (2010); Nourimand et al. (2012)
Plantago ovate (Plantaginaceae)	Root and shoot	Used as a emollient, demulcent, and a laxative	Flavonoids	Flavonoids saponins and proline	Salinity increases	Increase	Haghighi et al. (2012)
Capsicum sp. (*Solanaceae*)	Fruit	Used for rheumatoid arthritis, osteoarthritis, and other painful conditions	Phenolic compound	Capsaicin	Salinity increases	Increase	Arrowsmith et al. (2012)
Artemisia annua L. (Asteraceae)	Leaves	Used as antimalarial, anti-inflammatory, and anticancer	Tarpenoids and flavonoids	Artemisinin, arteanuin, artemether, arteether, artemetin, casticin, chrysoplenetin, and cirsilineol	Less salinity	SMs concentration increased	Weathers and Towler (2012); Aftab et al. (2010)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Salinity	Concentration variation	Key references
Origanum vulgare (Lamiaceae)	Leaves	Used as antiseptic, antispasmodic, carminative, cholagogue, diaphoretic, emmenagogue, expectorant, stimulant, and stomachic	Essential oil	Carvacrol, p-cymene, and γ-terpinene	Salt stress	Decreases	Said-Al Ahl and Hussein (2010)
Satureja hortensis (Lamiaceae)	Aerial parts	Used as antirheumatic, antiseptic, aromatic, carminative, digestive, expectorant, stings, and stomachic	Phenolic compound Terpinene	Carvacrol α-terpinene	Salt concentration increases Salt concentration increases	Increases Decreases	Najafi and Khavari-Nejad (2010)
Lycopersicon esculentum (*Solanaceae*)	Leaf	Used as first-aid treatment for burns/scalds and sunburn	–	Sorbitol and jasmonic acid	Salinity increases	Decreases	Tari et al. (2010)
Origanum majorana (Lamiaceae)	Shoots	Used for digestive problems like nausea, bloating, loss of appetite, intestinal spasm, diarrhea, and flatulence	Monoterpenes/ essential oils	(i) Oil contents (ii) *Trans*-sabinene Hydrate and γ-Terpinene (iii) *cis*-Sabinene Hydrate and linalyl acetate	(i) Salinity increases (ii) Salinity increases (iii) Salinity increases	(i) Decreases (ii) Decreases (iii) Increase	Baatour et al. (2010)
Mentha pulegium (Lamiaceae)	Aerial parts	Used as antiseptic, antispasmodic, carminative, diaphoretic, emmenagogue, sedative, and stimulant	Phenolic acid	Caffeic acid and rosmarinic acid	Salt stress	Increases	Queslati et al. (2010)

(continued)

Table 19.4 (continued)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Salinity	Concentration variation	Key references
Achillea fragratissima (Compositae)	Whole plant	Used for treatment of wounds, bleedings, headache, inflammation, pains, spasmodic diseases, flatulence, and dyspepsia	Phenolics alkaloid	Tannin	Salinity increases	Increase	Abd EL-Azim and Ahmed (2009)
Ricinus communis (Euphorbiaceae)	Shoot	Used for abdominal disorders, arthritis, backache, muscle aches, bilharziasis, chronic backache and sciatica, chronic headache, constipation, expulsion of placenta, gallbladder pain, period pain, menstrual cramps, rheumatism, sleeplessness, and insomnia	Alkaloids	Recinine alkaloids	Salinity increases	Increase	Ali et al. (2008)
Coriandrum sativum (Apiaceae)	Leaf	Used as an analgesic, carminative, digestive, antirheumatic, and antispasmodic agent	Monoterpenes/ essential oils	(i) Oil contents (ii) Octanal, Borneol and (*E*)-2-Nonenal (iii) α-Pinene and (*Z*)-Myroxide	(i) High salinity (ii) Salinity increases (iii) Salinity increases	(i) Decreases (ii) Increase (iii) Decreases	Neffati and Marzouk (2008)
Matricaria recutita Asteraceae	Flower	Use against gastrointestinal problems; and to treat irritation of the skin	Essential oil	α-bisabolol oxide	Salt stress	Increases	Baghalian et al. (2008)
Solanum nigrum L. (Solanaceae)	Fruits, leaves, roots	Used in chronic enlargement of liver, cough, skin disease, rheumatism, gout, and eye diseases	Steroidal alkaloid	Solasodine	Salinity increased	SMs concentration increased	Bhat et al. (2008)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Salinity	Concentration variation	Key references
Aloysia citrodora (Verbenaceae)	Shoot	Used as digestive disorders such as flatulence, indigestion, and acidity	Essential oil	Geranial and neral	Salinity increases	Decreases	Tabatabaie and Nazari (2007)
Trachyspermum ammi (Apiaceae)	Whole plant	Used as atonic dyspepsia, diarrhea, abdominal tumors, abdominal pains, piles, and bronchial problems, asthma, antispasmodic, and carminative	Essential oil	Cadinene, longifolene, thymol, and carvacrol	Salt stress	Decreases	Ashraf and Orooj (2006)
Matricaria chamomilla (Asteraceae)	Leaves	Used as spasmolytic, anti-inflammatory, and antibiotic	Flavonoids	Herniarin and umbelliferone	Salinity increased	SMs concentration decreased by 40%	Eliasova et al. (2004)

Table 19.5 Medicinal plants and their response under different light intensity

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Light	Concentration variation	Key references
Mahonia breviracema (Berberidaceae)	Root and shoot	Used as diuretic and demulcent	Alkaloids	Alkaloids	Full sunlight	Increases	Li et al. (2018)
Mahonia breviracema (Berberidaceae)	Leaf	Used as diuretic and demulcent	–	Essential oil	Full sunlight	Increases	Li et al. (2018)
Mahonia bodinieri (Berberidaceae)	Leaf	Used orally in the treatment enteric infections, especially bacterial dysentery	Hexadecanoic acid		50% sunlight	Increases	Li et al. (2018)
Mahonia bodinieri (Berberidaceae)	Whole plant	Used orally in the treatment enteric infections, especially bacterial dysentery	Alkaloids	Alkaloids	30% and 50% sunlight	Increases	Kong et al. (2016)
Flourensia cernua (Asteraceae)	Leaf	Used to gastrointestinal conditions and respiratory disorders	Alkaloids	Sabinene, β-pinene, borneol, bornyl acetate, and Z-jasmone	50% shade	Increases	Estell et al. (2016)
Erigeron breviscapus (Asteraceae)	Leaf	Used for cardiovascular disease, cerebral blockages and hemorrhage, and digestive disorders	Phenols	Scutellarin	Full sunlight	Increases	Zhou et al. (2016)
Pinus contorta (Pinaceae)	Seedling	Used as antiseptic, diuretic, rubefacient, vermifuge and vulnerary and for treatment of kidney and bladder diseases and rheumatic affections	Phenols	Pelargonidin	Short day of light	Increases	Camm et al. (1993)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Light	Concentration variation	Key references
Ipomoea batatas (Convolvulaceae)	Leaves	Used for the treatment of diabetes, hypertension, dysentery, constipation, fatigue, arthritis, rheumatoid diseases, hydrocephaly, meningitis, kidney ailments	Phenols	Catechins	Long day of light	Increases	Carvalho et al. (2010)
Ipomoea batatas (Convolvulaceae)	Leaves	Used for the treatment of diabetes, hypertension, dysentery, constipation, fatigue, arthritis, rheumatoid diseases, hydrocephaly, meningitis, kidney ailments	Phenols	Hydroxybenzoic acid	Long day of light	Increases	Carvalho et al. (2010)
Vaccinium myrtillus (Ericaceae)	–	Used for treatment of gastrointestinal tract disorders and diabetes, cardiovascular conditions, diabetes, as vision aids, diarrhea	Phenols	Chlorogenic acid	Long day of light	Increases	Uleberg et al. (2012)
Cyanea acuminate (Campanulaceae)	Leaves	Used for treatments for psoriasis, liver and stomach ailments, and common colds, leukemia	Alkaloids	Camptothecin	27% Sunlight	Increases	Liu et al. (1997)
Cyanea acuminate (Campanulaceae)	Roots	Used for treatments for psoriasis, liver and stomach ailments, and common colds, leukemia	Alkaloids	Camptothecin	27% Sunlight	Decreases	Liu et al. (1997)
Centella asiatica (Apiaceae)	Leaves	Used to repair nervous tissue due to spinal injury, neuromuscular disorders, and to increase general brain function and memory	Phenols	Asiatic acid	70% Shade	Increases	Devkota et al. (2010)
Centella asiatica (Apiaceae)	Leaves	Used to repair nervous tissue due to spinal injury, neuromuscular disorders, and to increase general brain function and memory	Phenols	Asiaticoside	Full sunlight	Increases	Devkota et al. (2010)

