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Azamal Husen *Editors*

Augmenting Crop Productivity in Stress Environment

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Preface

Agriculture is the oldest occupation that has brought a settled life; and to a great extent, a control over the destiny in terms of food and nutritional security for mankind. At present, 1.5 billion ha, accounting for 11% share of the globe's surface, i.e., 13.4 billion ha, is arable land. An estimated area of 2.7 billion ha is also available as potential arable land. Nevertheless, a divergence between agriculture productivity and burgeoning population occurs. According to an estimate, it is anticipated that 50% more food is required to feed a billion people by 2050.

The so-called Green Revolution that ushered in the development of high-yielding cultivars along with high input of synthetic fertilizers and pesticides and intensive irrigation has started fading away with decline in crop productivity due to soil erosion and pollution in the past 40 years, affecting around one-third of global arable land. It is estimated that soil erosion has accelerated hundred times more than its formation. For example, the development of 2.5 cm top soil takes about 500 years. Soil degradation also leads to silting of rivers with reduction of their flow and availability of water. The intensive irrigation has had twin negative effects, i.e. salinization and waterlogging of the irrigated arable land to the tune of 30 million and 80 million ha, respectively. In addition, 40% of the arable land is naturally acidic due to rainfall exceeding evapotranspiration and displays toxicity of Al, Mn, and H and deficiency of Ca, Mg, and Mo. With the expansion of agriculture, there is a tremendous change in biodiversity composition and structure of top soil along with water resources.

The above situation warrants to re-engineer agriculture systems that must be inclusive for site improvement and restoration of biodiversity in addition to augmenting crop productivity. The rigorous ploughing and excessive use of fertilizers and pesticides destabilize soil structure and contaminate water resources. There is need to develop site-specific and multi-resilient cultivars of agriculture crops that may luxuriantly be cultivated on adverse sites without much inputs. Intercropping, such as various agroforestry systems, needs to be encouraged in place of monocrops. The potential additional arable land available in sub-Saharan Africa, Latin America, and some countries of East Asia suffers from various terrain constraints and abiotic stresses for which novel cropping systems are to be developed. Thus, the book focusses on the following thrust areas:

- Global land resources and their status for crop production
- Physiology of abiotic stresses in crop plants
- Role of growth regulators in combating abiotic stresses in crop plants
- Intensive land use strategies with emphasis on organic crop cultivation

The book incorporates chapters being crafted with academic authority, clarity of the discipline, reviewing up-to-date literature with lucid illustrations. The book would cater to the need of both graduate students as textbook and researchers as reference book.

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Contents

About the Editors

Shamim Akhtar Ansari Scientist G & Ex-Director, Institute of Forest Productivity, Ranchi, India, is an erudite academician and researcher with an experience of >38 years. Dr Ansari has specialized in Plant Physiology and Biochemistry during MS and doctoral work. Subsequently, he joined as Senior Scientist in Indian Council of Forestry Research and Education under Ministry of Environment, Forests and Climate Change, Government of India. He has conducted extensive research and developed expertise in Clonal Forestry or Forest Biotechnology, including Tissue Culture and Adventitious Rhizogenesis and Population (molecular) Genetics and Association Mapping of Tropical Deciduous Trees. He served as Assistant Editor of 'TFRI Newsletter' for 5 years (1997–2002) and Editor of peer-reviewed international 'Indian Journal of Tropical Biodiversity' for 10 years (2002–2012). He has edited two books and published >100 research papers/review articles/popular science articles and received global citations. He has also guided 11 students for doctorate programme. Dr Ansari has received several academic accolades; notable among them are University Gold Medal (Aligarh Muslim University, Aligarh) and R.D. Asana Gold Medal (Indian Society for Plant Physiology, New Delhi). Dr Ansari is an elected fellow of the Indian Botanical Society, the Indian Society for Plant Physiology, and the Linnean Society of London.

Mohammad Israil Ansari presently working at the Department of Botany, University of Lucknow, India. Dr Ansari is biologist with expertise in thrust areas, viz. Plant Stress Physiology, Plant Molecular Biology, Nanotechnology, Post-harvest and Agricultural Biotechnology. Before joining the University of Lucknow, Dr Ansari worked as Professor of Biotechnology at Amity Institute of Biotechnology, Amity University, Lucknow Campus, Lucknow, India (2007–2016). Since 2000–2007, Dr Ansari underwent international learning as Fellow of Academia Sinica and National Science Council Taiwan. Dr Ansari has been associated with the Institute of Botany, Academia Sinica, Taipei, Taiwan, Graduate Institute of Plant Biology, National Taiwan University, Taiwan, and Institute of Plant and Microbial Biology, Academia Sinica, Taipei, Taiwan. Dr Ansari graduated and post-graduated from the Department of Botany, Aligarh Muslim University, Aligarh, India, and doctoral degree from Dr. Ram Manohar Lohia Avadh University, Faizabad, India. Doctoral research work was carried out at the Indian Institute of Sugarcane Research, Lucknow. Dr Ansari has 29 years of research and 18 years of teaching experience with 109 research papers in international journals of high repute; he has authored and edited several books (Springer, Elsevier), book chapters, review articles, post-doctoral, PhD, post-graduate summer projects to his credit. Dr Ansari has completed several research projects funded by the Department of Science and Technology, Govt. of India. Presently, running a GABA-transaminase gene promoter project from Science and Engineering Research Board (SERB), DST, Government of India. Dr Ansari is editorial board member, reviewer of several international journals as well as member of several Academic Board/Faculty Board/ Board of Studies/Research and Development bodies. Dr Ansari has collaboration with several international group and delivered number of keynote address, invited lectures at national, international level.

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 the MSc Program and as 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 more than 20 years of experience in teaching, research, and administration. Dr Husen specializes in biogenic nanomaterial fabrication and application, plant responses to nanomaterials, plant adaptation to harsh environments at the physiological, biochemical, and molecular levels, herbal medicine, and clonal propagation for improvement of tree species. He has conducted several research projects sponsored by various funding agencies, including the World Bank, the Indian Council of Agricultural Research (ICAR), the Indian Council of Forestry Research and Education (ICFRE), and the Japan Bank for International Cooperation (JBIC). He has published over 150 research papers, review articles and book chapters, edited books of international repute, presented papers in several conferences, and produced over a dozen manuals and monographs. Dr Husen received four fellowships from India and a recognition award from the University of Gondar, Ethiopia, for excellent teaching, research, and community service. He has been an active organizer of seminars/conferences and an efficient evaluator of research projects and book proposals. Dr Husen has been on the editorial board and the panel of reviewers of several reputed journals published by Elsevier, Frontiers Media SA, Taylor & Francis, Springer Nature, RSC, Oxford University Press, Sciendo, The Royal Society, CSIRO, PLOS, and John Wiley & Sons. He is on the advisory board of Cambridge Scholars Publishing, UK. He is a Fellow of the Plantae group of the American Society of Plant Biologists and a Member of the International Society of Root Research, Asian Council of Science Editors, ISDS, and INPST. Dr Husen is Editor-in-Chief of the

American Journal of Plant Physiology. He is also working as Series Editor of ‘Exploring Medicinal Plants’, published by Taylor & Francis Group, USA; ‘Plant Biology, Sustainability, and Climate Change’, published by Elsevier Inc., MA 02139, USA; and ‘Smart Nanomaterials Technology’, published by Springer Nature Singapore Pte Ltd. Singapore.

Role of Nanosensors and Bionanosensors in Crop Abiotic Stress

1

Saima Amjad and Mohammad Serajuddin

Abstract

Plants have developed several defense mechanisms to overcome biotic and abiotic stresses. The external stresses (abiotic stress) included heavy metal toxicity, salinity, pollution, extremely low or high temperature, and water deficiency, which ultimately reduce crop quality and productivity. Currently, scientists are developing innovative technologies by combining configuration of biology, nanoscience, computers, and electronics to develop nanosensors and bionanosensors with powerful detecting abilities. Nanotechnology-based biosensor plays a vital role in crop disease management, and it helps in improving the quality and productivity of the crop. Several nanosensors and bionanosensors have been reported that are used for the detection of abiotic stresses in plants such as genetically encoded nanosensor, Surface-enhanced Raman scattering (SERS), fluorescence, carbon nanotubes, and nanoparticle-based bionanosensor, which detected the diseases in real time for precision farming. However, studies based on plant bionanosensors have recently gained momentum, and only a few research findings are available for the detection of abiotic stress. Additionally, more scientific studies are required for development and working of nanobiosensor in agriculture sector.

Keywords

Abiotic stresses · Nanosensor · Bionanosensor · Nanotechnology · Agriculture

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1.1 Introduction

Environmental stresses affected the plants in many ways, which limits the agricultural crop productivity and sustainability. Plants are confronted by two types of environmental stresses, which can be classified as abiotic and biotic stress. The environmental stresses inhibit plant augmentation, fertility, and vitality. The restricting abiotic stresses includes heavy metal toxicity, air pollution, mechanical damage, nutrient deficiency, drought, salinity, high UV radiation or low light, soil alkalinity or acidity, and extremely low or high temperatures (Iqbal et al. 2020). Annually, 16% of the crop is damaged due to microbial diseases (Moore et al. 2020) and crop loss due to plant diseases, ultimately a threat to world food security (Balodi et al. 2017). Therefore, it is necessary to detect the right stage of diseases in plants to control crop loss (Strange and Scott 2005). Hence, plant disease management in the agriculture sector is a difficult task because a large percentage of plant disorders are seen at the last stage of the disease. Application of pesticides and fungicides is used to deal with these problems. However, these plant protection products cause significant crop loss. Therefore, it is necessary to understand the proper amount and ideal time of pesticide application on plants, and accordingly, plant disease stage pesticide doses could be given and simultaneously get rid of residual pesticide toxicity and environmental hazard (Younas et al. 2020). Nanotechnology application provides much scope to tackle such kinds of problems and improved crop production in the agriculture sector by using nanomaterials (Robinson and Morrison 2009; Batsmanova et al. 2013).

Nanotechnology is the field of applied sciences, which manipulate matter on an atomic, molecular, and supramolecular scale, and it can provide such kind of tools and techniques, which revolutionized the agriculture sector. It is using new mechanisms to deliver agrochemical residues to reduce the pesticides toxic effects on nontargeted organisms (Amjad et al. 2018). Further applications consist of delivery of fertilizers, postharvest management, monitor plant growth, and diagnosis of agrochemical residues and disease causing pathogens in crops by nanosensors, crop improvement through genetic engineering of plants (Ghidan and Al Antary 2019; Sharma et al. 2019; Ansari et al. 2020). Nanoparticles and nanomaterials with at least one dimension are in the range of 1–100 nm (Roco 2003). They have different physical and chemical properties, high reactivity, and biochemical activities due to their very small from their original material (Nel et al. 2006; Dubchak et al. 2010).

Nanotechnology may have efficiency to provide and mainly make more efficient technologies at present used in environmental sensing, detection, and remediation (Manjunatha et al. 2016). Nanomaterials serve as an effective sensor for detection of biomarkers related to plant diseases and diagnosis (Sharma et al. 2021; Kumar et al. 2021, 2022; Khater et al. 2017; Fatmi et al. 2017; Khiyami et al. 2014). Nanosensors can also be used for sensing fertilizers, soil pH, moisture, and management of nutrients uptake and decreases the nutrient loss to enhance the crop yield (Kaushal and Wani 2017).

1.2 Abiotic Stress in Plants

Plants suffered from many abiotic stresses as shown in Fig. 1.1, which affect crop productivity in the whole world. The abiotic stresses occurring in plants are interrelated with each other in the form of plant cell homeostasis, osmotic stress, and malfunction of ion distribution (Gull et al. 2019).

Heat stress causes diversified effect on crops as it is a sessile organism, and high temperature causes alteration in plant growth and yield, physiological and developmental process (Lobell and Asner 2003; Lobell and Field 2007), and the main outcome of high temperature stress is oxidative stress due to excessive ROS (reactive oxygen species) generation (Hasanuzzaman et al. 2012, 2013). Cold stress is also harmful for plants as well as heat stress, and in low temperature condition, the water within plant cells freezes and expands as it turns to ice and cell membrane ruptures and leads to cell death. Plants can manage to cold temperature by activating metabolic pathways that protect plant cells from cold and freezing conditions (Kidokoro et al. 2017). Drought is another factor that critically threatens world crop productivity, and it depends on several factors in particular distribution and occurrence of rainfall, moisture holding capacity of soils, and evaporative demands (Farooq et al. 2009). High salinity stress causes impair crop production, and in response, several genes get upregulated, which are involved either directly or inversely proportional to the plant protection (Tuteja 2007). Heavy metal contamination of soil and water indirectly exposed to plants causes toxicity at the structural, physiological, and molecular levels and its constraint on the crop quality and productivity (Ovečka and Takáč 2014; Singh et al. 2016).

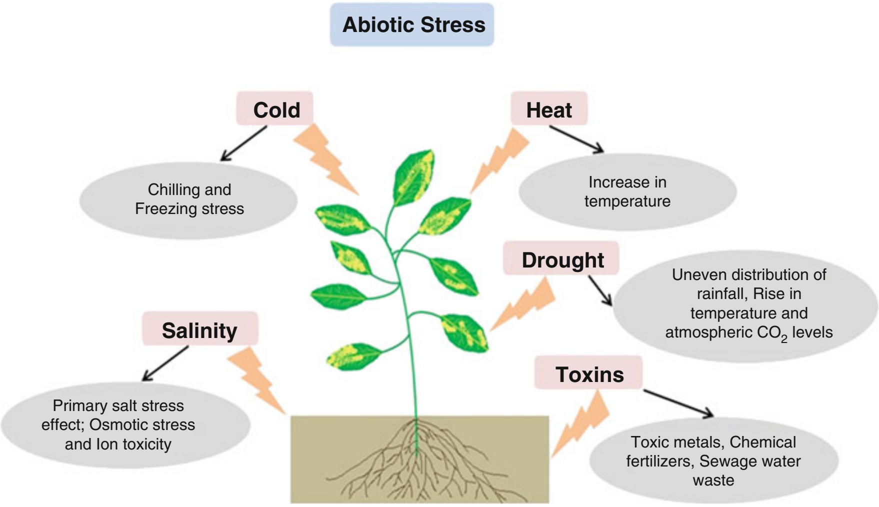

Fig. 1.1 Types of abiotic stress and their effects on plants

1.3 Nanosensors and Bionanosensors

Biosensor is defined as bioanalytical device that incorporates molecular entity linked with a physicochemical transducer (Tothill 2009). The first biosensor was invented by Leland C. Clark, Jr. in 1956 for oxygen detection (Heineman et al. 2006), which gave rise to advancement of various modified biosensors. Several biosensors have been designed to meet the necessities for a diverse range of applications in analyzing the disorders and disease (D'Orazio 2003), industrial process control (Baeumner 2003; Yu et al. 2005), food quality assurance, and environmental toxicant detection (Baeumner 2003; Terry et al. 2005; Yu et al. 2005). According to the report of Shawon et al. (2020) and Rai et al. (2012), history of biosensors broadly classified into three broad groups: first group included electrical response-based biosensors, second group included mediators between the reaction and the transducer, and the third group included mediator diffusion that is directly involved.

Nanosensor is defined as a chemical or mechanical sensor that measures the physical characteristics on a nanoscale or detects substances with at least one of their sensing dimensions is in the nanorange below 100 nm (Lim and Ramakrishna 2006). The application of nanosensors can be used in agriculture to detect chemical compounds in concentrations as low as one part per billion (Roman et al. 2004; Schedin et al. 2007).

The physical, chemical, and biological configuration of devices at nanoscale level developed bionanosensor. It is the advanced model of biosensor; it has a promising potential to sense minute amounts of biologically derived sensitized element (bacteria or virus) and chemical toxins, in agriculture and food system (Saranya et al. 2019; Turner 2000). In the last few decades, nanosensor is an emerging research area after the growing application of nanotechnology in the agricultural field, which approaches immeasurable potential advancement in sensitivity, speed, and selectivity as compared with conventional chemical and biological methods (Yusof and Isha 2020). Several types of nano-inspired biosensors are available and classified on the basis of rapid detection of abiotic stress, metabolic content, phytohormones, infections (fungal, viral, and bacterial), miRNAs, and genetically modified (GM) plants to transcriptional and genetically encoded biosensors (Kumar and Arora 2020). Wang et al. (2019) have reported biosensor to determine the alteration in electrochemical impedance for specific biomarkers, vitronectin-like (VN) proteins, which is secreted by the damage of plant cells. It helps for the detection of heavy metal stress such as cadmium and lead in *Arabidopsis* and soybean plants.