cadmium, the concentration of chlorogenic acid increases in *Vaccinium corymbosum* plantlets, while Sá et al. (2015) reported in their study that the production of carvone (essential oils) in *Mentha crispa* gets stimulated in the presence of lead. De and De (2011) investigated the impact of the treatment of chromium, nickel, cadmium, and copper on *Trigonella foenum-graecum* and found that the production of steroids, that is, diosgenin, gets inhibited by chromium and nickel, whereas cadmium and copper stimulated its production. Effect of chromium on the concentration of secondary metabolites of *Phyllanthus amarus* was studied by Rai and Mehrotra (2008). They have concluded that the concentration of phyllanthin and hypophyllanthin increases under chromium exposure. Sinha and Saxena (2006) found that in the presence of iron, the production of bacoside-A in roots and leaves of *Bacopa monnieri* increases, whereas the production of cysteine in roots increases and there is no effect in the production of cysteine in leaves. Similarly, in the presence of cadmium, there is no effect on the concentration of umbelliferone in *Matricaria chamomilla* (Kováčik et al. 2006). Narula et al. (2005) studied the plant culture of *Dioscorea bulbifera* and found that in the presence of copper, the production of diosgenin increases. The production of Eugenol (in the whole plant) and proline (in leaves) of *Ocimum tenuiflorum* increases in the presence of chromium (Rai et al. 2004). Murch et al. (2003) reported that the production of pseudohypericin and hypericin decreases in the presence of nickel in *Hypericum perforatum*, whereas the production of hyperforin gets completely inhibited under similar conditions. Further details associated with medicinal plants and their response to heavy metals are given in Table 19.6.

4 Conclusion

Human beings depend on plants for fulfilling their various needs. Medicinal/herbal plants are a good source of secondary metabolites used in pharmaceutical industries for drug synthesis and formulation. Concentration and content of secondary metabolites depend (increase/decrease) on harvest time, seasons, soil type, nutrient supply, altitude, geographical location, stage of plant (juvenile/mature), and genotypes or cultivars. Their production is under biotic (by the attack of herbivores, pets, and pathogens) and abiotic (such as temperature variation, drought, salinity, light intensity, and heavy metals) stresses. Secondary metabolites have a significant role in the tolerance and adaptation of plants to adverse environmental conditions. However, their synthesis mechanism is not fully examined, and further investigation is required to obtain the maximum production of secondary metabolites from important medicinal plants under normal as well as adverse environmental conditions.

Table 19.6 Medicinal plants and their response under heavy metals stress

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Heavy metals	Concentration variation	Key references
Vaccinium corymbosum (Ericaceae)	Plantlet	For treatment of wounds, skin diseases, and used to reduce pimples	Phenolic compound	Chlorogenic acid	Presence of cadmium	Increases	Manquian-Cerda et al. (2016)
Mentha crispa (Lamiaceae)	Leaves	Used for digestive disorders including gas, indigestion, nausea, diarrhea, upper gastrointestinal tract spasms, irritable bowel syndrome, bile duct and gallbladder swelling (inflammation), and gallstones	Essential oils	Carvone	Presence of lead	Increases	Sá et al. (2015)
Trigonella foenum-graecum (Fabaaceae)	Whole plant	Used as antibacterial, a gastric stimulant, an antidiabetic, and a galactagogue and to combat anorexia	Steroids	Diosgenin	Presence of cadmium and copper	Increases	De and De (2011)
Trigonella foenum-graecum (Fabaaceae)	Whole plant	Used as antibacterial, a gastric stimulant, an antidiabetic, and a galactagogue, and to combat anorexia	Steroids	Diosgenin	Presence of chromium and nickel	Inhibits the production	De and De (2011)
Phyllanthus amarus (Phyllanthaceae)	Whole plant	Used in the problems of stomach, genitourinary system, liver, kidney, and spleen	–	Phyllanthin, Hypophyllanthin	Presence of chromium	Increases	Rai and Mehrotra (2008)
Bacopa monnieri (Plantaginaceae)	Root and leaves	Contains powerful antioxidants, reduce inflammation, blood pressure, attention deficit hyperactivity disorder symptoms, anxiety and stress, and boost brain function	Saponins	Bacoside-A	Presence of iron	Increases	Sinha and Saxena (2006)

(continued)

Table 19.6 (continued)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Heavy metals	Concentration variation	Key references
Bacopa monnieri (Plantaginaceae)	Roots	Contains powerful antioxidants, reduce inflammation, blood pressure, attention-deficit hyperactivity disorder symptoms, anxiety and stress, and boost brain function	–	Cysteine	Presence of iron	Increases	Sinha and Saxena (2006)
Bacopa monnieri (Plantaginaceae)	Leaves	Contains powerful antioxidants, reduce inflammation, blood pressure, attention deficit hyperactivity disorder symptoms, anxiety and stress, and boost brain function	–	Cysteine	Presence of iron	No effect	Sinha and Saxena (2006)
Matricaria chamomilla (Asteraceae)	Whole plant	For treatment of sore stomach, skin care, irritable bowel syndrome, and as a gentle sleep aid	Phenylpropanoids	Umbelliferone	Presence of cadmium	No effect	Kováčik et al. (2006)
Dioscorea bulbifera (Dioscoreaceae)	Plant culture	For the treatment of piles, dysentery, syphilis, ulcers, cough, leprosy, diabetes, asthma, and cancer	Steroids	Diosgenin	Presence of copper	Increases	Narula et al. (2005)
Phyllanthus amarus (Phyllanthaceae)	Whole plant	Used in the problems of stomach, genitourinary system, liver, kidney, and spleen	–	Phyllanthin, hypophyllanthin	Cadmium stress	Increases	Rai et al. (2005)
Ocimum tenuiflorum (Lamiaceae)	Leaves	For the treatment of bronchitis, malaria, diarrhea, dysentery, skin disease, arthritis, eye diseases, and insect bites	–	Proline	Chromium treated	Increases	Rai et al. (2004)

Medicinal plant (family)	Plant part	Medicinal uses	Major class of secondary metabolite	Name of metabolite	Heavy metals	Concentration variation	Key references
Ocimum tenuiflorum (Lamiaceae)	Whole plant	For the treatment of bronchitis, malaria, diarrhea, dysentery, skin disease, arthritis, eye diseases, and insect bites	Phenol	Eugenol	Chromium stress	Increases	Rai et al. (2004)
Hypericum perforatum (Hypericaceae)	Whole plant	For the treatment of several disorders, such as minor burns, anxiety, and mild-to-moderate depression	Terpenes	Hyperforin	Presence of nickel	Inhibits the production	Murch et al. (2003)
Hypericum perforatum (Hypericaceae)	Whole plant	For the treatment of several disorders, such as minor burns, anxiety, and mild-to-moderate depression	Terpenes	Pseudohypericin, hypericin	Presence of nickel	Decreases	Murch et al. (2003)

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Chapter 20
Progresses and Major Research Challenges Under Changing Environmental Conditions

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Contents

Abbreviations

CFCs	Chlorofluorocarbons
CO_2	Carbon dioxide
COVID-19	Coronavirus disease 2019
DDT	Dichlorodiphenyltrichloroethane
EH	Environmental Health
MEA	Multilateral environmental agreements
SARS	Severe acute respiratory syndrome
UV	Ultraviolet
WHO	World Health Organization

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1 Introduction

The environmental variations include various things including human health, natural shelter, and social cohesion. It is a system threatened by changing and successive events such as strong and persistent storms and rising sea levels. Some regions also suffer from severe flooding, while others suffer from severe droughts. Besides, species extinction occurs at unprecedented rates (Warner et al. 2010). Safe drinking water has also become increasingly restricted, hindering economic activity and land degradation, as well as putting the lives of millions of people at risk. It is worth noting that the United Nations mentioned in 2019 report on the water that around 2.1 billion people around the world lack access to safe drinking water services. Defining concepts is vital for any researcher to determine the framework from which he works or to determine the base upon which he is based, as the concepts are only the product of many experiences and organized efforts by researchers (Organization 2014). "Environment" is a term or a term commonly used in scientific circles at present, as it is commonly used by the general public, and in light of that generality, we find several definitions that differ according to the human relationship with the environment (Mebratu 1998).

Environment is a term used to denote the surrounding conditions that influence growth and development. It is also used to express natural conditions such as air, water, and the land in which a person lives, but in terms of the practical point of view, it is the place that surrounds a person and affects his feelings, morals, and thoughts. In addition to the word environment, also means ecology. The word ecology from the Greek term "Oikos" which means household, or home, of the living (biological) and non-living (chemical and physical) factors that result in relationships that may be positive or negative or both; specifically, it is a science that studies the natural relations that exist between living organisms and the environment in which they live, as well as examines the mutual relationship between them and the effect of some of them on others (Krull et al. 2003). Accordingly, the environment is that space in which humans practice various activities of their lives and includes within this framework all living things, including animals and plants, with which humans coexist and together form a continuum between them. The term environment indicates all the elements that a human to be satisfied with all their various dimensions (Krull et al. 2003). Therefore, the purpose of the ecosystem is to increase the advantages of life, to develop the quality of the individual, and to achieve a better life.

These goals that a human seeks in the environment are to integrate all the different elements and components of the environment in a joint and equal manner in a form of balance for the comprehensive and integrated ecosystem (Tilbury 1995). Environmental studies are not only a mixture of geographical, biological, historical, and social studies but also a factor in advancing the direction and behavior of the mind to change the interest or benefit of the environment in general and comprehensively. Environmental protection is one of the values of a society that legal systems generally seek to emphasize, and the authorities must accomplish that this purpose is a complex value in which different elements overlap (Sherbinin et al. 2007).

2 Pollution and Ecological Imbalance

There are two types of changes that affect bio-societies, which are quantitative and qualitative changes (Meloni 2014). These changes occur either at the level of the ecosystem or bio-communities, which are called ecological succession, as a result of the change in both non-living and living factors (Santra 1994). This succession from the viewpoint of environmental scientists is an organized development that leads to the emergence of a new biological society in the same environment and it also helps biological diversity, and this succession is either autogenic if it occurs within the ecosystem, or a heterogenic if it enters new types from outside the ecosystem (Sharma and Sharma 2012). If the first life appeared in any region of the world, it is called the first sequence, and is called the second succession if it happened in a region that was inhabited by neighborhoods and was subjected to destruction by human intervention or natural factors such as drought or desert crawl and fires and others, and returned Life in it again because of improved environmental conditions and the arrival of water in it (Walker and Del Moral 2003).

One of the issues that occupy the world today is the issue of preserving the ecological balance so that the environment remains able to give and secure environmental safety. The ecosystem is defined as: "the systematic, and continuous interaction between the components of the living and non-living environment" (Katsanevakis et al. 2011). It can also be defined as a matrix of complementary interactive relationships within a specific environmental unit between its natural inorganic (inanimate) components and its organic (living) components according to a precise and balanced system through a subjective dynamism governed by divine cosmic laws that control its movement and interaction in a way that gives the system the ability to support life (Folke et al. 2007). The ecosystem in which all organisms live in a system that achieves balance and stability (Folke et al. 2007).

Environmental balance means "the continuation or the survival of the elements of the natural environment, without any fundamental change in its characteristics, whether quantitative or qualitative" (Jochim 2013). This means that if a person enters the environment and causes a change in the characteristics of its elements, whether from a quantitative or qualitative point of view, the relationship between the elements of the system is disturbed and what we call imbalance or loss of environmental equilibrium, and the consequence of this imbalance is the occurrence of many environmental problems (Hellawell 2012). From the environmental perspective, the problem indicates an imbalance or a deterioration in the array of ecosystems and the resulting hazards that harm all aspects of life, whether this danger is direct or indirect (Millennium Ecosystem Assessment 2005).

When certain areas become dehydrated, the balance of their environments is disturbed as a result of the destruction that surrounds the green covering these areas and the consequent harmful effects on environmental animals (Newsome et al. 2012). Introducing an organism into a new environment, where it is a problem due to the lack of life conditions and its natural enemies, leads to an imbalance (Newsome et al. 2012). The elimination of some environmental organisms causes an imbalance, as these organisms may have a major role in some environmental reactions, or they may be in rings in food chains. Unsustainable human intervention in the environment disturbs its balance, drying lakes, uprooting forests, filling ponds, and swamps. All of this leads to an environmental imbalance that continues to affect until the environment regains its balance again. Air consists of a mixture of different gases, such as oxygen, carbon dioxide, and nitrogen, and these gases are present in a certain percentage (Sharma 2014). When there is an imbalance in the proportions of these gases, air pollution occurs (Sharma 2014). Air pollution sources can be categorized into natural sources, such as dust storms, volcanic ash, degradation of organic matter, and man-made sources, such as population explosion, deforestation, urbanization, and industrialization (Mohapatra 2010). Burning fossil fuels increases carbon dioxide emissions and the effect of the resulting global warming raises global average temperatures enough to alter agricultural production areas and raise the sea level to flood coastal cities and disrupt national economies (Arora et al. 2018). Environmental problems in the atmosphere are very complex and critically affect human health and surroundings. The various major and secondary pollutants are released and accumulated in the atmosphere, and whereby long they last are dangerous. It is conveyed to various and branched distances, and this is a critical factor that shows how dangerous it affects the environment. Those substances whose very short lifespans affect the quality of indoor and local air, and materials that last longer from days to weeks, raise local and regional problems, and those that last longer than weeks to months raise continental problems (Seinfeld and Pandis 2016).

Earth's atmosphere raises global problems, and that has been there for several years. Some greenhouse gases have serious repercussions on the human communities and economics, as well as on the integrity of the ecosystem and productivity (Freedman 2013). Human-made greenhouse gas emissions, the most dangerous of which is carbon dioxide and methane, are already causing climate change. Global eruptions are nevertheless progressing and their impact will be felt in all regions of the world, with altering weather patterns and sea-level rise and their impact on coastal human settlements, disease patterns, food production, and ecosystem services (Harlan et al. 2015). Air pollution continues to cause many people to die. However, the air quality in some cities has improved significantly over the past 20 years.