1.4 Types of Nanosensor and Bionanosensor on the Basic Mechanism of Function

The latest development in merging nanotechnology and synthetic chemistry has been constructed high-quality nanomaterials in the form of nanocomposites, nanoarrays, and nanoparticles such as nanotubes, nanorods, nanospheres, nanowires,

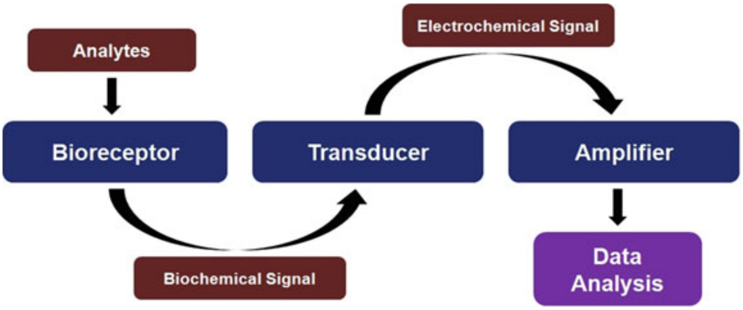

Fig. 1.2 Bionanosensor basic configuration and mechanism of action

etc. (Hu et al. 2010; Xianmao et al. 2008). The application of nanomaterials has been used for biosensor development because of the significant advantages of nanoparticles such as large surface area to volume ratio, shape-dependent properties, quantum size properties, low cost, lesser energy consumption, and small scale biosensors (Jaiswal et al. 2003; Liu and Lu 2003; Vaseashta and Dimova-Malinovska 2005; Wang 2005; Xu et al. 2009; Aguilar et al. 2010a; Aguilar et al. 2010b; Xu et al. 2011; Byers and Hitchman 2011). Currently, several bionanosensors are at various stages of their development (Fogel and Limson 2016) such as tool modifications, measures, fabrication procedures, and imaging of nanoscale materials. Several types of approaches are used for the manufacturing of nanosensor, which includes molecular configuration, top-down lithography, and bottom-up congregation (Foster 2006). Bionanosensors are basically composed of three components: a bioreceptor that recognizes the analytes (like enzymes and nucleic acid probes, e.g., substrates or the enzyme-substrate complex, complementary DNA, and antigens), which produces signals, transducer that transforms biochemical signals into electrical signals and connects with electronic device, or amplifier which amplifies the signals as shown in Fig. 1.2 (Grieshaber et al. 2008) and data is collected by electronic device.

The signal strength emitted may be directly or inversely proportional to the concentration of the analytes (Patra et al. 2019). The classification of nanosensors is very diverse as shown in Fig. 1.3. Several particular nanosensor types have been used including carbon-based electrochemical nanosensors (Qureshi et al. 2009), fluorescence resonance energy transfer (FRET)–based nanosensors (Stanisavljevic et al. 2015; Chen et al. 2013; Okumoto et al. 2012), antibody nanosensors (Wujcik et al. 2014), nanowire nanosensors (Patolsky and Lieber 2005), and plasmonic nanosensors (Choi and Choi 2012).

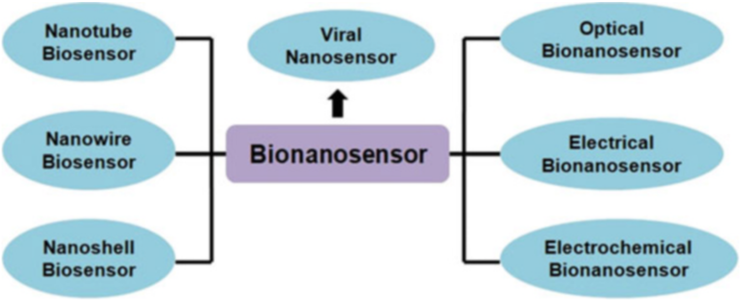

Fig. 1.3 Classification of bionanosensor

1.5 Application of Nanosensor and Bionanosensor for Detection of Abiotic Stress in Crops

Nanobiotechnology has the potential approach to design and synthesized smart bionanosensors that communicate with and actuate electronic tools for enhancement of agriculture productivity (Giraldo et al. 2019). Abiotic stress has a negative impact on the crop, and through continuous exposure of nonliving factors, it leads to changes in usual functioning of plant growth, which eventually lethal for plant. Therefore, identification of abiotic stress in crop plants is necessary, and these stress effects have been observed through visible changes in plants, thermal analysis, proteins, decrease in normal functions, expression of some new receptors, reactive oxygen species, etc.

Ali et al. (2020) constructed a genetically modified nanosensor (FLIP-H_2O_2), which was highly selective to H_2O_2 and pH stable and not sensitive to other oxidants such as superoxide anions, peroxynitrite, and nitric oxide. It has been based on fluorescence resonance energy transfer (FRET) in configuration with regulatory domain of OxyR between two fluorescent moieties, namely, ECFP and mVenus. H_2O_2 act as fundamental regulatory functions in metabolic processes and during stress condition, and the level of H_2O_2 enhances in the cells and causes oxidative stress, which interferes with regular growth in plants and animals cell. FRET nanosensor has capability for noninvasive real-time monitoring of H_2O_2 in any cell type. Additionally, FLIP-H_2O_2 can be attached to cellular organelles, like mitochondria and chloroplasts, and it can be used for monitoring for in vivo subcellular signal targeting (Ali et al. 2020).

Alova et al. (2020) have developed oxygen nanosensors for electrochemical measurement of oxygen content in *Chara corallina* internodal cells made up of quartz micropipettes carbon-filled with platinum-coated tips. The platinum nanoelectrodes are beneficial to understand the cell oxygen metabolism, and it measured the drastic decrease in oxygen concentration of microinjury occurred in *Chara corallina* cells (Alova et al. 2020).

Massachusetts Institute of Technology (MIT) engineers have designed and developed single-wall carbon nanotubes (SWCNT) nanosensors and implanted inside the plant leaves, which identify and communicate various stress conditions through nIR optical signals, and these signals can be received through e-mails and text messages on smartphone (MIT 2020).

Wang and Li (2008) synthesized ZrO_2/Au (zirconium dioxide/gold) nanocomposite films by sol–gel method and its application based on voltammetric sensing, which detect organophosphate pesticides. The strong sensitivity and selectivity of phosphate group on parathion molecules are detected by ZrO_2/Au nanosensor film electrode, which gives signals in wave voltammetry.

Soil humidity and its temperature are important components in maintaining the exchange of water and temperature between the soil surface and the environment through evaporation and transportation. Microelectromechnical systems (MEMS)–based nanosensor has been developed to work on a shear stress principal, in which the microsensor chip joins a proprietary polymer sensing component and piezoresistor circuit that is Wheatstone bridge to transport two DC output voltages that are linearly proportional to moisture and temperature (Jackson et al. 2008).

Liposome bionanosensor can be used for monitoring the organophosphorus (dichlorvos and paraoxon) pesticides (Vamvakaki and Chaniotakis 2007). The identification of particular toxins occurred at very low level in sewage sludge, herbicide, and contaminants of urban and industrial effluents causing pollution can be easily detected (Giardi and Piletska 2006). The latest development of nanosensor based on the FRET configuration was used for the detection of acetylcholinesterase (AChE) activity and toxic Cd^{2+} (Cadmium ions) in water samples.

Silicon nanoparticles (Si-NPs) exhibit immense potential in agriculture and may effort better in alleviating different abiotic stresses (Tripathi et al. 2015, 2017; Cui et al. 2017; Abdel-Haliem et al. 2017). According to Rastogi et al. (2019), Si-NPs can also be used as delivery agents for nucleotides and proteins and used for detection of toxins in plants by incorporation with nanozeolite and nanosensors. Additionally, the core–shell of Si-NPs gives extensive advantages when used as nanosensor in terms of sensor stability, sensitivity, and accuracy (Sun et al. 2016). Si-NPs may be effectively used in drought stress conditions for increasing the water holding capacity of soil particles. Liu et al. (2014) synthesized dual-emission nanosensor by coating carbon dots on the surface of rhodamine B-doped Si-NPs and successfully used application for the recognition of toxic copper ions (Cu^{2+}) in water.

Formaldehyde is a widespread environmental contamination and commonly found in industrial pollutant. It is one of the abiotic stresses occurred by formaldehyde in plants and altered many factors including chlorophyll content, ascorbate peroxidase (APX), carotenoid content, the activity of peroxidase (POD), soluble protein and sugar contents, the superoxide anion production, and lipid peroxidation rate (Erofeeva 2018). Silver nanoparticles (AgNPs) and gold nanoparticles (AuNPs) are developed as surface enhanced Raman-active substrates sensor for detection of formaldehyde analysis by SERS (Qu et al. 2012; Zhang et al. 2014; Ma et al. 2014; Lv et al. 2014).

Table 1.1 Types of nanosensor/bionanosensor for plant disease detection

Nanosensor/ bionanosensor	Mechanism	References
FRET nanosensor	Real-time monitoring of H_2O_2 and pH stable	Ali et al. (2020)
	Sensing of acetylcholinesterase (AChE) activity and toxic Cd^{2+} in water sample	Fang et al. (2017)
Oxygen nanosensor	Measured cell oxygen metabolism and drastic decrease in oxygen concentration due to microinjury occurred in *Chara corallina* cells	Alova et al. (2020)
SWCNT nanosensor	Identify and communicate various stress conditions	MIT (2020)
ZrO_2/au nanocomposite films	Detection of organophosphate pesticides gives signals in wave voltammetry	Wang and Li (2008)
Microelectromechnical systems (MEMS)	Soil moisture detection	Jackson et al. (2008)
Liposome bionanosensor	Monitoring the organophosphorus (dichlorvos and paraoxon) pesticides	Vamvakaki and Chaniotakis (2007)
Si-NPs nanosensor	Detection of toxic metals and water holding capacity	Sun et al. (2016)
Carbon dots coated rhodamine B-doped Si-NPs	Detection of toxic copper ions (Cu^{2+}) in water	Liu et al. (2014)
AgNPs and AuNPs SERS	Formaldehyde detection	Qu et al. (2012), Zhang et al. (2014), Ma et al. (2014), Lv et al. (2014)

The importance of abiotic stress detection at early stage by nano-inspired biosensor improves plant health (Table 1.1). The existing technology, tools, and ongoing researches in the area of nanosensor and bionanosensor provide better and advanced machines for monitoring of plant health and growth.

1.6 Conclusion and Future Prospects

The widespread application of nanosensors and bionanosensors advances smart agriculture systems and improves crop quality and its productivity. Nano-inspired biosensors already developed various diagnosis techniques to analyze diseases in medical studies and toxicants in the environment and agriculture sector. Nano-inspired biosensors can help and detect several agricultural problems in real-time and implement solutions not only for abiotic stresses but also for biotic stresses including plant phytopathology, temperature, and soil contamination by chemicals and heavy metals. The future nano-inspired biosensor can be configured with GPS and robotics systems to synthesize smart sensors to detect trace and treat plants in the agriculture field earlier to or during the starting of symptoms. Additionally, to survive under stress conditions, extremely sophisticated and competent tolerance mechanisms sensors have been developed already such as genetically modified nanosensor (FLIP-H_2O_2), carbon nanotubes, liposome-based bionanosensors, and nanoparticle-based sensors that have been evolved to adapt to the stresses. However, these studies are limited to the laboratory environments; therefore, more studies are needed to approach these experiments in regular agriculture practices to overcome the abiotic stress for better plant growth and development.

References

Abdel-Haliem MEF, Hegazy HS, Hassan NS, Naguib DM (2017) Effect of silica ions and nano silica on rice plants under salinity stress. Ecol Eng 99:282–289

Aguilar Z, Aguilar Y, Xu H, Jones B, Dixon J, Xu H, Wang A (2010a) Nanomaterials in medicine. Electrochem Soc Trans 33:69–74

Aguilar Z, Xu H, Jones B, Dixon J, Wang A (2010b) Semiconductor quantum dots for cell imaging. Mater Res Soc Symp Proc 1237:1206–1201

Ali HM, Ahmad M, Salem MZ, Ahmad A (2020) Construction of a nanosensor for non-invasive imaging of hydrogen peroxide levels in living cells. Biology 9(12):430

Alova A, Erofeev A, Gorelkin P, Bibikova T, Korchev Y, Majouga A, Bulychev A (2020) Prolonged oxygen depletion in microwounded cells of *Chara corallina* detected with novel oxygen nanosensors. J Exp Bot 71(1):386–398

Amjad S, Sharma AK, Serajuddin M (2018) Toxicity assessment of cypermethrin nanoparticles in *Channa punctatus*: behavioural response, micronuclei induction and enzyme alteration. Regul Toxicol Pharmacol 100:127–133

Ansari M, Shahzadi K, Ahmed S (2020) Nanotechnology: a breakthrough in agronomy. In: Nanoagronomy. Springer, Cham, pp 1–21

Baeumner AJ (2003) Biosensors for environmental pollutants and food contaminants. Anal Bioanal Chem 377:434e445

Balodi R, Bisht S, Ghatak A, Rao KH (2017) Plant disease diagnosis: technological advancements and challenges. Ind Phyto 70(3):275–281

Batsmanova LM, Gonchar LM, Taran NY, Okanenko AA (2013) Using a colloidal solution of metal nanoparticles as micronutrient fertilizer for cereals. Doctoral dissertation, Sumy State University

Byers R, Hitchman E (2011) Quantum dots brighten biological imaging. Prog Histochem Cytochem 45:201–237

Chen G, Song F, Xiong X, Peng X (2013) Fluorescent nanosensors based on fluorescence resonance energy transfer (FRET). Ind Eng Chem Res 52:11228–11245

Choi I, Choi Y (2012) Plasmonic nanosensors: review and prospect. IEEE Quantum Electron 18: 1110–1122

Cui J, Liu T, Li F, Yi J, Liu C, Yu H (2017) Silica nanoparticles alleviate cadmium toxicity in rice cells: mechanisms and size effects. Environ Pollut 228:363–369

D'Orazio P (2003) Biosensors in clinical chemistry. Clin Chim Acta 334:41e69

Dubchak S, Ogar A, Mietelski JW, Turnau K (2010) Influence of silver and titanium nanoparticles on arbuscular mycorrhiza colonization and accumulation of radiocaesium in *Helianthus annuus* span. J Agric Res 8:S103–S108

Erofeeva EA (2018) Hormesis and paradoxical effects of pea (*Pisum sativum* L.) parameters upon exposure to formaldehyde in a wide range of doses. Ecology 27:569–577

Farooq M, Wahid A, Kobayashi N, Fujita DBSMA, Basra SMA (2009) Plant drought stress: effects, mechanisms and management. In: Sustainable agriculture. Springer, Dordrecht, pp 153–188

Fatmi M, Walcott RR, Schaad NW (2017) Detection of plant-pathogenic bacteria in seed and other planting material. APS Press, St. Paul

Fogel R, Limson J (2016) Developing biosensors in developing countries: South Africa as a case study. Biosensors 6(1):5

Foster LE (2006) Medical nanotechnology: science, innovation, and opportunity. Pearson Education, Upper Saddle River

Ghidan AY, Al Antary TM (2019) Applications of nanotechnology in agriculture. In: Applications of nanobiotechnology. IntechOpen, Rijeka

Giardi MT, Piletska EV (2006) Biotechnological applications of photosynthetic proteins: biochips, biosensors and biodevices. In: Biotechnology intelligence unit. Springer, New York

Giraldo JP, Wu H, Newkirk GM, Kruss S (2019) Nanobiotechnology approaches for engineering smart plant sensors. Nat Nanotechnol 14(6):541–553

Grieshaber D, MacKenzie R, Vörös J, Reimhult E (2008) Electrochemical biosensors-sensor principles and architectures. Sensors 8(3):1400–1458

Gull A, Lone AA, Wani NUI (2019) Biotic and abiotic stresses in plants. In: Abiotic and biotic stress in plants. IntechOpen, Rijeka

Hasanuzzaman M, Hossain MA, da Silva JAT, Fujita M (2012) Plant responses and tolerance to abiotic oxidative stress: antioxidant defenses is a key factor. In: Crop stress and its management: perspectives and strategies. Springer, Berlin, pp 261–316

Hasanuzzaman M, Nahar K, Fujita M (2013) Extreme temperatures, oxidative stress and antioxidant defense in plants. In: Abiotic stress—plant responses and applications in agriculture. InTech, Rijeka, pp 169–205

Heineman WR, Jensen WB, Clark LC Jr (2006) Biosensors. Bioelectron 21:1403–1404

Hu L, Kim H, Lee J, Peumans P, Cui Y (2010) Scalable coating and properties of transparent, flexible, silver nanowire electrodes. ACS Nano 4:2955–2963

Iqbal S, Waheed Z, Naseem A (2020) Nanotechnology and abiotic stresses. In: Nanoagronomy. Springer, Cham, pp 37–52

Jackson T, Mansfield K, Saafi M, Colman T, Romine P (2008) Measuring soil temperature and moisture using wireless MEMS sensors. Measurement 41(4):381–390

Jaiswal J, Mattoussi H, Mauro J, Simon S (2003) Long-term multiple color imaging of live cells using quantum dot bioconjugates. Nat Biotechnol 21:47–51

Kaushal M, Wani SP (2017) Nanosensors: frontiers in precision agriculture. In: Nanotechnology. Springer, Singapore, pp 279–291

Khater M, de la Escosura-Muniz A, Merkoc A (2017) Biosensors for plant pathogen detection. In: Biosensors and bioelectronics. Elsevier, Essex

Khiyami MA, Almoammar H, Awad YM, Alghuthaymi MA, Abd-Elsalam KA (2014) Plant pathogen nanodiagnostic techniques: forthcoming changes? Biotech & Biotechnolo Equip 28(5):775–785

Kidokoro S, Yoneda K, Takasaki H, Takahashi F, Shinozaki K, Yamaguchi-Shinozaki K (2017) Different cold-signaling pathways function in the responses to rapid and gradual decreases in temperature. Cell 29(4):760–774

Kumar V, Arora K (2020) Trends in nano-inspired biosensors for plants. Mater Sci Ene Technol 3: 255–273

Kumar A, Choudhary A, Kaur H, Mehta S, Husen A (2021) Metal-based nanoparticles, sensors and their multifaceted application in food packaging. J Nanobiotechnol 19:256. https://doi.org/10.1186/s12951-021-00996-0

Kumar A, Choudhary A, Kaur H, Guha S, Mehta S, Husen A (2022) Potential applications of engineered nanoparticles in plant disease management: a critical update. Chemosphere. https://doi.org/10.1016/j.chemosphere.2022.133798

Lim TC, Ramakrishna S (2006) A conceptual review of nanosensors. Zeitschrift für Naturforschung 61:402–412

Liu J, Lu YA (2003) Colorimetric Lead biosensor using DNAzyme-directed assembly of gold nanoparticles. J Am Chem Soc 125:6642–6643

Liu X, Zhang N, Bing T, Shangguan D (2014) Carbon dots based dual-emission silica nanoparticles as a ratiometric nanosensor for Cu^{2+}. Anal Chem 86(5):2289–2296

Lobell DB, Asner GP (2003) Climate and management contributions to recent trends in U.-S. agricultural yields. Science 299:1078475

Lobell DB, Field CB (2007) Global scale climate–crop yield relationships and the impacts of recent warming. Environ Res Lett 2:5

Lv ZY, Mei LP, Chen WY, Feng JJ, Chen JY, Wang AJ (2014) Shaped-controlled electrosynthesis of gold nanodendrites for highly selective and sensitive SERS detection of formaldehyde. Sens Actuator B-Chem 201:92–99

Ma P, Liang F, Wang D, Yang Q, Ding Y, Yu Y, Gao D, Song D, Wang X (2014) Ultrasensitive determination of formaldehyde in environmental waters and food samples after derivatization and using silver nanoparticle assisted SERS. Microchim Acta 182:863–869

Manjunatha SB, Biradar DP, Aladakatti YR (2016) Nanotechnology and its applications in agriculture: a review. J Farm Sci 29(1):1–13

Massachusetts Institute of Technology (MIT) (2020) Nanosensor can alert a smartphone when plants are stressed: carbon nanotubes embedded in leaves detect chemical signals that are produced when a plant is damaged. Science daily. https://www.sciencedaily.com/releases/2020/04/200415133512.htm

Moore D, Robson GD, Trinci AP (2020) 21st century guide book to fungi. Cambridge University Press, Cambridge

Nel A, Xia T, Madler L, Li N (2006) Toxic potential of materials at the nanolevel. Science 311: 622e627

Okumoto S, Jones A, Frommer WB (2012) Quantitative imaging with fluorescent biosensors. Annu Rev Plant Biol 63:663–706

Ovečka M, Takáč T (2014) Managing heavy metal toxicity stress in plants: biological and biotechnological tools. Biotechn Advan 32(1):73–86

Patolsky F, Lieber CM (2005) Nanowire nanosensors. Mater Today 8:20–28

Patra JK, Mahato DK, Kumar P (2019) Biosensor technology—advanced scientific tools, with special reference to nanobiosensors and plant-and food-based biosensors. In: Nanomaterials in plants, algae and microorganisms. Academic Press, Amsterdam, pp 287–303

Qu WG, Lu LQ, Lin L, Xu AW (2012) A silver nanoparticle based surface enhanced resonance Raman scattering (SERS) probe for the ultrasensitive and selective detection of formaldehyde. Nanoscale 4:7358–7361

Qureshi A, Kang WP, Davidson JL, Gurbuz Y (2009) Review on carbon-derived, solid-state, micro and nano sensors for electrochemical sensing applications. Diamond Relat Mater 18:1401–1420

Rai V, Acharya S, Dey N (2012) Implications of nanobiosensors in agriculture. J Biomater Nanobiotechnol 3:315

Rastogi A, Tripathi DK, Yadav S, Chauhan DK, Živčák M, Ghorbanpour M, Brestic M (2019) Application of silicon nanoparticles in agriculture. 3 Biotech 9(3):90

Robinson DKR, Morrison M (2009) Nanotechnology developments for the Agrifood sector report

Roco MC (2003) Broader societal issue of nanotechnology. J Nanopart Res 5:181e189

Roman C, Ciontu F, Courtois B (2004) Single molecule detection and macromolecular weighting using an all-carbon-nanotube nanoelectromechanical sensor. In 4th IEEE conference on Nanotechnology, pp 263–266

Saranya S, Aswani R, Remakanthan A, Radhakrishnan EK (2019) Nanotechnology in agriculture. In: Nanotechnology for agriculture. Springer, Singapore, pp 1–17

Schedin F, Geim AK, Morozov SV, Hill EW, Blake P, Katsnelson MI, Novoselov KS (2007) Detection of individual gas molecules adsorbed on graphene. Nat Mater 6(9):652–655

Sharma D, Sharma J, Dhuriya YK (2019) Nanotechnology: a novel strategy against plant pathogens. In: Nanotechnology for agriculture: crop production & protection. Springer, Singapore, pp 153–170

Sharma P, Pandey V, Sharma MMM, Patra A, Singh B, Mehta S, Husen A (2021) A review on biosensors and nanosensors application in agroecosystems. Nanoscale Res Lett 16:136. https://doi.org/10.1186/s11671-021-03593-0

Shawon ZBZ, Hoque ME, Chowdhury SR (2020) Nanosensors and nanobiosensors: agricultural and food technology aspects. In: Nanofabrication for smart nanosensor applications. Elsevier, Amsterdam, pp 135–161

Singh S, Parihar P, Singh R, Singh VP, Prasad SM (2016) Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics, and ionomics. Front Plant Sci 6:1143

Stanisavljevic M, Krizkova S, Vaculovicova M, Kizek R, Adam V (2015) Quantum dots-fluorescence resonance energy transfer-based nanosensors and their application. Biosens Bioelectron 74:562–574

Strange RN, Scott PR (2005) Plant disease: a threat to global food security. Annu Rev Phytopathol 43:83–116

Sun D, Hussain HI, Yi Z, Rookes JE, Kong L, Cahill DM (2016) Mesoporous silica nanoparticles enhance seedling growth and photosynthesis in wheat and lupin. Chemosphere 152:81–91

Terry LA, White SF, Tigwell LJ (2005) The application of biosensors to fresh produce and the wider food industry. J Agric Food Chem 53:1309e1316

Tothill IT (2009) Review: biosensors for cancer markers diagnostics. Semin Cell Dev Biol 20:55–62

Tripathi DK, Singh S, Singh VP, Prasad SM, Dubey NK, Chauhan DK (2017) Silicon nanoparticles more effectively alleviated UV-B stress than silicon in wheat (*Triticum aestivum*) seedlings. Plant Physiol Biochem 110:70–81

Tripathi DK, Singh VP, Prasad SM, Chauhan DK, Dubey NK (2015) Silicon nanoparticles (SiNp) alleviate chromium (VI) phytotoxicity in *Pisum sativum* (L.) seedlings. Plant Physiol Biochem 96:189–198

Turner AP (2000) Biosensors-sense and sensitivity. Science 290(5495):1315–1317

Tuteja N (2007) Mechanisms of high salinity tolerance in plants. In methods in enzymology. Academic Press 428:419–438

Vamvakaki V, Chaniotakis NA (2007) Pesticide detection with a liposome-based nano-biosensor. Biosens Bioelectron 22(12):2848–2853

Vaseashta A, Dimova-Malinovska D (2005) Nanostructured and nanoscale devices, sensors and detectors. Sci Technol Adv Mat 6:312–318

Wang J (2005) Nanomaterial-based electrochemical biosensors. Analyst 130:421–426

Wang M, Li Z (2008) Nano-composite ZrO_2/au film electrode for voltammetric detection of parathion. Sens Actuators B 133(2):607–612

Wang X, Cheng M, Yang Q, Wei H, Xia A, Wang L, Ben Y, Zhou Q, Yang Z, Huang X (2019) A living plant cell-based biosensor for real-time monitoring invisible damage of plant cells under heavy metal stress. Sci Env 697:134097

Wujcik EK, Wei H, Zhang X, Guo Y, Yan X et al (2014) Antibody nanosensors: a detailed review. RSC Adv 4:43725–43745

Xianmao L, Yavuz M, Tuan H, Korgel B, Xia Y (2008) Ultrathin gold nanowires can be obtained by reducing polymeric strands of oleylamine-AuCl complexes formed via aurophilic interaction. J Am Chem Soc 130:8900–8901

Xu H, Aguilar Z, Dixon J, Jones B, Wang A, Wei H (2009) Breast cancer cell imaging using semiconductor quantum dots. Electrochem Soc Trans 25:69–77

Xu H, Aguilar Z, Wei H, Wang A (2011) Development of semiconductor nanomaterial whole cell imaging sensor on silanized microscope slides. Front Biosci E3:1013–1024

Younas A, Yousaf Z, Rashid M, Riaz N, Fiaz S, Aftab A, Haung S (2020) Nanotechnology and plant disease diagnosis and management. In: Nanoagronomy. Springer, Cham, pp 101–123

Yu D, Blankert B, Vire JC, Kauffmann JM (2005) Biosensors in drug discovery and drug analysis. Anal Lett 38:1687e1701

Yusof NA, Isha A (2020) Nanosensors for early detection of plant diseases. In: Nanomaterials for agriculture and forestry applications. Elsevier, Amsterdam, pp 407–419

Zhang Z, Zhao C, Ma Y, Li G (2014) Rapid analysis of trace volatile formaldehyde in aquatic products by derivatization reaction-based surface enhanced Raman spectroscopy. Analyst 139: 3614–3621

Role of Environment Stress Leaf Senescence and Crop Productivity

2

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Abstract

Senescence is known to be an ending event of leaf development that is represented by the formative age and impacted by the various environmental stress conditions. Leaf senescence is a factor that limits the shelf life of foliar vegetables starting most quickly in the outer, physiologically older leaves. Its adverse effects limited not only on crops productivity during harvesting but also on vegetable crops and ornamental plants after harvest decreases the quality of the crops during storage, transportation, and on the shelves; several nutrients in senescing leaves are degraded. Postharvest storage is an important aspect of plant senescence, and controlling the time of ripening and improving the shelf life of postharvest vegetables could be accomplished by regulating the key genes of senescence. Substantial development in the physiological and molecular understanding of senescence has made it probable to develop strategies to manipulate senescence for agricultural improvement to prolong the storing and shelf-life of several leafy vegetables and ornamental plants.

Keywords

Leaf senescence · Internal and external factors · Adverse environmental conditions · Physiological and molecular strategies

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2.1 Introduction

Leaf senescence is the last and important developmentally coordinated process of plant, which includes various integrated events at several levels of plant; it encourages the transportation of the nutrients to emerging parts of the plant and involves constant changes in the function or composition of several cellular components with a change in expression of most of genes (Jalil et al. 2017, 2019). These events of leaf senescence process involve first the degeneration of chloroplasts and the interruption in photosynthesis that are trailed by deterioration and membrane leakiness, which at last results in debasement of macromolecules and attrition of mitochondria and nuclei (Jing et al. 2003; Lim et al. 2007). The chlorophyll and protein turnover are impaired and usually many metabolites decline.

Leaf senescence can be trigged by various internal and external factors, adverse environmental conditions, and biological stress such as high temperature, inadequate light, cold stress, drought, nutrient inadequacy, and pathogen attack, which are responsible for leaf senescence. Internal factors include developmental progresses, phytohormone, and age. Flowering and fruit ripening can trigger leaf senescence, especially in monocarpic plants (Nooden 1988).

The nutrients are restored in special tissue of the trunk in the deciduous trees, whereas in annually growing crops, the nutrients are stored as integral component of the germinating seeds. Leaf senescence process is important for the longevity of the plant in the favorable conditions. The important role of senescence in plants is recycling and mobilization of nutrients. Large amount of nutrients are produced in the development and growth period of young leaves in plant. When the leaf senescence process is initiated, the senescence leaves remobilized or recycled all its nutrients to the growing and developing part of plant (Smart 1994; Nam 1997; Himelblau and Amasino 2001; Lim et al. 2007; Ansari and Chen 2011).

Dyeing of leaves is the last phase of senescence process, but this phase will not occur until nutrients present in the senescence leaves have been remobilized by senescence. It is proved by several investigations that leaf senescence is a reversible process, if it is environmentally induced. Due to exposure of different treatments, fully yellow leaves that have recycled all its nutrients can be changed into green leaves (Thomas and Donnison 2000). The regreening can be obtained by cytokinins or gibberellins application. The chloroplasts have capability to reconstruct its structure, chloroplast proteins begin to synthesize, and photosynthesis is reinitiated. These features display that a senescing leaf is regulated from the initiation to the completion of the process. Similar to the developmental stage, senescence process can also be occurred prematurely by various environmental stresses. Plants cannot completely fight with adverse conditions, and only the mechanism of senescence has capability to compete with this situation. Some plant organs sacrificed itself to increases the possibility of vitality of the other part of the plant. Similarly, infection of microbes on one leaf resulted to induced senescence in that leaf. Thus, it permits the plant to move nutrients far from the developing pathogen, to recover the nutrients previously the leaf is disposed of to expel the source of contamination from the region of the still uninfected parts of the plant (Buchanan-Wollaston et al. 2003).

Moreover, stress conditions such as nutrient restriction or starvation, oxidative stress, salt stress, or drought induced premature senescence, short lifespan of leaves or the complete plant.

2.1.1 Onset of Leaf Senescence

The mechanism of leaf senescence is completed in highly coordinated manner, and the components of cell are disassembled in an ordered progression. Degradation of chlorophyll is the first and momentous step of leaf senescence; however, when yellowing of the leaves can be seen, most of the events of the senescence have happened (Buchanan-Wollaston et al. 2003). In particular, the chlorophyll decline is due to the reduction of chlorophyll biosynthesis. During the first stage of senescence, the chlorophyll the total chlorophyll does not decline because part of the chl b is converted in chla. It means that in the first stage, the total chlorophyll does not change but change the ratio chla/chl b with a reduction of chl b concentration. The degradation of protein and other macromolecules followed by decline in the activity of photosystem, nutrients, and minerals remobilized from the senescent leaf to the developing part of plants (Lim et al. 2007; Ansari et al. 2005, 2014). The total protein content declines, and the type of proteins changes. In particular, the protein involved in the degradation or defense from the oxidative stress increases as shown in Fig.2.1.

2.1.2 Degradation of Chlorophyll

Scientists investigated the mechanism of proteins and chlorophyll degradation during the process of senescence. In the last few years, many studies have been done on pathway for degradation of chlorophyll, and various genes were cloned, which was associated with this pathway. However, none of these genes expressed during senescence process (Takamiya et al. 2000). An important pathway enzyme is identified as p recycled heophorbide α-oxygenase that cleaved the ring of tetrapyrrole and form RCC (red chlorophyll catabolite) (Hortensteiner 1998).

Pheophorbide *A* oxygenase knock out mutant of *Festuca pratensis*(*sid*) is stay-green phenotype and accumulated pheophorbide *a* (Vicentini et al. 1995). During the senescence process, activity of pheophorbide *a* oxygenase enzyme elevated, indicating that this enzyme acts as a control point in this process. Characterization and cloning of this gene will be an important step to underlying mechanisms for the regulation of chlorophyll degradation. The last product of catabolism of chlorophyll was NCCs (non-fluorescent chlorophyll catabolites) that deposited in the vacuole and not recycled nitrogen that stored in it. Thus, the energy-taking step of chlorophyll degradation was not involved in the recycling of the nutrients, while detoxified the highly reactive products of pigment-protein complexes. Therefore, this is important for the plant cell viability during leaf senescence process.