The problems of regional air pollution with oxidation have decreased in Europe and North America, according to the WHO report for 2017, but there is an increasing focus of policy in parts of Asia, where acid precipitation has increased. The lower levels of the atmosphere cause the ground level to decrease in agricultural yield production and quality. The passage of pollutants across the northern hemisphere, particularly lower ozone from the atmosphere, is considered a further significant issue (Pierrehumbert 2014). Notwithstanding attempts to tackle air pollution since 1987, emissions of various air pollutants into the atmosphere continue to cause ozone-depleting substances, such as CFCs. The weakening of the ozone layer at the top of the atmosphere causes increased UV rays that reach the surface from the earth (Pierrehumbert 2014). There is no doubting the actual phenomenon which is proceeding, which is the widening of the ozone hole, or the depletion of stratospheric ozone in late winter and early spring over the Antarctic as well as the northern (Bais et al. 2018). Increasing short-term UV radiation affects the incidence of skin, eye, and causes immune system cancer, and therefore has serious public health implications (Weatherhead and Andersen 2006). There are concerns about the impact of short-term UV rays on human health as a reflection of the ecological systems, such as the impacts on submerged plants and marine food reticulations (Solomon et al. 2016). Exposing humans and the environment to air pollution is a major challenge and an issue that raises global concerns for public health. The World Health Organization (WHO) has determined that approximately 4.2 million die each year due to fine particles (Organization 2016). This includes 800,000 deaths due to fine particles less than 10 microns in the urban outdoor air, and 6.1 million due to microparticles less than 10 microns in indoor air, although the study did not cover all the causes of death likely linked to air pollution (Pope III and Dockery 2006).

The most considerable number of precocious and estimated mortality happens annually in developing countries, in Asia and Pacific countries. There are increased global emissions of sulfur dioxide and nitrogen oxides. It is stated that airborne particles cause about 2% of cardiovascular disease deaths in adults, 5% of tracheal cancer, lung cancer, and deaths from acute respiratory infections in children, which amount to about 1% of premature deaths in the world annually (Epstein et al. 2002).

The contamination of groundwater with microbes due to sewage leakage, and the high concentration of nutrients in marine and coastal waters, due to runoff are among the most common environmental problems that cause an environmental imbalance (Boesch et al. 2001). Water contamination has been divided into two main parts: The first section is for deterioration caused by natural causes such as changes in water temperature, increased percentage of suspended matter, or increased salinity. The second section refers to chemical causes such as pollution caused by oil and sewage spills, as well as pollution caused by agricultural waste after the use of fertilizers, fungicides, and pesticides, as well as industrial waste. Many causes may lead to water contamination and make it unusable, among the most important of which are various human activities (Anju et al. 2010).

Sewage disposal is the first requirement that many organizations have started to do. However, this is complicated in developed countries because many people cannot meet this requirement. Waste manufacturing is a source of water contamination, as it has adverse consequences on the environment that are often long term (Rajaram and Das 2008). On the other hand, many industrial companies leave all their waste in natural places such as rivers and oceans, causing the accumulation of all chemical waste used in waterways such as groundwater. Industrial waste often contains asbestos, lead, mercury, nitrates, sulfur, and oils, which are the most notable components that alter the water composition immediately (Gleick 1994). When water contamination leads to the depravity of marine life, this pollution affects marine life that lies beneath this surface. The influence of air pollution on the environment is that gases mixed in the atmosphere accumulate with carbon dioxide, sulfur dioxide, and nitrogen oxides that provoke the production of some acids with a severe impact on the ecosystem (Berner and Berner 2012). Air deterioration from water vapor absorbs more industrial gases, leading to the formation of acid rain. Thus, generating a completely polluted water cycle has a long-term influence on the protection of water, including freshwater (Smith 2017).

By altering the conditions and the general condition of seawater and all its sources, the effectiveness of the natural food series changes gradually, due to the presence of various pollutants, especially heavy metals such as lead and cadmium as well as trace elements, materials that are consumed by small animals (Kleiber et al. 2011). The problem lies with large animals that eat small animals that have already died by eating these harmful substances, which cause the same effect on them and then on humans, when they are hunted. Consequently, the food chain is significantly disrupted, becoming more pronounced over the years as a result of severe water pollution. Most of the ecosystems on the planet are affected because they change both the vegetation and its climate and everything that makes the species in this environment alive. Therefore, various animal and plant species will deteriorate; these species must change some of the habits they are used to stay in this natural environment because animals die or change their habits to survive. Acid rain is a pollution problem caused by the release of acidic gases into the atmosphere. Besides, the water fumes from this condensation are in the clouds, and this causes acid rain. The presence of this type of water not only damages the surface of the earth but also degrades the ecosystem (Kleiber et al. 2011).

3 The Biological Diversity and Ecosystem Resilience

Ecosystems comprise multiple complicated synergies between members of different species (Persha et al. 2011). These interactions often create negative feedback loops, keeping the ecosystem in approximately the same state (Cumming et al. 2015). For example, if numbers of a particular type of plant begin to grow, the numbers of animals eating that plant may also begin to rise, thus reducing the number of the plant. Ecosystems contain as many interactions like this one, and these interactions are essential to understanding the importance of individual species to biodiversity (Maron and Crone 2006). In ecosystem diversity, the species interact with each other and with the other factors, such as light, air, and water to form an ecosystem. From the Arctic tundra to tropical forests and estuaries to the deep-water environment in the seas, the Earth encompasses a torrent of ecosystems in which the challenge is often not explicit and apparent (Ramirez-Llodra et al. 2010). An ecosystem can be as large as a great reef or as small as a group of sponges, algae, and worms in the shell of a spider crab. While there is a clear division between the coastal forest and the depths of the sea, there is no point marking the line between the end of the forest boundary and the beginning of the savanna. The races within the ecosystem compete with each other for sources of light and food, but at the same time, they depend on each other (Sutton and Yingling 2020); 87 percent of flowering plants are pollinated by animals, while coral reefs provide shelter for 25% of marine life. The bacteria recycle the dead materials into the nitrate compounds from which the plant can form a protein. Ecosystems provide a support life forms inside and outside the system. Humans cannot survive without those services that include clean air, water, waste decomposition, and pollination of plants (Meadows et al. 2012).

Biodiversity is not compatible with the abundance of life on planet Earth, as it means preserving environmental resilience and ease of adaptation as a whole (Gomiero et al. 2011). We find that just as genetic diversity provides species with the ability to adapt to environmental change, so does the diversity of species double the adaptive capacity of ecosystems. Promoting biodiversity around agricultural fields is essential to ensuring more abundant and stable food production. Green areas that are characterized by the abundance and diversity of their components such as crops, trees, and meadows enhance the wild pollination processes, also to improving biological resistance to harmful pests and insects (Garratt et al. 2017). Consequently, agricultural productivity increases with the continuous global changes, and the increase of critical climates, the biodiversity value of agricultural lands becomes more important, to ensure the resilience of these areas in the face of environmental disturbances. Pollination is an essential service in ecosystems, and in many cases, it is the result of intertwining relationships between plants and animals, and if either of them is affected, this will affect the survival of both parties. One-third of the world's crops depend on pollination by insects or other animals (Helmer 2019). Consequently, pollinators are a fundamental factor in the diversity of food colors and the preservation of natural resources. Biodiversity plays an important role in sustainable agricultural production, as increased production is closely linked to the extent to which it can be achieved in protecting the environment and ensuring the provision of ecosystem services sustainably. The diversity of plants in the environment, in farms and orchards, brings different benefits (Garratt et al. 2017). One of the most important of these is the continuity and durability of benefit and giving. It is known that each type of plant has a specific season and time in which it is fruitful, and its fruits ripen in this season for the benefit of humans and all living things. Therefore, the different types of plants work to continue giving throughout the year, for one type produces its fruits in the summer, another type produces its fruits in the winter, and another type also produces in the spring. The second benefit of plant diversity is the diversity of plants that help protect the plantation from pests. The lack of fruits and the lack of plant crops after the fruit has taken place, is often only when these plants are exposed to two factors, namely the infection of plants with pests and diseases and lack of nutrients. With different types of plants in the same environment, plants in that environment are often not exposed to these two factors (Sugio et al. 2011). In addition, restricting the environment or the agricultural field to one type of plants helps to spread plant diseases and epidemics that reduce the yield or eliminate plants, and the cultivation of one type of crop on a large scale in large areas in several countries of the world has led to devastation of their crops (Smith and Crews 2014). It has been found that pathogenic genes can destroy the entire crop, so planting more than one crop is considered to protect crops against epidemiology. On the scale of forests, it has been found that natural forest plants produce refreshing scents and different substances that differ according to different plants, which inhibit the activity and growth of bacteria and viruses, and these secretions reduce the number of microbes in the forest air. Therefore, the number of bacteria in forest air is 200–250 times less than the number in urban air, while it was found that industrial forests in which one type of tree was planted, they were devoid of natural biological diversity, completely lacking plant and animal organisms and no longer endemic to them (Osman 2013). Certain types of birds and animals can make do with this type of plants as their main food. These specific plants have become vulnerable to pests and diseases as a result of the low air content of substances affecting the growth of microbes and secreted by various plants, and also as a result of the proliferation and spread of insects that cause tree diseases and their death, and because the elements of the natural balance have disappeared, because the birds and animals that feed on these insects have disappeared (Mahmood et al. 2016).