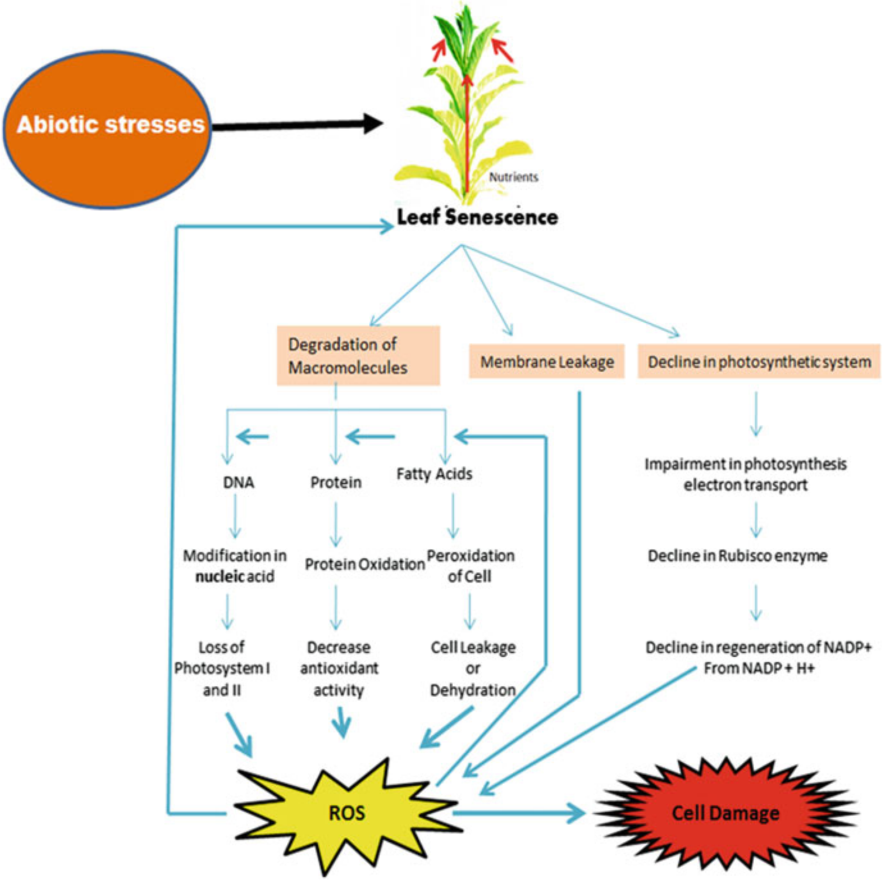

Fig. 2.1 During leaf senescence process, production of free radicals that leads to cell damage

Chlorophyll degradation is important during senescence process, which proved by the characterization of gene *accelerated cell death 2* (*Acd2*); enzyme of this gene plays important in chlorophyll degradation. Disruption in the activity of this enzyme causes rapid cell death by the accumulation of phytotoxic chlorophyll products, i.e., RCC (Hortensteiner 1998; Buchanan-Wollaston et al. 2003).

2.1.3 Degradation of Protein

During leaf senescence, approximately 75% protein of chloroplast in leaves is degraded and recycled, and the mechanism of this process is still unclear. Several genes encoding for protease are upregulated during senescence, while it is observed that these gene encoding enzymes are present in the vacuole. Thus, they are not connected with proteins of chloroplast till the leakage of membranes occurs due to senescence (Buchanan-Wollaston et al. 2003). Many studies proved that proteins that localized in stroma such as glutamine synthetase and RuBisCO degraded by ROS in photooxidative stress conditions of chloroplasts (Ishida et al. 1999). However, it is still unclear whether enhanced ROS production is involved in degradation of RuBisCO during senescence. However, increased ROS production during senescence is caused by the degradation of macromolecules and thus takes place after the initiation of lipid and protein degradation.

2.1.4 Degradation of Lipids

The functional and structural integrity of the cell membrane is deteriorated during leaf senescence due to the acceleration of membrane lipid metabolism. Several enzymes such as phosphatidic acid phosphatase, lipoxygenase, phospholipase D, and lytic acyl hydrolase are involved in this process; many genes that encoded these enzymes were highly expressed in leaf senescence (He and Gan 2002). During senescence, abundant source of carbon is released from the thylakoid membranes that can be recycled and used as a source of energy. Mature leaves possess peroxisomal fatty acid β-oxidation-associated enzymes, and this pathway becomes important when the source of carbohydrate decreased during leaf senescence. Enzyme-encoding genes that expressed enhanced senescence were utilized for β-oxidation, and it shows that these pathways were essential for the degradation and remobilization of lipid while the signals involved in these pathways during senescence are still unclear.

Breakdown of fatty acid generates acetyl CoA that directly utilized for respiration or, acetyl CoA derived from gluconeogenesis and glyoxylate pathway used for the synthesis of sugars that was transported. Pyruvate orthophosphate dikinase enzyme encoding senescence-enhanced expression gene converted pyruvate to sugars by gluconeogenesis pathway, which shows that this pathway metabolized in leaf senescence. It has been reported that leaf senescence was affected by the modification of acyl hydrolase genes that was associated with lipid degradation. Transformed *Arabidopsis thaliana* plants that had limited concentration of a senescence-enhanced lipase expressed late leaf senescence (Hong et al. 2000). Similarly, antisense suppression of acyl hydrolase gene (*SAG101*) of *Arabidopsis thaliana* shows delayed leaf senescence (He and Gan 2002). Moreover, overexpression of this gene induced the leaf senescence process.

Analysis of nutrient mobilization from *Arabidopsis thaliana* leaves showed that the concentration of various elementary compounds such as Cr, Mo, S, Fe, Zn, and Cu decreased up to 50% in senescent leaves in comparison with green leaves. Concentration of the macronutrients like K, N, and P reduced up to 80% (Himelblau and Amasino 2001). Genes that encode enzymes involved in the mobilization processes are not elucidated. Glutamine synthetase (GS) level increased in cytosol during senescence; this enzyme is likely to play important role in the transamination of amino acids to glutamine that enhanced nitrogen transport efficiency. Glutamine level has been increased in leaves of *Brassica napus* plant in the final phase of leaf senescence process.

2.1.5 Mitochondria and Loss of Cellular Organization

Mitochondria play a key role in accumulating its nutrients and providing energy for this development (Buchanan-Wollaston et al. 2003). As senescence progresses, size increases, the shape becomes round, and the number decreases, leading to various morphological changes in mitochondria (Keech et al. 2007). In addition to these changes and the significant loss of their protein, mitochondrial retention is a high function, levels of energy transfer, and carbohydrates backbones may be maintained (Thompson et al. 1987; Keech et al. 2007, 2010). Moreover, without microtubule interference (Keech et al. 2010), mitochondria maintain residual motility. These dynamic activities suggest that cytoplasmic propagation is maintained at least partially until the end of the senescence of the leaves by the protection of actin filaments (Keech 2011). The processes described above lead to critical condition, which are tonoplast rupture and rupture of the lytic contents of the cytoplasm. The residual contents of the cytoplasm cause rapid damage to the structure of the remaining cells and ultimately results to cell damage (Van Doorn and Woltering 2004).

2.2 Factors Affecting Leaf Senescence

There are different types of plant senescence, each of which is caused by certain factors. The first classification of this process (Leopold 1961) defined senescence as somatic (whole plant), upper (stem and leaf), deciduous (leaf only), or continuous (partial). Nowadays, with the growing information of the various factors that can trigger leaf senescence, it is very common to refer to a leaf senescence depending on its causal factor. The most notable feature of this is autumn (Keskitalo et al. 2005), which has recently been shown to make senescence by reducing the length of days (Fracheboud et al. 2009). Other factors are caused by biotic (Smart 1994) and abiotic stress conditions (Rivero et al. 2007; Miller and McBride 1999; Rousseaux et al. 1996; Weaver and Amasino 2001) and postharvest factors. In addition, the process of senescence is also regulated by phytohormones such as ethylene, cytokinins, and ABA (Smart 1994).

2.2.1 Age-Dependent Senescence

In monocarpic annual crop, leaf senescence of single leaves or complete senescence in plants is associated with development of mature seeds that upon production initiate the next-generation of lifespan (Nooden 1988). The leaf functionality is directly connected with energy production for the reproduction and seed dispersal.

It has been observed in soybean that the senescence of particular leaves is highly regulated by reproductive and developmental parts of the plant. This indicated that all part of an organism associated with each other in relation to regulated developmental processes, including senescence process of complete plant is an example of correlative control (Nooden 1988). Thus, the regulation of senescence by the reproductive part has been observed in most of the annual crop plants. However, in *Arabidopsis thaliana*, the life cycle of single leaves is independent from the development of reproductive organ (Noodén and Penney 2001). It supposed that other species of the Brassicaceae family also share similar characteristics (Noodén and Penney 2001).

Life cycle of leaf consists of three main stages from its origination to termination that are an expansion stage, a maturity stage, and a senescence stage (Guiboileau et al. 2010). In the maturity stage, the leaf depends on the environmental and physiological signals that communicate from other parts of the plant that activates the reversible events. Subsequently, development of leaf indicates the beginning of irreversible senescence process, finishing with the leaf death (Lim et al. 2007). The leaf senescence efficiency ultimately causes death of tissues that involved in the photosystem that is intricate and highly controlled mechanism, which involves various translocating and catabolic mechanisms (Gan and Amasin 1997; Guo and Gan 2014; Hörtensteiner and Feller 2002; Buchanan-Wollaston et al. 2003; Lim et al. 2007; Guiboileau et al. 2010; Fischer 2012).

Eventually, the proceeding senescence process are developmentally programmed, and the adverse environmental condition effects on the mechanism indicate that leaf senescence regulation is assimilate and affected by the regulatory pathways involve in stress (Jansson and Thomas 2008). However, the studies of various gene expression profiling indicate that the regulatory mechanism involved in leaf senescence process are conserved in monocot and dicot plants because of the upregulation of same catabolic pathways (Buchanan-Wollaston et al. 2005; Jukanti et al. 2008; Gregersen et al. 2008; Breeze et al. 2011). Moreover, some studies indicate that certain group members of upregulated transcription factors such as WRKY, C2H2 zinc-finger, NAC,AP2/EREBP, MYB, and bZIP families involved in the regulation of leaf senescence process (Buchanan-Wollaston et al. 2005; Balzadeh et al. 2008; Guo and Gan 2014; Breeze et al. 2011).

2.2.2 Stress-Induced Senescence

In general, plants are exposed to adverse environmental conditions and are certainly susceptible to different abiotic and biotic stress during the growing season, which results in a decline in the production of the most important economically viable plants (Bray et al. 2000). Adverse environmental conditions can cause small leaf defects that limit the uniformity, ultimately prolonging the whole plant maturation process (Gan 2003; Guo and Gan 2014), which negatively affects plant production. There is a significant difference in the plant’s rapid response to stress and the process of senescence at the level of genetic control; therefore, various stressful situations suggest developing a synthetic system similar to the senescence leaf process (Guo and Gan 2014). Stressful conditions have created many pathways to show to encourage leaf senescence, but the control of these pathways is unclear; however, they include certain phytohormones such as ethylene, abscisic acid, salicylic acid, and jasmonic acid, which are also associated with stress conditions (Robert-Seilaniantz et al. 2011; Peleg et al. 2011). Control of these signaling pathways is important in crop production.

2.2.2.1 Relationship Between Plant Senescence and Abiotic and Biotic Stress

Age-dependent senescence and stress-induced senescence are often difficult to separate since many biochemical processes involved in these are similar and both ultimately result in plant death. It is often seen that plants form a defense mechanism due to hostile environmental conditions, where the plants inhibit the growth of shoots and disrupt vital cellular functions. Another aspect of coping with stress is the process of leaf senescence, called stress-induced senescence. The process of senescence has many similarities in abiotic stress in relation to plant reactions such as plant morphology, chemical and physical properties, and genetic pattern. Therefore, environmental stress conditions and senescence processes have a negative impact on global yields. Climate change, however, poses a serious threat to economic and global conditions.

The effect of abiotic stress-induced senescence is the limit of crop yields. Likewise, research and development are equally needed. Abiotic stress conditions such as heat, drought, waterlogging, cold, and salt are the main reasons for the decline in crop growth and yields. Various methods involved in plants to tolerate different stressful situations. Understandably, sophisticated approaches to the development of stress-induced stress, many strategies can be established to develop plants that are more resistant to stress-induced senescence (Gepstein and Glick 2013).

Plant diseases are major limiting factors for crop yield by severely affecting the plant. They induced prolonged defense responses or disease symptoms in the plants that promote the acceleration of the leaf senescence process (Nooden 1988). The disease-causing responses of plants involve signaling via phytohormones that are also utilized in leaf senescence regulation (Robert-Seilaniantz et al. 2011), which explain the association of biotic stress responses with leaf senescence acceleration.

2.2.3 Influence of Phytohormone on Senescence

Plant hormones are chemical messengers that naturally synthesize in plants and act as signal compounds; its intricate hormone signaling systems and capability to crosstalk are considered as perfect candidate for facilitating defense responses toward hostile environmental condition (Jalil and Ansari 2019). Ethylene is known as a promoter of various forms of senescence (Abeles et al. 1992; Grbic and Bleecker 1995; Weaver et al. 1998) and genes associated with its biological properties, such as ACC (1-aminocyclopropane-1-carboxylic i -acid) oxidase or ACC synthase that is highly regulated in leaf extract (Lim et al. 2007; van der Graaff et al. 2006). Inhibition of ethylene biosynthesis similarly results in prolonged leaf expansion and continuous chlorophyll production in tomatoes (John et al. 1995). In *Arabidopsis thaliana*, the senescence process is also delayed in the etr1 (ethylene resistant 1) mutant (Grbic and Bleecker 1995), as well as the conversion of ethylene signals similar to the insensitive ethylene 2 (ein2) (Oh et al. 1997). However, plants that are continuously grown under high ethylene or mutant organisms with ethylene signal transfer (ctr1) do not show premature leaf emergence (Kleber-Janke and Knrpinska 1997). The reaction associated with senescence in ethylene appears to be related to leaf age since mutations that show a different onset of leaf (old) mortality show mutations in ethylene (Jing et al. 2002, 2005). However, the effect of ethylene varies from species to species and is directly correlated with plant sensitivity to this hormone. It has been found that exogenous application of ethylene accelerates leaf yellowing (chlorophyll degradation) in wild type of *A. thaliana*, causing leaf yellowing (Zacarias and Reid 1990). Leaf senescence of *Arabidopsis thaliana* has been isolated with many senescence-associated genes (SAGs), and among them only the see1 was strongly induced by ethylene. The expression of this gene was inversely proportional to chlorophyll degradation. Some other SAGs were also affected by ethylene (such as SAG 13, 14 and 20), but their expression was less strong in younger leaves (Oh et al. 1997).

Abscisic acid (ABA) is best known for causing closing of stomata and improving leaf shedding and senescence (Weaver et al. 1998; Lee et al. 2011). In the leaf senescence, the level of ABA elevated (Gepstein and Thimann 1980) and RPK1 (ABA-inducible Receptor-like Protein Kinase) has been recognized as the age-sensitive senescence process (Lee et al. 2011).

Cytokinins are well-known inhibitors of leaf senescence (Zavaleta-Mancera et al. 1999). The presence of cytokinins triggers the transfer of amino acids to the application site and promotes the recording of essential elements in nitrate metabolism, carbon metabolism, and synthesis (Sakakibara et al. 2006). In addition, in *Chenopodium rubrum L.*, cytokinins promote the expression of extracellular invertase CIN1 and hexokinase transporters CST2 and 3, which are associated with increased sugar (Ehness and Roitsch 1997). Further studies on tobacco showed that leaf senescence inhibition by cytokinins depends on improved expression of the cellular invertase and the reduction of sugar from phloem (Balibrea Lara et al. 2004).

Leaf senescence is usually associated with cytokinins concentration reduction in leaves. Cytokinin biosynthesis may have two different pathways. The first comes through N6-isopentenyladenosine monophosphate that is produced by hydroxylase. The latter is also called indirect pathway, in which cytokinins are synthesized from the catabolism of tRNA. The first evidence that cytokinins were able to inhibit leaf senescence was observed in detached *Xanthium* leaves (Richmond and Lang 1957). Many studies have been carried out to understand the role of cytokinins in chlorophyll degradation. It is well known that etiolated cotyledons or leaves incubated in dark conditions and treated with cytokinins regreen when they are exposed to light. This has been reported for several cut flowers, and detached leaves have been intensively used for understanding the chlorophyll degradation process, because they show leaf yellowing few days after harvest. This postharvest disorder is associated with the roots removal that induces cytokinins reduction in leaves because preferential cytokinins biosynthesis occurs in roots. Hence, detached leaves do receive neither nutrients nor hormones from the roots. These lacks lead to hormones unbalance and alteration of physiological processes that accelerate senescence. During senescence, the endogenous level of cytokinins decreases and exogenous applications can delay leaf yellowing. In cut flowers, the concentration of cytokinins does not decrease in homogenous way. These results have a large commercial application for preserving cut flowers from chlorophyll degradation. The decapitation of *Nicotiana rustica* plants above a single senescent leaf and treated with cytokinins induced regreening if low light intensity was applied. The decline in leaf protein content and increase in protease activity, typically markers during senescence, were reversed in treated leaves. The chlorophyll degradation can be efficiently inhibited even with substances with cytokinin-like activity such as phenyl urea derivates. Thidiazuron (TDZ) a synthetic herbicide and plant regulator applied to cut *Alstroemeria* flowers was able to extend the leaf longevity for more than 2 months (Ferrante et al. 2002). The TDZ has been also successfully used to avoid the leaf yellowing in potted geranium during dark transportation (Toscano et al. 2018).

The role of cytokinins during leaf senescence and yellowing has been widely investigated by molecular tools. Results obtained using a molecular biology approach did not give a complete description of genes turned on or off by cytokinins. Many genes have been identified to be up- or downregulated by cytokinins that could be directly or indirectly correlated with chlorophyll metabolism. Among the SAGs isolated during leaf senescence in *Arabidopsis* plants, the Sen1 seems to be strongly associated with chlorophyll degradation. Treatment with 0.1 mM cytokinins was able to repress significantly the mRNA levels and delayed loss of chlorophyll but not that of photochemical efficiency (Oh et al. 1997). In *Lolium multiflorum* leaves, a cysteine protease (See1) was found to increase during leaf senescence, and treatments with cytokinins were able to reduce the See1 mRNA expression and chlorophyll degradation (Li et al. 2000). Analogous experiments carried out on cucumber cotyledons showed that benzyladenine (BA) applied in darkness increased the chlorophyll content on subsequent exposure to light. At molecular level, it has been found that in etiolated cotyledons, BA remarkably increased the transcript of protochlorophyllide reductase (POR), which catalyzes the photo reduction of protochlorophyllide to chlorophyllide (Masuda and Takamiya 2004; Heyes and Hunter 2005). The same effect was found when BA was applied to etiolated *Lupinus luteus* (L.) cotyledons. BA induced greening and increased POR gene expression when etiolated lupine cotyledons were illuminated. The POR transcripts were highly expressed in etiolated cotyledons and at low levels in green leaves and no expression in senescent leaves. Further investigations performed on barley have demonstrated that there are two genes encoding light-dependent POR. They are named POR A and POR B and are differentially regulated by light (Holtorf et al. 1995). The POR A is mainly expressed in darkness, while the POR B is especially present in light-grown leaf tissues.

The DNA-recombinant technology has been used to induce artificially the cytokinin biosynthesis in senescing leaves in order to avoid senescence. The gene that encodes for the key enzyme of cytokinins biosynthesis isopentenyl transferase (IPT, enzyme that catalyzes the rate-limiting step in cytokinin biosynthesis) has been isolated and used for generating transgenic plants. The *IPT* gene has been cloned and inserted in plants with tissue-specific promoters and transgenic plants produced higher amount of cytokinins in the area where the promoter was expressed. In *Arabidopsis thaliana*, the expression analysis of many SAGs was performed under different senescence promoters and greatly delayed the leaf senescence. The *SAG12* has been found commonly expressed under leaf senescence independently trigger. It encodes for a cysteine endopeptidase specifically expressed in senescing *Arabidopsis* leaves. The promoter of SAG12 has been used for driving the expression of *IPT* using a construct *SAG12/IPT*. The transgenic plants enhanced the cytokinins biosynthesis at first symptom of leaf senescence in an autoregulated manner. The increase of endogenous cytokinins inhibited the leaf senescence, and contemporarily *SAG12* promoter was repressed avoiding overexpression (Gan and Amasin 1997).

2.3 Synthesis of Free Radicals During Leaf Senescence

It has been postulated the relation of free radicals and leaf senescence in the “free radical theory of aging” (Harman 1956). It has been reported that the production of free radicals increases during leaf senescence (Zimmermann and Zentgraf 2005). Leaf senescence is an unintended and program aging that is recognized as the last stage of plant development that leads to the death of cell. This is an important and highly regulated process in the plant life cycle followed by a series of events such as mitochondria and cellular loss, disruption of photosynthesis, chlorophyll and macromolecule depletion, and leakage of membranes that cause oxidative cell damage (Fig. 2.1) (Kinnersley and Turano 2000).

Free radicals react with many biological molecules that are damaged during senescence such as oxidize proteins, inadequate fatty acids, and DNA (Jajic et al. 2015) (Fig. 2.1). Lipid peroxidation is a characteristic feature of leaf senescence and can be caused by ROS or lipoxygenase enzymes (Swanson and Gilroy 2010). Oxygen radicals are highly active and cytotoxic; when they react with unsatisfactory fatty acids, the effects of fluid retention lead to cell peroxidation leading to cell leakage and dehydration (Zimmermann and Zentgraf 2005). It has also been reported that the fatty acid stimulation of the phospholipid membrane acts as a substrate for the lipoxygenase enzyme that includes lipid peroxidation and the synthesis of free radicals (Fig. 2.1) (Gan and Amasin 1997; Sharma et al. 2012).

During leaf senescence, cell function is also associated with the electron transport of photosystems I and II, free radicals that respond to DNA causing the conversion of nucleic acids into an important factor responsible for the loss of cellular system function that can cause cell death (Dhindsa et al. 1981). Loss of photosystem activity during leaf senescence can cause photosystem electron transport imbalances, due to reduced RuBisCO enzyme activity (Thompson et al. 1987) that affects the synthesis of NADP + from NADP and H + (Fig. 2.1); during leaf senescence, it leads to the formation of ROS and eventually to cell damage (Bhattacharjee 2005).

2.4 Stress-Induced Senescence and Crop Productivity

Hostile environment conditions cause loss of about 20%–70% in agrarian crop productivity around the world (Datta 2004). Drought, salinity, water logging, soil alkalinity, nutrient deficiency, and cold are foremost factors restricting crop production as shown in Fig. 2.2 and influencing crop quality (Zhu 2016). In field, crops faced with different environmental conditions at same time (Mittler 2006). Changes in environmental conditions will possibly expand the recurrence of most thrilling climate proceedings (Porter and Semenov 2005), engendering additional stressful environments and serious harm. This tendency is also highlighted in environmental variation contrasted with crop productivity system, and these variations will generate reduced crop productivity (Mickelbart et al. 2015; Jalil and Ansari 2020a), indicating a substitution challenge for crop improvement for the occasion of latest crop varieties with improved resistance to adverse environment conditions. Ecological factors influence different plant development pathways (Wang et al. 2003; Jalil and Ansari 2020b). These factors contribute to productivity by altering the homeostasis of plants and altering the source-sink relationships of the metabolic source (Albacete et al. 2014). Legal measures included in the transformation of the sinking relationship during hostile environment conditions are (1) abiotic stresses that induces the onset of senescence because of the degradation photosynthetic pigments of chloroplast, resulting in a decrease in photosynthetic activity in the source tissue (reduced source) (Pérez-Alfocea et al. 2010) and (2) reduced use within sink tissues promotes interaction with the leaves of the source, highlighting the inhibition of the photosynthesis response (Albacete et al. 2014). Both progressions are integrated and interrelated, and control of these progressions can create significant mechanism for

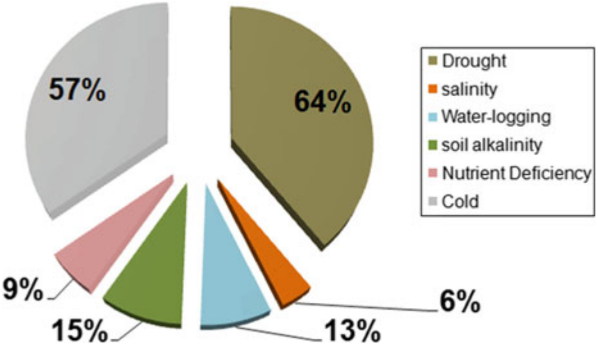

Fig. 2.2 FAO data on the worldwide land area affected by abiotic stresses, viz., drought, salinity, waterlogging, soil alkalinity, nutrient deficiency, and cold that negatively influenced the crop production

enhancement of crop production and quality (Albacete et al. 2014). It has been observed that the development of sink function through controlling the various genes linked to carbon metabolism can improve the resistance of various plants to hazardous conditions (Koonjul et al. 2005; Oliver et al. 2005; Wang et al. 2003).

With respect to source strength, the inhibition of survival and storage of photosynthetic energy through grain filling is linked with improved yields in drought condition (Gregersen et al. 2013). Moreover, incorporating transit from the source to sink, enhancing the capacity of the sink, and evading input barriers can increase and reduce leaf senescence and consequently increase plant production in different abiotic conditions (Pérez-Alfocea et al. 2010). Therefore, reducing the availability of transport sensitivity during stress-induced senescence is a barrier to development and efficiency.

Various techniques have been used to reverse the tendency in plants to grow. The synthesis of cytokinin and abscisic acid hormones is related to the regulation of leaf senescence and source-sink interactions (Peleg and Blumwald 2011). In *Triticum aestivum*, abscisic acid and cytokinin regulated drought-induced senescence; more precisely, higher amount of abscisic acid improves leaf senescence as well as carbon regeneration, which follows the rate of grain refill (Yang et al. 2003). *Oryza sativa* seedlings over-define CCCH-couple zinc protein (OsTZF1), which shows drought and salt tolerance, which is accomplished via reversing abscisic acid–induced senescence, probably by regulating RNA metabolism of stress-response genes (Yang et al. 2003). Changes in the hormonal balance increases grain quantity via reducing stress-induced stress (Peleg et al. 2011; Reguera et al. 2013). It has been reported that mutant rice crops produce a type of IPT (incorporating cytokinin biosynthesis enzyme) under the control of a SARK stimulant. Stress-induced modification in cytokinin content creates variability in the balance of plant-derived hormones, which affect the control of spring-sink interactions and produce strong source energy for variable plants under drought stress, with improved quantity and quality of crop (Peleg et al. 2011).

The disturbance in photosynthesis and deterioration of photosynthetic elements are main impacts of adverse environmental conditions (Dangl et al. 2000). Therefore, chloroplast protection and maintenance methods help to support plant production under hostile environmental conditions. Numerous researches on crops have revealed a positive connection between delayed senescence and crop productivity under adverse conditions (Hafsi et al. 2000; Fu et al. 2011; Messmer et al. 2011). The reduction of OsCV in *Oryza sativa* promotes chloroplast dilapidation, protracted photosynthetic activity, and improved crop productivity under drought stress. Reversal of chloroplast revenues can affect nitrogen regeneration in growing tissues (Liu et al. 2008). While late senescence can produce high grain yields, it may also reduce the effectiveness of nitrogen remobilization (NRE), which results in a reduction in protein content (Masclaux-Daubresse et al. 2008; Havé et al. 2016). A feasible way to solve this problem is to change the senescence of the leaves during stressful situations using stress-induced stimulants or chemical-based stimulants (Xu et al. 2009; Merewitz et al. 2010; Kuppu et al. 2013; Décima Oneto et al. 2016).

Regarding sink capacity, efforts in improving crop yields during stressful situations have included the regulation of carbon metabolism and the transformation of photo assimilates into the sink. For example, promotion of starch synthesis in source and sinks focused on carbon source synthesis and inhibiting the response through photosynthesis, reversing senescence, and, at the same time, strengthening the cutting ability to absorb carbon (Peleg et al. 2011; Albacete et al. 2014). Carbon metabolism and fluxes regulated during hostile conditions is an intricate process involving hormone homeostasis (Albacete et al. 2014). For example, enhancing the regulation of cell wall invertase (CIN1) by a SAG12-induced senescence facilitator activates carbohydrate mutations that suppress ethylene biosynthesis (Munné-Bosch and Alegre 2004), resulting in late sensitivity (Balibrea Lara et al. 2004). Phytohormones are involved in regulating cell wall invertase, encouraging the ability to cut, and synthesizing well-developed tissue (Roitsch and González 2004). Excessive CIN1 overdose by a tomato fruit-promoting promoter leads to higher water efficiency (WUE) and improves water resistance, by increasing photosynthetic activity in the source and lowering water consumption due to lowering of air (Albacete et al. 2014). It is thought that these possessions are due to the changes in the CK/ABA ratio or that there may be changes in the activities of sucrolytic enzyme in the leaves (Albacete et al. 2014).

2.5 Conclusion

Intensifying our facts on the plant responses associated with stress-induced senescence will subsidize the development of new crop plants able to lessen the yield losses under the hostile environment. During senescence, sequences of events promote the stimulated biosynthesis of free radicals that causes oxidative damage to cellular macromolecules leading to cell death that effect the productivity of crops. Therefore, altering plant responses toward stress-induced senescence appears to be suitable approach to enhance crop productivity. Remarkably, perennial crops are characterized by different source-sink signaling as compare with annual crops, and their stress-induced senescence is regulated inversely. Consequently, the biotechnological modification of plant senescence and source-sink signaling in crop plants can deliver innovative approaches for food and feedstock productivity in a global environment change situation.

References

Abeles FB, Morgan PW, Saltveit ME Jr (1992) Ethylene in plant biology. Academic Press, New York

Albacete AA, Martínez-Andújar C, Pérez-Alfocea F (2014) Hormonal and metabolic regulation of source–sink relations under salinity and drought: from plant survival to crop yield stability. Biotechnol Adv 32:12–30

Ansari MI, Chen SCG (2011) Leaf senescence-an overview. Int J Recent Trend Sci Technol 1:110–114

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

Ansari MI, Lee RH, Chen SC-G (2005) A novel senescence-associated gene encoding g-aminobutyric acid (GABA):pyruvate transaminase is upregulated during rice leaf senescence. Physiol Plant 123:1–8

Balibrea Lara ME, Gonzalez Garcia MC, Fatima T, Ehness R, Lee TK, Proels R et al (2004) Extracellular invertase is an essential component of cytokinin-mediated delay of senescence. Plant Cell 16:1276–1287

Balzadeh S, Riano-Pachon DM, Mueller-Roeber B (2008) Transcription factors regulating leaf senescence in *Arabidopsis thaliana*. Plant Biol 10:63–75

Bhattacharjee S (2005) Reactive oxygen species and oxidative burst: roles in stress, senescence and signal transduction in plants. Curr Sci 89:1113–1121

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

Breeze E, Harrison E, McHattie S, Hughes L, Hickman R, Hill C (2011) High-resolution temporal profiling of transcripts during *Arabidopsis* leaf senescence reveals a distinct chronology of processes and regulation. Plant Cell 23:873–894

Buchanan-Wollaston V, Earl E, Harrison E, Mathas S, Navabpour T, Page D (2003) The molecular analysis of leaf senescence—a genomics approach. Plant Biotechnol J 1:3–22

Buchanan-Wollaston V, Page T, Harrison E, Breeze E, Lim PO, Nam HG, Lin JF, Wu SH, Swidzinski J, Ishizaki K et al (2005) Comparative transcriptome analysis reveals significant differences in gene expression and signalling pathways between developmental and dark/starvation-induced senescence in *Arabidopsis*. Plant J 42:567–585

Dangl J, Dietrich R, Thomas H (2000) Senescence and programmed cell death. In: Buchanan B, Gruissem W, Jones R (eds) Biochemistry and molecular biology of plants. American Society of Plant Physiologists, Rockville, MD, pp 1044–1100

Datta SK (2004) Rice biotechnology: a need for developing countries. Ag Bio Forum 7:31–35

Décima Oneto C, Otegui ME, Baroli I, Beznec A, Faccio P, Bossio E, Blumwald E, Lewi D (2016) Water deficit stress tolerance in maize conferred by expression of an isopentenyltransferase (IPT) gene driven by a stress- and maturation-induced promoter. J Biotechnol 220:66–77

Dhindsa RJ, Dhindsa PP, Thorpe TA (1981) Leaf senescence: correlated with increased level of membrane permeability and lipid peroxidation and decreased level of superoxide dismutase and catalase. J Exp Bot 32:93–101

Ehness R, Roitsch T (1997) Co-ordinated induction of mRNAs for extracellular invertase and a glucose transporter in *Chenopodium rubrum* by cytokinins. Plant J 11:539–548