The third benefit of plant biodiversity is the work to increase soil fertility. It has been observed that natural forest soils have remained fertile hundreds or even thousands of years rich in mineral salts and organic materials, flooded with enormous production of huge, gigantic plants and trees. Some forests have produced types of trees up to more than 110 meters in length, that is, a 37-storey building, such as redwood trees (Gomiero et al. 2011). Moreover, other types of trees have a trunk thickness of more than 12 meters, such as simple cypress trees, and other trees that are resistant to all harsh conditions, such as ambo trees that can withstand harsh conditions. It can withstand drought, resist insect pests and severe storms, and high temperatures and its wood are resistant to fire, which has the advantage of impeding its cutting or spreading. It has been observed that the soils of farms and agricultural fields lose their fertility and weaken with the passage of years, even though humans take care of it. The results of studies and research indicated that the sustained cultivation of one type of plant weakens the soil and reduces its fertility. For example, scientists have found that growing a single crop consumes the mineral salts and organic matter in the soil if it is grown in the field year after year (Coleman 2018). It has also been found that growing different types of crops in the field according to a regular schedule provides an opportunity to compensate for most of the mineral salts and organic materials consumed, and helps to reduce plant diseases, and the life cycle of insects (Coleman 2018). It is known in botany that all plants need nitrogen, which is in the form of certain compounds, and it must be present in the soil. It is worth noting that some plants take nitrogen salts from the soil and cannot replace them, while other plants can excrete these compounds and excrete them into the soil (Mauseth 2014). Therefore, the diversity of plants in the environment provides the soil with an opportunity to inject it with nitrogen compounds, utilizing plants and microorganisms that can take advantage of the nitrogen gas present in the air we breathe and convert it into the basic compounds necessary for the growth and reproduction of plants (Zinger et al. 2011). The fourth benefit is protection from wind and storms and soil erosion. The diversity of plants in the environment leads to other benefits, including protecting plants against each other from the physical factors that damage plants and plants. One of the most important elements of protection in this regard is the protection of plants from winds and storms (Mithöfer and Boland 2012). Palms and trees are generally considered natural buffers against high winds and severe storms, especially in open areas where strong winds prevail, and to protect plantings and crops and obtain an abundant and uncompromised crop. Environmental engineering and agricultural science studies have indicated that it is necessary to plant trees around farms and orchards to be protective green belts that protect crops and improve the atmosphere surrounding the plants by reducing wind speed and working to moderate its temperature (Smith et al. 2013). Trees and plants that can withstand the local weather conditions should be chosen. In environments where high temperatures and desert weather conditions prevail, palm trees are considered to be trees that endure these harsh conditions and that benefit planting and crops when they are used as green belts that surround orchards and farms in open areas. Fertile soils are exposed to natural runoff through many factors, including rainwater runoff on the soil surface, strong winds, and dune encroachment (Smith et al. 2013). Trees are used to preserve the environment, as they help preserve the soil, prevent soil erosion by winds, and their roots hinder soil erosion in the event of heavy rains, and severe water flows to the surface of the earth (Miller et al. 2010). Many types of trees help stop the spread of deserts, and to stand in front of the encroachment of dunes, thus preventing moving sand from creeping into agricultural areas and cities, by planting trees and various plants in the edges of agricultural areas and cities subject to the encroachment of dunes in the form of strips or more to be as green packages (Quante et al. 2016). People knew the benefits of plant diversity in farms and forests. People also knew the benefits of green belts, which led to the expansion of their use in this era, not only to protect farms and orchards but also to protect cities from sand encroachment. The different experiences related to protecting cities and villages from the encroachment of shifting sand by various means and methods have indicated that the establishment of green belts and afforestation, in general, has proven its feasibility and effectiveness (Larsson 2010). Also, this method has good effectiveness in stopping sand encroachment over all other methods, and its application is easier compared to other methods. As it appeared from these experiences that other means are only temporary measures that lead to fixing moving dunes temporarily so that afforestation and the cultivation with plants. Those plants that include trees, shrubs, and herbs are distinguished by their ability to suit sandy soil conditions, extreme climate, and soil poverty with mineral salts and organic compounds. Sandy plants are also distinguished by their roots that grow deep into the wet layer or spread over the surface of the earth, thus working to hold the soil together (Van Bruggen and Finckh 2016). It is known that the type and structure of plant roots and the depth of their extension in the soil vary with different plants, some extend over the soil surface, some extend deep into the soil for a short distance, and others dive a lot deep into the soil (Nawaz et al. 2013). All plant roots leave in the soil what they excrete from organic chemicals or what remains of them from roots, dead roots, and various organic residues, then they are decomposed and disintegrated by microorganisms, and this works to add substances or organic compounds in the soil, which is scientifically termed as increasing the organic content (Nawaz et al. 2013). Organic compounds have a very high ability to absorb and hold water, and plant roots, especially those that have roots, also have a high capacity to store water in large quantities (Kuzyakov and Xu 2013). In this way, it increases the organic content in the soil and the roots of the plants to increase the efficiency of the soil to conserve and hold water in it, at the surface level and in the depths of the soil that the roots reach. Therefore, in the event of interruption of rain and interruption of water access to plants, various plants serve each other to withstand these harsh conditions, so the plants remain alive for a longer time when exposed to such conditions (Kuzyakov and Xu 2013). Hence, biological diversity contributes to maintaining the continuity of life in forests and agricultural environments. Fifth, the diversity of plants provides shelter and habitat suited to the diversity of living things. The diversity of plants in the environment not only serves man but also all living things in the environment. The different types of plants provide sustenance and shelter commensurate with the diversity of living things, insects, animals, and birds. Some people may think that providing sustenance and shelter to different organisms means realizing the existence of causes that harm trees and plants and harm the environment (Freeman 2003). This is far from right. Not all living things in the environment are harmful, but the vast majority of them have innumerable benefits that benefit humans and benefit the environment.

The diversity of plants in the environment is the hindrance to the spread of fire in the event of its outbreak or the burning of one or some plants, as the natural biological diversity of plants does not allow the leaves of all trees to fall at the same time (Harris et al. 2016). Each type sheds its leaves at a specific seasonal time, hence the presence of one type of tree in forest works to shed the leaves of all these trees in one season and time, so the forest floor is covered with a thick layer of leaves that dry out after that. If these dry leaves were exposed to a fiery flame or lightning, they ignite quickly and cause a forest fire. Therefore, the rate of fires in forests that contain one type of tree is much higher than the rate of fires recorded in natural forests of great biodiversity (Wilson 2013). Hence, the diversity of trees and plants in an industrial or natural forest is considered the best way to limit the spread of fires in forests, as not all trees are exposed to leaf loss at the same time, so if a fire breaks out at a dry tree, the moisture and greenness of the tree next to it is an obstacle to the spread of flames (Wilson 2013). The diversity of plants does not cause the leaves to fall on the ground from all trees at one time. Rather, the time of leaf fall varies according to the type of plants, so the leaves do not accumulate and accumulate in large quantities on the ground. Moreover, the presence of one type of plant in the environment or field means that its leaves fall at the same time, and this leads to the accumulation of leaves in abundance, which increases the effort to address this problem (Polgar and Primack 2011).