Ferrante A, Donald A, Hunter DA, Hackett WP (2002) Thidiazuron—a potent inhibitor of leaf senescence in *Alstroemeria*. Postharvest Biol Technol 25:333–338

Fischer AM (2012) The complex regulation of senescence. Crit Rev Plant Sci 31:124–147

Fracheboud Y, Luquez V, Bjorken L, Sjodin A, Tuominen H, Jansson S (2009) The control of autumn senescence in European aspen. Plant Physiol 149:1982–1991

Fu JD, Yan YF, Kim MY, Lee SH, Lee BW (2011) Population-specific quantitative trait loci mapping for functional stay-green trait in rice (*Oryza sativa* L.). Genome 54:235–243

Gan S (2003) Mitotic and postmitotic senescence in plants. Sci Aging Knowledge Environ 38:Re7

Gan S, Amasin RM (1997) Making sense of senescence (molecular genetic regulation and manipulation of leaf senescence). Plant Physiol 113:313–319

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

Gepstein S, Thimann KV (1980) Changes in the abscisic acid content of oat leaves during senescence. Proc Natl Acad Sci U S A 77:2050–2053

Grbic V, Bleecker AB (1995) Ethylene regulates the timing of leaf senescence in *Arabidopsis*. Plant J 8:595–602

Gregersen PL, Culetic A, Boschian L, Krupinska K (2013) Plant senescence and crop productivity. Plant Mol Biol 82:603–622

Gregersen PL, Holm PB, Krupinska K (2008) Leaf senescence and nutrient remobilisation in barley and wheat. Plant Biol 10:37–49

Guiboileau A, Sormani R, Meyer C, Masclaux-Daubresse C (2010) Senescence and death of plant organs: nutrient recycling and developmental regulation. C R Biol 333:382–391

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

Hafsi M, Mechmeche W, Bouamama L, Djekoune A, Zaharieva M, Monneveux P (2000) Flag leaf senescence, as evaluated by numerical image analysis, and its relationship with yield under drought in durum wheat. J Agron Crop Sci 185:275–280

Harman D (1956) Aging: a theory based on free radical and radiation chemistry. J Gerontol 11:298–300

Havé M, Marmagne A, Chardon F, Masclaux-Daubresse C (2016) Nitrogen remobilisation during leaf senescence: lessons from *Arabidopsis* to crops. J Exp Bot 68:2513. https://doi.org/10.1093/jxb/erw365

He Y, Gan SA (2002) Gene encoding an acyl hydrolase is involved in leaf senescence in *Arabidopsis*. Plant Cell 14:805–815

Heyes DJ, Hunter CN (2005) Making light work of enzyme catalysis: protochlorophyllide oxidoreductase. Trends Biochem Sci 30:642–649

Himelblau E, Amasino RM (2001) Nutrients mobilized from leaves of *Arabidopsis thaliana* during leaf senescence. J Plant Physiol 158:1317–1323

Holtorf H, Reinbothe S, Reinbothe C, Bereza B, Apel K (1995) Two routes of chlorophyllide synthesis that are differentially regulated by light in barley (*Hordeum vulgare* L). Proc Natl Acad Sci U S A 92:3254–3258

Hong Y, Wang T-W, Hudak KA, Schade F, Froese CD, Thompson JE (2000) An ethylene-induced cDNA encoding a lipase expressed at the onset of senescence. Proc Natl Acad Sci U S A 97: 8717–8722

Hortensteiner S (1998) NCC malonyltransferase catalyses the final step in chlorophyll breakdown in rape (*Brassica napus*). Phytochemistry 49:953–956

Hörtensteiner S, Feller U (2002) Nitrogen metabolism and remobilization during senescence. J Exp Bot 53:927–937

Ishida H, Makino A, Mae T (1999) Fragmentation of the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase by reactive oxygen species occurs near Gly-329. J Biol Chem 274: 5222–5226

Jajic I, Sarna T, Strzalka K (2015) Senescence, stress, and reactive oxygen species. Plan Theory 4: 393–411

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

Jalil SU, Ansari MI (2019) Role of phytohormones in recuperating salt stress. In: Salt stress, microbes, and plant interaction: mechanism and molecular approaches. Springer, Singapore, pp 91–104

Jalil SU, Ansari MI (2020a) Stress implication and crop productivity. In: Plant ecophysiology and adaptation under climate change: mechanism and prespectives. Springer, Singapore, pp 73–86

Jalil SU, Ansari MI (2020b) Isoprenoids in plant protection against abiotic stress. In: Protective chemical agents in the amelioration of plant abiotic stress: biochemical and molecular perspectives. Wiley, London, pp 424–436

Jalil SU, Khan MIR, Ansari MI (2019) Role of GABA transaminase in the regulation of development and senescence in *Arabidopsis thaliana*. Curr Plant Biol 19:100119

Jansson S, Thomas H (2008) Senescence: developmental program or timetable? New Phytol 179: 575–579

Jing H, Schippers JHM, Hille J, Dijkwel PP (2005) Ethylene-induced leaf senescence depends on age-related changes and OLD genes in *Arabidopsis*. J Exp Bot 56:2915–2923

Jing H, Sturre MJG, Hille J, Dijkwel PP (2002) *Arabidopsis* onset of leaf death mutants identify a regulatory pathway controlling leaf senescence. Plant J 32:51–63

Jing HC, Hille J, Dijkwel RR (2003) Ageing in plants: conserved strategies and novel pathways. Plant Biol 5:455–464

John I, Drake R, Farrell A, Cooper W, Lee P, Horton P, Grierson D (1995) Delayed leaf senescence in ethylene-deficient ACC-oxidase antisense tomato plants: molecular and physiological analysis. Plant J 7:483–490

Jukanti AK, Heidlebaugh NM, Parrott DL, Fischer IA, McInnerney K, Fischer AM (2008) Comparative transcriptome profiling of nearisogenic barley (*Hordeum vulgare*) lines differing in the allelic state of a major grain protein content locus identifies genes with possible roles in leaf senescence and nitrogen reallocation. New Phytol 177:333–349

Keech O (2011) The conserved mobility of mitochondria during leaf senescence reflects differential regulation of the cytoskeletal components in *Arabidopsis thaliana*. Plant Signal Behav 6:147–150

Keech O, Pesquet E, Ahad A, Askne A, Nordvall DAG, Vodnala SM et al (2007) The different fates of mitochondria and chloroplasts during dark-induced senescence in *Arabidopsis* leaves. Plant Cell Environ 30:1523–1534

Keech O, Pesquet E, Gutierrez L, Ahad A, Bellini C, Smith SM et al (2010) Leaf senescence is accompanied by an early disruption of the microtubule network in *Arabidopsis thaliana*. Plant Physiol 110:163402

Keskitalo J, Bergquist G, Gardeström P, Jansson S (2005) A cellular timetable of autumn senescence. Plant Physiol 139:1635–1648

Kinnersley AM, Turano FJ (2000) G-aminobutyric acid (GABA) and plant responses to stress. Crit Rev Plant Sci 19:479–509

Kleber-Janke T, Knrpinska K (1997) Isolation of cDNA clones for genes showing enhanced expression in barley leaves during dark-induced senescence as well as during senescence under field condition. Planta 203:332–340

Koonjul PK, Minhas JS, Nunes C, Sheoran IS, Saini HS (2005) Selective transcriptional down-regulation of anther invertases precedes the failure of pollen development in water-stressed wheat. J Exp Bot 56:179–190

Kuppu S, Mishra N, Hu R, Sun L, Zhu X, Shen G, Blumwald E, Payton P, Zhang H (2013) Water-deficit inducible expression of a cytokinin biosynthetic gene IPT improves drought tolerance in cotton. PLoS One 8:e64190

Lee IC, Hong SW, Whang SS, Lim PO, Nam HG, Koo JC (2011) Age-dependent action of an ABA-inducible receptor kinase, RPK1, as a positive regulator of senescence in *Arabidopsis* leaves. Plant Cell Physiol 52:651–662

Leopold AC (1961) Senescence in plant development. Science 134:1727–1732

Li Q, Bettany AJ, Donnison I, Griffiths CM, Thomas H, Scott IM (2000) Characterization of a cysteine protease cDNA from *Lolium multiflorum* leaves and its expression during senescence and cytokinin treatment. Biochim Biophys Acta 1492:233–236

Lim PO, Kim HJ, Nam HG (2007) Leaf senescence. Annu Rev Plant Biol 58:115

Liu L, Zhou Y, Zhou G, Ye R, Zhao L, Li X, Lin Y (2008) Identification of early senescence-associated genes in rice flag leaves. Plant Mol Biol 67:37–55

Masclaux-Daubresse C, Reisdorf-Cren M, Orsel M (2008) Leaf nitrogen remobilisation for plant development and grain filling. Plant Biol 10:23–36

Masuda T, Takamiya K (2004) Novel insights into the enzymology, regulation and physiological functions of light-dependent protochlorophyllide oxidoreductase in angiosperms. Photosynth Res 81:1–29

Merewitz EB, Gianfagna T, Huang B (2010) Effects of SAG12-ipt and HSP18.2-ipt expression on cytokinin production, root growth, and leaf senescence in creeping bentgrass exposed to drought stress. J Am Soc Hortic Sci 135:230–239

Messmer R, Fracheboud Y, Bänziger M, Stamp P, Ribaut JM (2011) Drought stress and tropical maize: QTLs for leaf greenness, plant senescence, and root capacitance. Field Crop Res 124:93–103

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

Miller, P.R., McBride, J.R. (eds)., 1999. Oxidant air pollution impacts in the Montane Forests of Southern California, Springer, New York 397–416

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

Munné-Bosch S, Alegre L (2004) Die and let live: leaf senescence contributes to plant survival under drought stress. Funct Plant Biol 31:203–216

Nam HG (1997) The molecular genetic analysis of leaf senescence. Curr Opin Biotechnol 8(8): 200–207

Nooden LD (1988) In: Nooden LD, Leopold SC (eds) Whole plant senescence. In senescence and aging in plants. Academic Press, San Diego, pp 391–439

Noodén LD, Penney JP (2001) Correlative controls of senescence and plant death in *Arabidopsis thaliana* (Brassicaceae). J Exp Bot 52:2151–2159

Oh SA, Lee SY, Chung KK, Lee CH, Nam HG (1997) A senescence-associated gene of *Arabidopsis thaliana* is distinctively regulated during natural and artificially induced leaf senescence. Plant Mol Biol 30:739–754

Oliver SN, Van Dongen JT, Alfred SC et al (2005) Cold-induced repression of the rice anther-specific cell wall invertase gene OSINV4 is correlated with sucrose accumulation and pollen sterility. Plant Cell Environ 28:1534–1551

Peleg Z, Blumwald E (2011) Hormone balance and abiotic stress tolerance in crop plants. Curr Opin Plant Biol 14:290–295

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

Pérez-Alfocea F, Albacete A, Ghanem ME, Dodd IC (2010) Hormonal regulation of source: sink relations to maintain crop productivity under salinity: a case study of root-to-shoot signalling in tomato. Funct Plant Biol 37:592–603

Porter JR, Semenov MA (2005) Crop responses to climatic variation. Philos Trans Roy Soc London 360:2021–2035

Reguera M, Peleg Z, Abdel-Tawab YM, Tumimbang EB, Delatorre CA, Blumwald E (2013) Stress-induced cytokinin synthesis increases drought tolerance through the coordinated regulation of carbon and nitrogen assimilation in rice. Plant Physiol 163:1609–1622

Richmond AE, Lang A (1957) Effect of kinetin on protein content and survival of detached *Xanthium* leaves. Science 125:650–651

Rivero RM, Kojima M, Gepstein A, Sakakibara H, Mittler R, Gepstein S, Blumwald E (2007) Delayed leaf senescence induces extreme drought tolerance in a flowering plant. Proc Natl Acad Sci U S A 104:19631–19636

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

Roitsch T, González MC (2004) Function and regulation of plant invertases: sweet sensations. Trends Plant Sci 9:606–613

Rousseaux MC, Hall AJ, Sanchez RA (1996) Far-red enrichment and photosynthetically active radiation level influence leaf senescence in field-grown sunflower. Physiol Plant 96:217–224

Sakakibara H, Takei K, Hirose N (2006) Interactions between nitrogen and cytokinin in the regulation of metabolism and development. Trends Plant Sci 11:440–448

Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot 2012:1–26

Smart CM (1994) Gene expression during leaf senescence. New Phytol 126:419–448

Swanson S, Gilroy S (2010) ROS in plant development. Physiol Plant 138:384–392

Takamiya K, Tsuchiya T, Ohta H (2000) Degradation pathway(s) of chlorophyll: what has gene cloning revealed? Trends Plant Sci 5:426–431

Thomas H, Donnison I (2000) Back from the brink: plant senescence and its reversibility. In: Bryant JA, Hughes SG, Garland JM (eds) Programmed cell death in animals and plants. Bios, Oxford, pp 149–162

Thompson JE, Legge RE, Barber RF (1987) Role of free radicals in senescence and wounding. New Phytol 105:313–344

Toscano S, Trivellini A, Ferrante A, Romano D (2018) Physiological mechanisms for delaying the leaf yellowing of potted geranium plants. Sci Hortic 242:146–154

Van der Graaff E, Schwacke R, Schneider A, Desimone M, Flugge UI, Kunze R (2006) Transcription analysis of *Arabidopsis* membrane transporters and hormone pathways during developmental and induced leaf senescence. Plant Physiol 141:776–792

Van Doorn WG, Woltering E (2004) Senescence and programmed cell death: substance or semantics? J Exp Bot 55:2147–2153

Vicentini F, Hortensteiner S, Schellenberg M, Thomas H, Matile P (1995) Chlorophyll breakdown in senescent leaves: identification of the biochemical lesion in a stay-green genotype of *Festuca pratensis* Huds. New Phytol 129:247–252

Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218:1–14

Weaver LM, Amasino RM (2001) Senescence is induced in individually darkened *Arabidopsis* leaves, but inhibited in whole darkened plants. Plant Physiol 127:876–886

Weaver LM, Gan S, Quirino B, Amasino RM (1998) A comparison of the expression patterns of several senescence associated genes in response to stress and hormone treatment. Plant Mol Biol 37:455–469

Xu Y, Tian J, Gianfagna T, Huang B (2009) Effects of SAG12-ipt expression on cytokinin production, growth and senescence of creeping bentgrass (*Agrostis stolonifera* L.) under heat stress. Plant Growth Regul 57:281–291

Yang JC, Zhang JH, Wang ZQ, Zhu QS, Liu LJ (2003) Involvement of abscisic acid and cytokinins in the senescence and remobilization of carbon reserves in wheat subjected to water stress during grain filling. Plant Cell Environ 26:1621–1631

Zacarias L, Reid MS (1990) Role of growth regulators in the senescence of *Arabidopsis thaliana* leaves. Physiol Plant 80:549–554

Zavaleta-Mancera HA, Thomas BJ, Thomas H, Scott IM (1999) Regreening of senescent *Nicotiana* leaves: II Redifferentiation of plastids. J Exp Bot 50:1683–1689

Zhu JK (2016) Abiotic stress signaling and responses in plants. Cell 167:313–324

Zimmermann P, Zentgraf U (2005) The correlation between oxidative stress and leaf senescence during plant development. Cell Mol Biol Lett 10:515–534

Genomics in Enhancing Crop Productivity Against Stresses

3

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Abstract

Compared with the world's 1.8 billion people, the population in the last century has quadrupled and may surpass five times by 2050. On the other hand, climate variability and climate change are further compounding problems toward achieving higher yield. High-throughput genotyping and phenotyping have enabled genetic dissection of crop plants. Mapping of agronomically important quantitative trait loci and genomic selection enabled the development of genomics-assisted breeding. The availability of whole-genome sequencing in many crops has provided opportunity for molecular marker development and genomic-assisted breeding for rapid development of stress resistant/tolerant genotypes. This present book chapter deals with recent advances in these genomic technologies for enhancing crop productivity in stress environment.

Keyword

Molecular markers · Genomic-assisted breeding (GAB) · Marker-assisted selection (MAS) · Genomic selection (GS) · Transcriptomics · Transcript signature

3.1 Introduction

The projected global food demand until 2050 needs significant increases in crop yield. Furthermore, climate change has impacted adversely on crop productivity, which is evident in the form of extreme temperatures, altered rainfall patterns, and other extreme weather conditions. As a result, there is increased attack of pathogens

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and pests and abiotic stresses. In order to mitigate climate variability and climate change, it is therefore necessary to develop and deploy crop varieties that are resilience to climatic variation and climate change.

Trait or gene is the hereditary unit located on chromosome. The rediscovery of Mendel's laws of inheritance (1900) and Darwin's theory of natural selection (1859) can be considered as fundamental basis of plant breeding. Furthermore, the discovery of structure of DNA was a landmark, which opened up new area—the molecular biology. The success of plant breeding in wheat and rice has led to "Green Revolution". It is well known that DNA sequence of genes and nongene sequences control agronomically useful traits and are responsible for genetic variability (Thottathil et al. 2016). Most of these traits are governed by quantitative trait loci (QTL). The idea of flagging QTLs to genetic markers will enable tracking their inheritance at the molecular level. This concept known as marker-assisted selection came into prominence during late 1990s and has been used for the indirect selection of phenotypes in plant breeding programs (Dreher et al. 2009; Gupta and Roy 2002; Nayak et al. 2017). In a marked development, at the beginning of the twenty-first century, the next-generation high-performance sequence technologies (NGS) (Goodwin et al. 2016) have accelerated marker development throughout the genome and enabled genotyping (Davey et al. 2011; Depristo et al. 2011), especially genome-wide availability of SNPs (Kumar et al. 2012; Bhat et al. 2016). It is now being realized that marker-assisted selection (MAS) are effective for few major effect genes but are not very successful with many small effect genes (Heffner et al. 2009). With whole genome sequencing and transcriptomics, genome-wide markers are available that can strengthen molecular breeding works. Marker-assisted breeding (MAB), which comprises several breeding schemes such as marker-assisted selection (MAS), gene pyramiding, marker-assisted backcrossing (MABC), and genome-wide selection (GWS) or genomic, seems to be future breeding strategy for accelerated crop improvement (Leng et al. 2017; Goddard 2009). In addition to DNA sequencing, RNA-seq is revolutionizing global gene expression studies through transcriptomics approach for unraveling gene function under abiotic stresses (An et al. 2012; Raney 2012; Li et al. 2016a, b, c; Kang et al. 2020). Currently, CRISPR/Cas technique emerged as an effective tool for targeted genome editing. Given the emerging agricultural challenges in the climate change regimes, the aim of this book chapter was to explore recent technological advances in crop genomics.

3.2 DNA Sequencing Technologies

Sequencing crop genomes can be considered as a gateway to crop improvement (Thottathil et al. 2016). It is extremely useful for QTL identification and genetic variability. Various second generation sequencing technologies (NGS), i.e., Solexa-Illumina, 454(Roche)/FLX, and ABSOLiD followed by third generation sequencing technologies such as single-molecule real-time (SMRT) sequencing (Ardui et al. 2018), Helicos genetic analysis system (Milos 2009), and Nanopore sequencing

(Kulski 2016; Kono and Arakawa 2019) are revolutionizing crop genomics. In fact, NGS technologies have provided opportunities to develop millions of novel markers for molecular breeding (Edwards and Batley 2010; Bolger et al. 2014). Sequencing/resequencing the whole genome of a large number of accessions is the definitive method for the analysis of the polymorphism in the crop (Bhat et al. 2016) and harnessing of the genetic variability for crop improvement.

3.3 Genomics for Crop Improvement

3.3.1 Marker-Assisted Selection (MAS)

Plant breeders traditionally select plants based on their visible or measurable traits, called the phenotype that are difficult to select accurately, for the whole process of phenotypic selection is slow and is influenced by environment. With the advent of DNA marker technology during 1980s, it has been now possible to utilize them in molecular breeding of crop plants. The genetic marker is a gene or DNA sequence with a known chromosome location controlling a particular gene or trait. The major allelic variations within a genome of a particular species can be due to differences in the number of SSRs at a particular locus, InDels, and SNPs (Mammadov et al. 2012). Nowadays, researchers are using molecular markers to track these variations in the progeny at DNA level. A plethora of molecular markers such as RFLP (Botstein et al. 1980), RAPD (Welsh and Mcclelland 1990), AFLP (Vos et al. 1995), SSRs (Tautz 1989; Powell et al. 1995), and SNP (Thomson 2014) have developed to detect the polymorphisms. Marker-assisted selection (MAS) technology has been extensively used in crop breeding for enhancing crop productivity against biotic and abiotic stresses. The success of MAS depends on several factors, including the number of target genes to be transferred and the distance between the flanking markers and the target gene. The identification of QTLs is a prerequisite for MAS technology. Biparental QTL mapping and genome-wide association study (GWAS) are being used for detection of QTLs (Xu et al. 2017; Alqudah et al. 2020). Some important steps involved in marker-assisted selection are given in Fig. 3.1. Table 3.1 presents in a nutshell the application of MAS in different crops. A list of various software used in MAS selection is given in Table 3.2.

The limitations of MAS include the following: (1) it is only applicable for genes with large QTL effects, and (2) major success using this technology is achieved with qualitative traits such as disease resistance, but it has not been successful with complex quantitative traits as they may be specific to the environment and/or genetic background (Wang et al. 2016).

3.3.2 Genomic Selection (GS)

Genome-wide selection (GWS), also called genomic, is based on prediction of total genetic value (Meuwissen et al. 2001) that take into account the additive effects of all

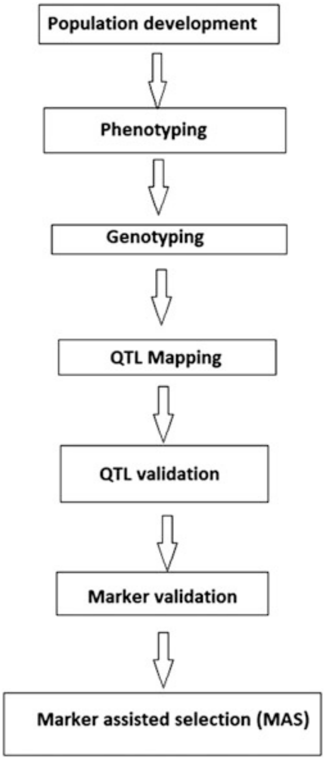

Fig. 3.1 Some steps in marker-assisted selection

genes. Mapping of minor effect QTLs is very difficult. Contrary to MAS, genomic selection (GS) uses genome-wide markers to estimate the effect of all loci for predicting the genetic values of untested population. Thus, GS is a specialized form of MAS where marker alleles covering entire genome are used and the effect of all marker loci are estimated. A comparison of MAS and GS is presented in the Table 3.3. The steps in genomic selection are: creation of training population, genotyping training population, phenotyping training population, model training, genotyping of breeding population, calculation of GEPV value, and selection of superior lines/individuals (Heffner et al. 2009). In training population, both phenotypes and molecular marker scores are determined. Genotype and phenotype data are used for training GS model. The other population in GS, i.e., testing population, is required, which is a set of individuals whose merit we wish to determine. This population is only genotyped and is used for prediction of GEBVs for individuals/lines for genomic selection (Fig. 3.2).

The suitable markers used for genotyping in GS are molecular makers based on chip technology such as SNP, DArT (Diversity Array Technology) and genotyping by sequencing (GBS). GBS is a suitable marker platform for genetic selection since it accesses regulatory regions and sequence tag mapping, flexibility and low cost, and high genomic prediction accuracy and imputes missing data and highly

Table 3.1 Selected applications of MAS technology in plant breeding

Crops	Trait	Gene/QTL	Reference
Rice	Blast resistance	Rice blast resistance genes *Pi2* and *Pi9*	Luo et al. (2017)
	Bacterial blight resistance	Bacterial blight resistant genes, viz., *xa5*, *xa13*, and *Xa21*	Khan et al. (2014)
	Rice blast and brown plant hopper resistance	Blast resistance genes *Pi9*, *Pi47*, *Pi48*, and *Pi49* and two BPH resistance genes *Bph14* and *Bph15*	Chen et al. (2020)
	Submerged tolerance in rice	*Sub1A* and *Sub1C*	Septiningsih et al. (2009)
	Salt resistance	*hst1* gene, transferring salinity tolerance; *Saltol*	Rana et al. (2019), Waziri et al. (2016)
	Drought tolerance	$qDTY_{1.1}$, $qDTY_{2.1}$	Siangliw et al. (2007), Steele et al. (2006), Muthu et al. (2020)
Wheat	Fusarium head blight resistance	QTL *Fhb1*	Steiner et al. (2017)
	Stripe and stem rust resistance	Rust resistance genes *Yr51*, *Yr57*, *Sr22*, *Sr26*, and *Sr50*	
	Powdery mildew resistance	*Pm21*	Ye et al. (2019)

multiplexed (Elshire et al. 2011; Shamshad and Sharma 2018). The relative merits of various genomic prediction models such as stepwise regression, ridge regression, and Bayesian estimation model to estimate additive genetic is reviewed (Meuwissen et al. 2001; Wang et al. 2018). The advantages of GS are: (1) QTL discovery and mapping is not required, (2) greater genetic gain per unit time than phenotypic selection, (3) it is even effective for low heritability traits, and (4) it reduces the rate of inbreeding depression and loss of genetic variability. GS is recently incorporated in plant breeding and is ideally suited for polygenetic traits. The studies in plants have shown GWS to be more effective than other strategies, such as MAS and MARS that use only a subset of markers with significant effects. GS approach is currently being practiced in many crops such as maize (Liu et al. 2020), barley (Nielsen et al. 2016), wheat (Juliana et al. 2020), and rice (Cui et al. 2020). The list of software used in GS is given in the Table 3.4.

3.3.3 Transcriptomics Technologies

The transcriptome describes the sum of all RNAs transcribed by a specific cell or tissue, which include mRNA and noncoding RNA. It involves two main techniques, i.e., microarrays and RNA sequencing (RNA-Seq). Until late 2000s, microarray technology, spotted oligonucleotide microarrays, and Affymetrix microarray are the favored tool for transcriptional profiling (Bumgarner 2013). The most useful

Table 3.2 List of various software used in MAS technology

Linkage map construction	MAPMAKER/EXP (Lander et al. 1987);
	JoinMap (Stam 1993)
	AntMap (Iwata and Ninomiya 2006)
	MSTMAP (Wu et al. 2008a, b)
	MergeMap (Mace et al. 2009)
	MultiPoint (Wu et al. 2008a, b)
QTL discovery	MAPL
	PLABQTL (Utz and Melchinger 1996)
	MapQTL (van Ooijen and Maliepaard 1996)
	QGene (Nelson 1997)
	QTL (Berry 1998)
	Map Manager QTX (Manly et al. 2014)
	Window QTL Catographer (Wang et al. 2005)
	MCQTL
	GMM
	ICIM
	QTL Network
	R/QTL (Broman and Sen 2009)
LD analysis	STRUCTURE (Pritchard et al. 2000)
	EIGENSTRAT (Price et al. 2006)
	GeneRecon (Mailund et al. 2006)
	GENOMIZER (Franke et al. 2006)
	BMap Builder (Abad-Grau et al. 2006)
	CaTS (Skol et al. 2006)
	MIDAS (Gaunt et al. 2006)
	TASSEL (Bradbury et al. 2007)
	InStruct (Gao et al. 2007)
	PLINK (Purcell et al. 2007)
	GenAMP (Curtis et al. 2011)
	GWAPP (Seren et al. 2012)
	ALDER (Loh et al. 2013)

approach for the discovery of genes is the expressed sequence tags (ESTs) and mRNA of protein coding gene. The Sanger sequencing-based generation of ESTs is costly and time-consuming. In the recent years, gene discovery using RNA-seq has become quick and cost-effective with NGS technologies, which generates million (s) of reads in a single sequencing run of few hours to few days. It requires only DNA/RNA fragments directly for sequencing without the requirement of cloning the fragments like earlier Sanger's sequencing. Recently, transcriptome analysis is done through RNA-Seq. It provides the information about number of genes that are upregulated/or downregulated in a particular cell, tissue, or organ of an individual at a particular time (Nejat et al. 2018). This technology is quite useful to gain information about the unknown genes that are differentially expressed in a particular

Table 3.3 Comparison of GS and MAS

Parameters	Marker-assisted selection (MAS)	Genomic selection (GS)
QTL	QTLs with significant and large effect	All QTLs whether significant or not, are used in GS
Selection criteria	Based on marker genotype	Based on GEBV of marker genotype
Number of markers used	Few markers that are linked to QTL	Large number of genome-wide markers
QTL discovery confirmation and validation	Required	Not required; only QTLs associated with markers are estimated
Model training	Not required	Required and is based on suitable training population
Phenotypic evaluation	QTL discovery confirmation and validation	Only done for training population
Ideal choice for breeding program	Suited for gene introgression/gene pyramiding	For quantitative trait improvement

Fig. 3.2 Steps in genetic selection (GS)

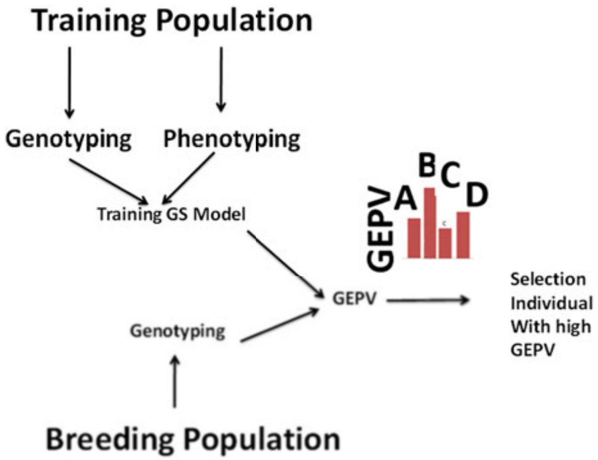

Table 3.4 The list of software used in GS

Model	Software for GS	Ref.
Bayesian genomic linear regression	BESSiE	Boerner and Tier (2016)
Convolutional neural network	DeepGS	Ma et al. (2018)
Machine learning	FaSTLMM	Lippert et al. (2011)
Extended genomic best linear unbiased prediction	GAPIT	Wang et al. (2005)
Ridge regression BLUP	RR-BLUP	Endelman (2011)

environment. Therefore, this technique is very promising in understanding system biology of complex stress tolerance in plants. In addition, transcript profile can also be used to link phenotypes for developing molecular signatures such in a maize mapping population (Baute et al. 2015; Baute et al. 2016) and also as a metabolite markers associated with drought tolerance in potato (Sprenger et al. 2018).

3.3.4 Genome Editing

The ability of the researcher to cut DNA at a given site has revolutionized biology. Genome editing allows targeted mutations in crop genomes with base-pair precision. It is alternative to both classical plant breeding and transgenic approach. A number of genome editing technologies have emerged in recent years, including zinc-finger nucleases (ZFNs), transcription activator–like effector nucleases (TALENs), and the RNA-guided CRISPR-Cas nuclease system (Ran et al. 2013). Genome editing tool, CRISPR/Cas9, has been used by bacteria and archaea to fight against viruses. It consists of two parts: a guide RNA and an enzyme Cas 9 that cuts DNA. A guide RNA takes the enzyme to the targeted sequence. The target sequence is complementary to Grna, and the Cas9 is recruited to target sequence and snips the DNA. CRISPR/Cas9 has the potential to cut and edit any animal or plant gene. CRISPR/ Cas tool may help by making farming more sustainable and safe. Recently, it has been gaining a lot of attention to modify DNA with great accuracy (Wang et al. 2019; Ansari et al. 2020). Some specific examples of applications CRISPR-Cas9 in genomic editing of crops plants with modified traits is presented in Table 3.5.

3.4 Conclusions and Future Prospects

High plant yield is influenced by various factors, including genotype, soil conditions, nutrient and water availability, infection by pathogens, and other environmental factors. Sustainable plant productivity for food security in the regimes of unpredictable global climatic changes seems to be challenging. In order to maximize crop production, it is therefore necessary to implement emerging next-generation sequencing technologies in association with marker-assisted selection (MAS), genetic selection (GS), transcriptomics, genome editing, and transgenics for development of tailored crop in a short period of time. In future, it seems possible that integrated platforms would be available to handle huge amount of data generated in genomics, transcriptomics, proteomics, and metabolomics and apply integrated approach for enhancing crop productivity against stress environments.