4 Physiology of Plants to Withstand Drought

The optimum environmental conditions for plants are rarely available, such as water, air, and nutrients. Rather, tension often occurs due to either extreme water stress, due to a lack of soil moisture, temperature, salinity, or toxicity with some elements or many other factors that may push living organisms to limited survival (Lombardini and Rossi 2019). The study of plants under such conditions has been known as "stress physiology," and this is important in terms of plant environment phylogeny (Meena et al. 2017). Often, the plant response to stress is based on changing life and physiological processes, as studying cases of tension phylogeny will provide us, in some of its aspects, with the importance of knowing the physiological mechanisms that occur in the presence of tension, especially that which occurs under normal conditions (Secchi et al. 2017). The study of the stress physiology on the agricultural side will contribute to an increased understanding of the factors that determine the distribution and spread of plants and the actual changes in the various life processes during the growth cycle (Sewelam et al. 2016). On the applied agricultural side, the ability of crops to maintain survival and the required plant density under stressful conditions is a major factor in determining the economic outcome (Meena et al. 2017). The studies and scientific knowledge on growing plants under natural conditions are many and varied. We are definitely in need of augmenting the scientific data that talk about the stress and environmental conditions, that is, the unusual and which are often not taken into consideration and affect the survival, vitality, and production of plants, particularly in light of the frequent climatic changes and global warming restrictions (Altieri et al. 2015). Trees and shrubs in the temperate latitudes of the northern hemisphere are exposed to extremely low temperatures during the winter, and the plants of the Alpine regions are exposed to cold, dry winds and high levels of ultraviolet radiation (Lütz 2010). It is also exposed to crop plants during one of the stages of their growth and maybe throughout the growth period, to drought conditions, or the high concentration of salts in the root zone (Lütz 2010). In recent years, we faced the problem of soil, water, and air pollution as a result of the improper uses of environmental resources by humans, which made matters worse and added other new factors, all of which lead to physiological stress during the plant life cycle (Khalid et al. 2018). The occurrence of a peak in any of the environmental parameters will create stress conditions on plants, which may have a fundamental impact on the issue of physiological development, that is, reaction and thus survival. The study of plant response to environmental stress has been of central importance to specialists in plant ecology and physiognomy in general and plant environment, as well as plant breeders and producers (Wesche et al. 2016). Because of the stress conditions that result in disturbing the nature of growth, such a loosening will put plant physiologists and others on the path that makes available to them the tools useful for studying the physiological foundations and the life technology of the stress state that they study (Huang et al. 2014; Khan et al. 2018). The manifestations of stress in life need to have implications for the general meaning more than they are. At the level of the ecosystem, for example, any external inhibitor determines productivity (including carbon capture in photosynthesis), and making it below the plant's genetic potential is a state of stress (Pinheiro and Chaves 2011). Perhaps this example represents the peculiarity of the case on the agricultural side, as mathematical models can be used to estimate the genetic potential under ideal environmental conditions (Perfecto and Vandermeer 2010). Therefore, without practical scientific applications for estimating genetic potential, it becomes difficult to determine or judge the effect of stress in such a case (Kievit et al. 2013). When estimating environmental stress, the plant species differ among themselves to a large degree in terms of the ideal environmental conditions that they need for growth and development and thus, their sensitivity to any change in these environmental conditions is also variable, especially when severe extremes occur in environmental conditions – for example, a change in temperature, water effort, or salinity (Nicotra et al. 2010). Therefore, it is perhaps the most useful and acceptable definition of life stress which speaks of the difference in stress or the effect that leads to the inhibition of the performance of life systems from performing their role normally. Plants respond to stress in many ways, some plants may evade the stress effect by completing their growth cycle during the period of absence of tension or its few effects, or they may suffer some damage from its effects and have no choice but to live with it by avoiding or resisting it (Stults-Kolehmainen and Sinha 2014). One of the examples is the difference in the productivity of a plant or a specific area cultivated with the same variety from year to year. Some believe that this difference is due to a specific environmental circumstance at a time when specialists explain that the difference in productivity is for the same genetic structure. Rather, it is the result of the interaction and interaction of the various influencing factors in the growth and life activities of the plant, that is, the method of tension that occurs during the plant growth cycle (Akula and Ravishankar 2011).

Plants are damaged by tension, that is, a defect in the performance of one or more of the life processes necessary to sustain growth and/or life (Gardiner et al. 2016). If the tension is moderate and for a short period, the damage may be temporary, and the plant will regain its normal position with the removal of the tension (Gardiner et al. 2016). On the other hand, if the tension is caused to a great extent, then the continuation of vegetative growth or flowering is affected. Some drought-tolerant plants, as their roots grow in dry soil, increase the production of a viscous gelatinous liquid around the roots (in the rhizosphere) (Squires 2017). As a result, loops of soil particles are formed that are lightly attached to the roots, and ketones bind due to the viscous nature of the gel-peptide fluid, and their influence decreases. Thus, the water conductivity is maintained between the soil and the root. There are other plants with thick leaves that store water and with a layer of thick cuticle, or the presence of fluff, which all reduce evaporation, or lead to modifications that help with water retention, or reduce water loss. In some cacti plants, thick stems obtain high photosynthesis (Tekle and Alemu 2016). Meanwhile, the leaves have turned into thorns as a defense to avoid dehydration. The stress caused by the lack of water represents the constant and continuous threat to plant survival, as many plants that undergo a phenotypic or physiological modification may not be able to continue and survive in the environment in which they live due to water stress or low soil moisture content (Araujo et al. 2015). This tension is related to the prevailing weather conditions (lack of rain, high temperature, increased wind speed, low relative humidity in the air, etc.), so soil dryness is defined as a lack of soil water necessary to the extent that its readiness for the plant decreases (that is, the threshold at which the plant is unable to perform water absorption or depletion at a speed that meets its requirements for carrying out vital activities, and photosynthesis that meets the requirements of evaporation-transpiration does not occur (Araujo et al. 2015). Conversely, water tightening may be a result of excess water (Chapman et al. 2013). An example of stretching due to excess water is flooding, which results in suffocation as a result of low oxygen concentration the equipment for the roots, which in turn will impede breathing. Generally speaking, tension due to lack of water is the most common, which has led specialists to call it "tightening of water shortage." Because water tightening occurs in natural environments as a result of trapped rain, such conditions are known as drought conditions (Chapman et al. 2013).

5 Phytosanitary Aspect in Resilient and Inflexible Environmental Conditions

Phytosanitary means not only the absence of disease but also a general state of well-being, which allows plants to achieve their full productive potential (Larkin 2015). Phytosanitary health, including disease prevention, pest deterrence, and removal, is an extremely important aspect of food production from aquaculture (Hine et al. 2010). Although the most important developments in phytosanitary have been achieved through the management of pathogens and pests, optimal nutrition, smart farming techniques, and appropriate environmental management are also essential factors for securing healthy plants (Gouda et al. 2018). Besides, knowledge about cultivated plants is essential to address various production issues. Integrated production and pest management is an ecosystem approach to soil-based agriculture and soilless plant production, conservation combining management strategies for the growth of healthy plants, and minimizing the use of various pesticides (Gruda 2019). It is a combination of mechanical, physical, chemical, biological, and microbial controls along with the resistance of host plants to insects (Gruda 2019).

Maintaining light, heat, and humidity at optimum conditions is important because they can easily change in protected cultivation in favor of healthy plant growth and unfavorable conditions for pests (Reddy 2016). Removing all plant debris, including roots, at the end of each harvest will help limit the spread of pests and diseases (Flint 2018), (Gruda 2019). Dead leaves and diseased branches should be removed frequently. In outdoor conditions, it is advisable to limit the vegetation surrounding the unit to the lowest possible level, to prevent pests from spreading in the biodynamic unit (Flint 2018).

Both temperature and humidity play an important role in plant health management (Elad and Pertot 2014). Optimum growth temperatures can be different from those of plants, and thus diseases occur in certain regions and periods during the year when environmental conditions are most favorable. It is worth noting that moisture plays a pivotal role in the germination of fungal spores, which require a thin layer of water that covers plant tissues (Paterson and Lima 2010). Similarly, the activation of some bacterial and fungal diseases is strongly linked to the presence of water (Limon et al. 2019). Therefore, control of relative humidity and moisture is essential to reduce the risk of disease outbreaks (Gómez et al. 2019). Controlling relative humidity, especially in greenhouses with an aquaculture unit, is especially important. This can be accomplished through dynamic or forced ventilation, and through windows and ventilation fans that create a horizontal airflow. This helps to reduce temperature differences and cold spots where condensation occurs. Also, the moving air is constantly mixed, and when it is mixed, it prevents the temperature from dropping below the dew point, and therefore, the water does not condense on the vegetables (Tariq et al. 2019).

Scientists recently demonstrated that plants have a delicate sensory network that can strike the right balance between water loss and gas uptake in drought conditions, through a complex network of sensors (Lombardini and Rossi 2019). When the light is abundant, plants open their pores to absorb carbon dioxide, and at the same time, water molecules escape in the form of vapor with more than a hundred times the carbon dioxide they absorb (Ganesh 2014).

Gas exchange is not a problem under natural conditions, but when the soil dries up in the middle of summer, the plant needs to switch to economic mode to save water, and in it, the plants open their pores only to have photosynthesis to stay alive (Niglas 2015; Tardieu et al. 2018). Pores are opened and closed by specialized guard cells surrounding them (Niglas 2015). The units made up of follicles and sentinel cells are called stomata. The stomata consist of two kidney-shaped cells that meet on the concave side and enclose between them an aperture, the stomatal aperture, from which gases (carbon dioxide and water vapor) are allowed to be exchanged between the plant and the atmosphere (Jalkanen and Salmi 2020). To measure photosynthesis and water supplies to respond appropriately to changing environmental conditions, plants have receptors to measure the carbon dioxide concentration within the leaf (Velásquez et al. 2018). When the gas value rises sharply, all stomata are closed to prevent unnecessary water evaporation, and as soon as its concentration drops, the stomata are reopened (Glime 2015). When water is scarce, plants produce abscisic acid and puts the control cycle of carbon dioxide into the water-saving mode, and this is achieved by sentinel cells equipped with abscisic acid receptors, and when the hormone concentration increases in the leaf, the stomata are closed (Marcińska et al. 2013). The research team wanted to shed light on the components of control cycles in sentinel cells, so they exposed Arabidopsis plants to elevated levels of carbon dioxide and abscisic acid for several hours, to stimulate reactions at the level of genes (Ruibal et al. 2020). Gene expression profiles were analyzed in sentinel cells using bioinformatics techniques (Xu et al. 2016). The researchers found that patterns of gene expression differ greatly at high concentrations of carbon dioxide or abscisic acid, and they observed that an excessive increase in carbon dioxide causes the expression of some abscisic acid genes to change (Xu et al. 2016).

6 Environmental Resilience and Research Challenges

Environmental scientists believe that the ability of these systems to achieve this balance depends on environmental resilience that occurs at the level of individuals and the environmental resistance that takes place at the level of the entire ecosystem through its possession of organic stock. Hence, whenever this system includes individuals with high environmental resilience, and stock adequate organic matter and phytonutrients, they become susceptible to maintain their mobility and balance significantly, and vice versa (Oliver et al. 2015).

Environmental resilience is one of the forms of resistance: the ability of a system (static, ecosystem, environmental shelter, and biosphere) to create or maintain a state of dynamic equilibrium after a certain stage of instability caused by external or internal disturbance (Marten 2001). Construction resilience in an ecosystem indicates serving to preserve the health and function of living organisms and their associated ecosystem processes (Jordan 2013). Stress may change the ecosystem to another, but if it returns to something functionally similar to what it was before, then it is flexible. Resistance and resilience can operate independently. It is said that more resilient/resilient ecosystems are more stable. It is worth noting that it is necessary to know the reasons that led to the creation of a more resistant ecosystem; it may be thermal pressure or drought pressure, but in these cases, it is not resistant to biological invasion (invasive species) (Ivits et al. 2016).

Each ecosystem is self-sustaining; if turbulence occurs, it will return to its original basin; it is like a ball. For example, you can move from an ecosystem dominated by coral reefs to an ecosystem dominated by algae, as well as a forest (like the Amazon, which can tip over to the savanna if a lot of trees are cut down. Once a change of ecosystem occurs, you cannot just remove the impact and return the system to where it was before (Yachi and Loreau 1999). The state of the new ecosystem, be it forest, savannah, or fishing without commercial fish, enhances itself. Beyond the threshold is an ecosystem that may alter stable states (Gross et al. 2014).

Resilience ecosystems often utilize a variety of approaches and techniques to adapt to change. For ecosystems, biodiversity and functional iteration can help the ecosystem be more resilient to environmental changes. This resistance can be measured from the extent of the disturbance that the environment can absorb before changing the system by altering the variables and processes that control behavior

(Spies et al. 2010). This type of resistance is usually defined as environmental resilience (Spies et al. 2010). Although the environmental integrity of a particular system may deteriorate at some point, the functional environmental interconnectedness of the system is one of the most important conditions necessary for the ecosystem's resilience and long-term stability.

Environmental health (EH) solicits to forestall diseases and make an environment that supports health. These definitions exclude behaviors that are not associated with the environment, like behaviors associated with social and cultural contexts. They also exclude behaviors resulting from heredity (Boesch 2006). The World Health Organization (WHO) defines environmental health as those issues correlated with human health and disease determined by environmental agents. EH also deals with theories and practical applications to assess factors within the environment that affect health and control it. It includes environmental health, as used by the WHO Regional Office in Europe, which includes direct pathological effects from chemicals, radioactive, and other biological materials. This is in addition to the effects that are often produced indirectly and affect human health and environmental health in general, whether physical, psychological, social, or cultural, which include, for example, housing, urban development, land use, and transportation (Organization 2015). According to the World Health Organization, environmental health services are defined as services that implement environmental health policies through monitoring and control activities. It also fulfills this role by promoting and improving environmental standards and encouraging the use of healthy and environmentally friendly technologies and behaviors. These services play a leading role in developing and proposing new areas (Organization 2015).

Environmental health, environmental safety, or environmental damage are symptoms of an imminent loss of ecosystem in terms of it carrying capacity or ability to implement environmental services or imminent environmental devastation, which is due to accumulated causes such as pollution. It can also be defined in terms of agriculture to reduce the negative effects of agricultural activities. The term health refers to awakening human concerns about environmental health, which are often very closely related (but as part of medicine and not ecology) (Lee et al. 2010). A While the term safety or damage appears to not correlate with this matter, it assumes that there is a definition of the term safety that can be said to apply to ecosystems. The political term, to a greater degree, environmental wisdom, refers not only to the realization of a level of health, safety, or potential harm but also to the decision not to do something to harm this ecosystem or its dependents. The ecosystem is in good condition if it can recover itself after suffering from external disturbances. This is called flexibility. Environmental health measures, such as more specific biodiversity principles, tend to relate specifically to an environmental area or even an ecosystem (Swanstrom 2008).

Biodiversity-dependent measures are valid indicators of environmental health, as stability and productivity are good indicators of environmental health, which are two of the environmental impacts of biodiversity (Tilman et al. 2014). Dependencies differ between the factions so much that it is hard to express them abstractly (Tilman et al. 2014). However, there are few universal symptoms of inadequate system health or illness to its integrity. The accumulation of waste matters and the reproduction of the more simplistic models of life (microorganism) that feed on them – but there is no resulting population growth in those species that feed them. The intimate relationship between the environment and pandemics has been known considering ancient eras. In the seventeenth century, it was found that microorganisms cause severe complications, which led to the start by using means to improve the environment to combat contagious diseases (caused by these microorganisms) such as cholera, typhoid fever, malaria, and others (White 2012). The procedures have emerged in our time, considering the form of health plans that deal with the fundamental elements of the environment that avoid infection with these disorders. For instance, authorized organizations emerged whose assignment is to make sure that the water is clean and secure to drink, that sterile milk is freed from germs, that food is ready healthily, which waste is disposed of during a way that forestalls the reproduction of insects and rats (White 2012). In these ways, many of the traditional environmental problems related to health have been overcome in many regions of the world, and in the modern era, new environmental problems have emerged that are different from those previously known and some of their causes.

Environmental pollutants resulting from industry and civilization development pose a threat to public health (Kraft 2017). What is most worrisome is the presence of large quantities of chemicals that pollute the environment. Chemicals that represent the characteristic of modern civilization are now one of these materials and hundreds of them are traded commercially. Its impact on health is not sufficiently known, and the risk lies in increasing the number of chemicals used in house paints and lead added to gasoline (Quadros and Marr 2010). Thus, heart diseases caused by carbon monoxide, nervous disorders caused by mercury, and various problems related to chemicals, including cancer, should receive attention. It has been found that there is a relationship between lung cancer and dust from some factories, and a type of liver cancer has been found that spreads among workers in converting (vinyl chloride) into polyvinyl chloride, which is a plastic material used for multiple purposes. However, the extent of the problem related to cancer and chemical compounds in the environment has not been confirmed. The incidence of various accidents has increased, and the deaths resulting from it, as well as poisonings and risks resulting from the expansion of the use of pesticides and fertilizers (Prüss-Ustün et al. 2011). Scientific progress was expected to enable mankind to address modern environmental hazards and the diseases they generate, but industrial technology created conditions and produced various methods and materials that were not previously known. Moreover, the emergence of mechanical methods is proceeding slowly compared to the rapid progress of technology and social changes in the developed world, which weakens the ability of humans to adapt to toxic and harmful products for chemicals and pollutants. The hope for survival and the struggle for life are based on efforts made to combat environmental pollution (Blaikie et al. 2014).

Ecosystems are changing at an unprecedented rate considerably globally because of human influences, including exploitation and use, pollutants, invasive species, changing turbulence systems, increased CO_2, and global climate change (Brierley and Kingsford 2009). Differences in species distribution and thus the emergence of state-of-the-art ecosystems are increasingly challenging our ability to manage the biodiversity system, the functioning of the ecosystem, and raise the human standard of living. Managing environmental flexibility necessarily requires a multi-domain strategy due to the hierarchical nested nature of complicated systems In applied ecology, ecological resilience is usually interpreted as a measure of the likelihood of a system to be restored to the specified state, that is the power of an ecosystem to revive distinct processes, structures, functions, and feedback after disturbances or management actions (Duru and Therond 2015). Affability management entails (a) effectively enhancing environmental processes, structural, and functional characteristics, and feedback for healthy or desirable states, (b) decaying the resilience of unwanted states and promoting transitions to desirable alternative states, and (c) increasing the capacity of systems to affect systems new or changing turmoil and global climate change (Chapin III et al. 2009).

The environmental and sustainability challenges that the world faces today are rooted in decades of global developments. During this period, the "tremendous acceleration" of social and economic activity has contributed to transforming the relationship of humankind with the environment since 1950. The world population has tripled to 5.7 billion, and the economic output expanded 12 times, accompanied by a similar increase in the use of nitrogen and phosphate fertilizers and potassium, and primary energy use has increased fivefold (Domazet and Marinović Jerolimov 2014).

There are many areas in which human activity influences and depends on the resilience of terrestrial, aquatic, and marine ecosystems (Chapin III et al. 2011). These include agriculture, deforestation, pollution, mining, recreation, overfishing, dumping at sea, and climate change (Chapin III et al. 2011). In this regard, awareness is growing that more understanding and an emphasis on the resilience of the ecosystem are needed to approach the purpose of sustainable development. A comparable result was attained by Perman et al., (2003) who used resilience to describe one of six concepts of sustainability: "It is the sustainable state that meets the minimum requirements for the resilience of an ecosystem over time." The science of resilience has evolved over the past decade and has expanded beyond the environment to reflect thinking systems in fields like economics and political science. As more people move to densely populated cities, utilizing massive quantities of water, energy, and other resources, the requirement to combine these restraints to consider the resilience of ecosystems and urban cities is crucial (Pickett et al. 2011).

The purpose of the proposed environmental resilience is ultimately about avoiding our extinction or being concerned with measuring the likelihood of extinction. Protecting the environment to "provide a range of services" must be a "necessary condition for the economy to be sustainable. Environmental flexibility and the thresholds through which resilience is determined are closely related to how they affect environmental policy-making and legislation and thus environmental management" (Van Jaarsveld et al. 2005). Resilience is ordinarily considered as the desired emergency feature and is increasingly included in environmental policy. On the contrary, socially or economically disadvantageous conditions can be considered flexible, for instance, diminished ecosystems invaded by invasive species such as exotic herbs. Human interventions that change system dynamics, for example, by increasing the frequency or intensity of disturbances beyond the capacity of normal recovery processes can create new conditions that lead to new ecosystem responses, so-called system shifts. The stability of the ecosystem and its dependency on natural and human interventions are the main factors which affect the resilience of the ecosystem and environmental memory. Likewise, altering the ecosystem's memory by removing the legacy of materials or information can lead to system shifts after the disturbance. Disorders, in the purpose of conditioning, may have a positive influence on the flexibility of the ecosystem when natural disturbance systems are preserved. The consequence may be counteractive when resilience is seriously diminished. Modernity in ecosystems is ubiquitous, but the level of modernity varies, as does the definition of what constitutes modernity. The recentness, though, does not mean change. With either of the two definitions, it appears likely that the low memory power of the ecosystem increases the susceptibility to new emerging conditions. Understanding how the data contribute to ecosystem memory and influencing responses to disturbances is critical to success in managing forests, restoring forest landscapes, and adapting to climate change.

7 Conclusion

Promoting sustainable natural and environmental resource management, resilience, and preparedness for natural disasters is imperative. Both the current situation and the challenges before us require a shift in the way we manage our environment, which shows that they are not sufficient to limit. The current approaches have laid the foundations for this, but we are concerned with health and wellness. Supportive and health-enhancing environments, and from them, a sustainable and effective environmental threat to health has arisen to advocate the development of a new strategy on health, environment, and climate change. Sustainable development calls for a future in which environmental, social, and economic considerations are balanced when seeking development and improving the quality of life. There must be a link between development and the environment to protect the environmental systems and manage natural resources, which are essential requirements to meet human needs and improve living conditions for all. Sustainable development depends on achieving two basic things: the right to development and the right to protect the environment, both of which are human rights so that the protection of the environment has become a basic requirement to support human rights in leading a decent life and enjoy the health that comes through the right to development. Environmentalists focus on maintaining integration ecosystems required for the overall stability of the global ecosystem and attention to measuring the units of natural, chemical, and biological organisms. Scientific research and its technological applications are closely related to development. The developed countries are distinguished in confirming this link and benefiting from it to the utmost extent. For example, the improvement in the standard of living of their citizens is 60–80%

mainly due to scientific and technological development, thanks to the huge potential that these countries provide to research institutions. Scientific development, innovations, and new products are the result of scientific research projects that contribute to a comprehensive solution to the obstacles that face sustainable development directly or indirectly through addressing issues that help provide a scientific base and an appropriate climate for the process of economic and social development alike. In developing countries, the weak system of scientific research and development is one of the main obstacles facing sustainable development.

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