Table 3.5 Applications CRISPR-Cas9 is presented in agriculture

Crop plant	Targeted gene	Target trait	Reference
Tomato	*PMR4*	Resistance against powdery mildew	Koseoglou (2017)
	CP and *rep* of virus	Resistance against tomato yellow leaf curl virus	Tashkandi et al. (2018)
	Solyc08g075770	Susceptibility to *Fusarium* wilt disease	Prihatna et al. (2018)
	SP5G	Generation of loss of day-length-sensitive tomato plants	Soyk et al. (2017)
	BZR1	Decrease in heat stress tolerance	Yin et al. (2018)
Potato	*StPPO2* gene	Reduced enzymatic browning in potato tubers	González et al. (2020)
Solanum melongena L.	*PPO* genes (*SmelPPO4, SmelPPO5, and SmelPPO6)*	Reduces fruit flesh browning	Maioli et al. (2020)
Banana	ORF region of virus	Resistance against banana streak virus	Tripathi (2019)
Papaya	*alEPIC8*	Resistance against *Phytophthora palmivora*	Gumtow et al. (2018)
Apple	*DIPM1, 2, 4*	Resistance against fire blight disease	Malnoy et al. (2016)
Wheat	Gliadins	Gluten proteins (gliadins and glutenins) cause coeliac disease (CD) in genetically predisposed individuals	Jouanin et al. (2020)
	TaMLO	Mildew resistance locus	Shan et al. (2014)
	TaEDR1	Disease resistance against powdery mildew	Zhang et al. (2017)
	TaGW2	Grain weight negative regulator	Liang et al. (2017)
Rice	*osPPKL1*	Increases length and yield	Zhang et al. (2012)
	OsMPK5	Various abiotic stress tolerance and disease resistance	Xie and Yang (2013)
	TMS5	Negative regulator of thermo-sensitive genic male sterility	Zhou et al. (2016)
	EPSPS	A key enzyme of aromatic amino acids biosynthesis	Li et al. (2016a, b, c)
	CSA	Negative regulator of photoperiod-sensitive Genic male sterility	Li et al. (2016a, b, c)
	ERF922	Rice blast resistance negative regulator	Wang et al. (2016)
	NRT1.1B	Nitrogen transporter	Lu and Zhu (2017)

(continued)

Table 3.5 (continued)

Crop plant	Targeted gene	Target trait	Reference
	OsRR22	Salinity tolerance	Zhang et al. (2019)
	OsITPK6	Low phytic acid	Jiang et al. (2019)
Maize	*ALS2*	Biosynthesis of branched-chain amino acids (major targets for herbicides)	Svitashev et al. (2015)
	ARGOS8	Increased grain yield under drought stress	Shi et al. (2017)

References

Alqudah AM, Sallam A, Baenziger PS, Börner A (2020) GWAS: fast-forwarding gene identification and characterization in temperate cereals: lessons from barley—a review. J Adv Res 22: 119–135

An D, Yang J, Zhang P (2012) Transcriptome profiling of low temperature-treated cassava apical shoots showed dynamic responses of tropical plant to cold stress. BMC Genomics 13(1):64

Ansari WA, Chandanshive SU, Bhatt V, Nadaf AB, Vats S, Katara JL et al (2020) Genome editing in cereals: approaches, applications and challenges. Int J Mol Sci 21(11):4040

Ardui S, Ameur A, Vermeesch JR, Hestand MS (2018) Single molecule real-time (SMRT) sequencing comes of age: applications and utilities for medical diagnostics. Nucleic Acids Res 46(5):2159–2168

Baute J, Herman D, Coppens F, De Block J, Slabbinck B, Dell'Acqua M, Pè ME, Maere S, Nelissen H, Inzé D (2015) Correlation analysis of the transcriptome of growing leaves with mature leaf parameters in a maize RIL population. Genome Biol 16(1):168

Baute J, Herman D, Coppens F, De Block J, Slabbinck B, Dell'Acqua M, Pè ME, Maere S, Nelissen H, Inzé D (2016) Combined large-scale phenotyping and transcriptomics in maize reveals a robust growth regulatory network. Plant Physiol 170(3):1848–1867

Berry CC (1998) Computationally efficient Bayesian QTL mapping in experimental crosses. In: Proceedings of the biometrics section of the American Statistical Association, pp 164–169

Bhat JA, Ali S, Salgotra RK, Mir ZA, Dutta S, Jadon V, Tyagi A, Mushtaq M, Jain N, Singh PK, Singh GP (2016) Genomic selection in the era of next generation sequencing for complex traits in plant breeding. Front Genet 7:221

Boerner V, Tier B (2016) BESSiE: a software for linear model BLUP and Bayesian MCMC analysis of large-scale genomic data. Genet Sel Evol 48:63

Bolger ME, Weisshaar B, Scholz U, Stein N, Usadel B, Mayer KFX (2014) Plant genome sequencing-applications for crop improvement. Plant Biotechnol J 8(1):2–9

Botstein D, White RL, Skolnick M, Davis RW (1980) Construction of a genetic linkage map in man using restriction fragment length polymorphisms. Am J Hum Genet 32(3):314

Bradbury PJ, Zhang Z, Kroon DE, Casstevens TM, Ramdoss Y, Buckler ES (2007) TASSEL: software for association mapping of complex traits in diverse samples. Bioinformatics 23(19):2633–2635

Broman KW, Sen Ś (2009) A guide to QTL mapping with R/qtl. Springer, New York

Bumgarner R (2013) Overview of DNA microarrays: types, applications, and their future. Curr Protoc Mol Biol 101:22–31

Chen Q, Zeng G, Hao M, Jiang H, Xiao Y (2020) Improvement of rice blast and brown planthopper resistance of PTGMS line C815S in two-line hybrid rice through marker-assisted selection. Mol Breed 40(2):21

Cui Y, Li R, Li G, Zhang F, Zhu T, Zhang Q, Ali J, Li Z, Xu S (2020) Hybrid breeding of rice via genomic selection. Plant Biotechnol J 18(1):57–67

Curtis RE, Kinnaird P, Xing EP (2011) GenA-map: visualization strategies for structured association mapping. In: 2011 IEEE symposium on biological data visualization (BioVis), pp 87–94

Davey JW, Hohenlohe PA, Etter PD, Boone JQ, Catchen JM, Blaxter ML (2011) Genome-wide genetic marker discovery and genotyping using next-generation sequencing. Nat Rev Genet 12: 499–510

Depristo MA, Banks E, Poplin R, Garimella KV, Maguire JR, Hartl C, Philippakis AA, Del AG, Rivas MA, Hanna M, McKenna A, Fennell TJ, Kernytsky AM, Sivachenko AY, Cibulskis K, Gabriel SB, Altshuler D, Daly MJ (2011) A framework for variation discovery and genotyping using next-generation DNA sequencing data. Nat Genet 43:491

Dreher K, Morris M, Khairallah M, Ribaut JM, Shivaji P, Ganesan S (2009) Is marker-assisted selection cost-effective compared with conventional plant breeding methods? The case of quality protein Maize. Proceedings of the 4th annual conference of the international consortium on agricultural biotechnology research (ICABR'00), pp 203–236

Edwards D, Batley J (2010) Plant genome sequencing: applications for crop improvement. Plant Biotechnol J 8(1):2–9

Elshire RJ, Jeffrey CG, Sun Q, Poland JA, Kawamoto K, Buckler ES, Mitchell SE (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS One 6(5): e19379

Endelman JB (2011) Ridge regression and other kernels for genomic selection with R package rrBLUP. Plant Genome 4:250–255

Franke A, Wollstein A, Teuber M, Wittig M, Lu T, Hoffmann K, Nürnberg P, Krawczak M, Schreiber S, Hampe J (2006) GENOMIZER: an integrated analysis system for genome-wide association data. Hum Mutat 27(6):583–588

Gao H, Williamson S, Busta-mante CD (2007) A Markov chain Monte Carlo approach for joint inference of population structure and inbreeding rates from multilocus genotype data. Genetics 176(3):1635–1651

Gaunt TR, Rodriguez S, Zapata C, Day IN (2006) MIDAS: software for analysis and visualisation of interallelic disequilibrium between multiallelic markers. BMC Bioinformatics 7(1):1–11

Goddard M (2009) Genomic selection: prediction of accuracy and maximisation of long term response. Genetica 136:245–257

González MN, Massa GA, Andersson M, Turesson H, Olsson N, Fält AS, Storani L, Décima Oneto CA, Hofvander P, Feingold SE (2020) Reduced enzymatic browning in potato tubers by specific editing of a polyphenol oxidase gene via ribonucleoprotein complexes delivery of the CRISPR/ Cas9 system. Front Plant Sci 10:1649

Goodwin S, McPherson JD, McCombie WR (2016) Coming of age: ten years of next-generation sequencing technologies. Nat Rev Genet 17(6):333

Grau A, María M, Montes R, Se-bastiani P (2006) Building chromosome-wide LD maps. Bioinformatics 22(16):1933–1934

Gumtow R, Wu D, Uchida J, Tian MA (2018) *Phytophthora palmivora* extracellular cystatin-like protease inhibitor targets papain to contribute to virulence on papaya. Mol Plant Microbe 31: 363–373

Gupta PK, Roy JK (2002) Molecular markers in crop improvement: present status and future needs in India. Plant Cell Tiss Org Cult 70(3):229–234

Heffner EL, Sorrells ME, Jannink JL (2009) Genomic selection for crop improvement. Crop Sci 49(1):1–12

Iwata H, Ninomiya S (2006) AntMap: constructing genetic linkage maps using an ant colony optimization algorithm. Breed Sci 56(4):371–377

Jiang M, Liu Y, Liu Y, Tan Y, Huang J, Shu Q (2019) Mutation of inositol 1, 3, 4-trisphosphate 5/6-kinase6 impairs plant growth and phytic acid synthesis in rice. Plant Theory 8:114

Jouanin A, Gilissen LJ, Schaart JG, Leigh FJ, Cockram J, Wallington EJ, Boyd LA, Van Den Broeck HC, Van der Meer IM, America AHP, RGF V (2020) CRISPR/Cas9 gene editing of gluten in wheat to reduce gluten content and exposure-Reviewing methods to screen for Coeliac safety. Front Nutr 2020:7

Juliana P, Singh RP, Braun HJ, Huerta-Espino J, Crespo-Herrera L, Govindan V, Mondal S, Poland J, Shrestha S (2020) Genomic selection for grain yield in the CIMMYT wheat breeding program-status and perspectives. Front Plant Sci 11:1418

Kang WH, Sim YM, Koo N, Nam JY, Lee J, Kim N, Jang H, Kim YM, Yeom SI (2020) Transcriptome profiling of abiotic responses to heat, cold, salt, and osmotic stress of *Capsicum annuum* L. Sci Data 7(1):1–7

Khan MA, Naeem M, Iqbal M (2014) Breeding approaches for bacterial leaf blight resistance in rice (*Oryza sativa* L.), current status and future directions. Eur J Plant Pathol 139(1):27–37

Kono N, Arakawa K (2019) Nanopore sequencing: review of potential applications in functional genomics. Dev Growth Differ 61(5):316–326

Koseoglou E (2017) The study of SlPMR4 CRISPR/Cas9-mediated tomato allelic series for resistance against powdery mildew. Master's thesis, Wageningen University, Wageningen

Kulski JK (2016) Next-generation sequencing—an overview of the history, tools, and omic applications. In: Next generation sequencing–advances, applications and challenges. InTech, Rijeka, pp 3–60

Kumar S, Banks TW, Cloutier S (2012) SNP discovery through next-generation sequencing and its applications. Int J Plant Genomics 2012:831460. https://doi.org/10.1155/2012/831460

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1(2):174–181

Leng PF, Lübberstedt T, Xu ML (2017) Genomics-assisted breeding–a revolutionary strategy for crop improvement. J Integr Agric 16(12):2674–2685

Li J, Meng X, Zong Y, Chen K, Zhang H, Liu J, Li J, Gao C (2016b) Gene replacements and insertions in rice by intron targeting using CRISPR-Cas9. Nat Plants 2:16139

Li M, Li X, Zhou Z, Wu P, Fang M, Pan X, Lin Q, Luo W, Wu G, Li H (2016c) Reassessment of the four yield-related genes Gn1a, DEP1, GS3, and IPA1 in rice using a CRISPR/Cas9 system. Front Plant Sci 7:377

Li Z, Hu G, Liu X, Zhou Y, Li Y, Zhang X, Yuan X, Zhang Q, Yang D, Wang T, Zhang Z (2016a) Transcriptome sequencing identified genes and gene ontologies associated with early freezing tolerance in maize. Front Plant Sci 7:1477

Liang Z, Chen K, Li T, Zhang Y, Wang Y, Zhao Q, Liu J, Zhang H, Liu C, Ran Y et al (2017) Efficient DNA-free genome editing of bread wheat using CRISPR/Cas9 ribonucleoprotein complexes. Nat Commun 8:14261

Lippert C, Listgarten J, Liu Y, Kadie CM, Davidson RI, Heckerman D (2011) FaST linear mixed models for genome-wide association studies. Nat Methods 8:833

Liu X, Hu X, Li K, Liu Z, Wu Y, Wang H, Huang C (2020) Genetic mapping and genomic selection for maize stalk strength. BMC Plant Biol 20:1–16

Loh PR, Lipson M, Patterson N, Moorjani P, Pickrell JK, Reich D, Berger B (2013) Inferring admixture histories of human populations using linkage disequilibrium. Genetics 2013:14

Lu Y, Zhu JK (2017) Precise editing of a target base in the rice genome using a modified CRISPR/Cas9 system. Mol Plant 10:523–525

Luo W, Huang M, Guo T, Xiao W, Wang J, Yang G, Liu Y, Wang H, Chen Z, Zhuang C (2017) Marker-assisted selection for rice blast resistance genes Pi2 and Pi9 through high-resolution melting of a gene-targeted amplicon. Plant Breed 136(1):67–73

Ma W, Qiu Z, Song J, Li J, Cheng Q, Zhai J, Ma C (2018) A deep convolutional neural network approach for predicting phenotypes from genotypes. Planta 248:1307–1318

Mace ES, Rami JF, Bouchet S, Klein PE, Klein RR, Kilian A, Wenzl P, Xia L, Halloran K, Jordan DR (2009) A consensus genetic map of sorghum that integrates multiple component maps and high-throughput diversity array technology (DArT) markers. BMC Plant Biol 9(1):13

Mailund T, Schierup MH, Pedersen CN, Madsen JN, Hein J, Schauser L (2006) GeneRecon-A coalescent based tool for fine-scale association mapping. Bioinformatics 22(18):2317–2318

Maioli A, Gianoglio S, Moglia A, Acquadro A, Valentino D, Milani AM, Prohens J, Orzaez D, Granell A, Lanteri S, Comino C (2020) Simultaneous CRISPR/Cas9 editing of three PPO genes reduces fruit flesh browning in *Solanum melongena* L. Front Plant Sci 11:1883

Malnoy M, Viola R, Jung MH, Koo OJ, Kim S, Kim JS, Velasco R, Nagamangala Kanchiswamy C (2016) DNA-free genetically edited grapevine and apple protoplast using CRISPR/Cas9 ribonucleoproteins. Front Plant Sci 7:1904

Mammadov J, Aggarwal R, Buyyarapu R, Kumpatla S (2012) SNP markers and their impact on plant breeding. Int J Plant Genomics 2012:1–11

Manly KF, Cudmore JRH, Meer JM (2014) Map manager QTX, cross-platform software for genetic mapping. Mamm Genome 12(12):930–932

Meuwissen TH, Hayes BJ, Goddard ME (2001) Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819–1829

Milos PM (2009) Emergence of single-molecule sequencing and potential for molecular diagnostic applications. Expert Rev Mol Diagn 9(7):659–666

Muthu V, Abbai R, Nallathambi J, Rahman H, Ramasamy S, Kambale R, Thulasinathan T, Ayyenar B, Muthurajan R (2020) Pyramiding QTLs controlling tolerance against drought, salinity, and submergence in rice through marker assisted breeding. PLoS One 15(1):e0227421

Nayak SN, Singh VK, Varshney RK (2017) Marker-assisted selection. In: Encyclopedia of applied plant sciences. Academic Press, Oxford, pp 183–197

Nejat N, Ramalingam A, Mantri N (2018) Advances in transcriptomics of plants. In: Plant genetics and molecular biology. Springer, Cham, pp 161–185

Nelson JC (1997) QGENE: software for marker-based genomic analysis and breeding. Mol Breed 3(3):239–245

Nielsen NH, Jahoor A, Jensen JD, Orabi J, Cericola F, Edriss V, Jensen J (2016) Genomic prediction of seed quality traits using advanced barley breeding lines. PLoS One 11(10): e0164494

Powell W, Morgante M, Andre C, McNicol JW, Machray GC, Doyle JJ, Tingey SV, Rafalski JA (1995) Hypervariable microsatellites provide a general source of polymorphic DNA markers for the chloroplast genome. Curr Biol 5(9):1023–1029

Price AL, Patterson NJ, Plenge RM, Weinblatt ME, Shadick NA, Reich D (2006) Principal components analysis corrects for stratification in genome-wide association studies. Nat Genet 38(8):904–909

Prihatna C, Barbetti MJ, Barker SJ (2018) A novel tomato *Fusarium* Wilt tolerance gene. Front Microbiol 9:1226

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155(2):945–959

Purcell S, Neale B, Todd-Brown K, Thomas L, Ferreira MA, Bender D, Maller J, Sklar P, De Bakker PI, Daly MJ, Sham PC (2007) PLINK: a tool set for whole-genome association and population-based linkage analyses. Am J Hum Genet 81(3):559–575

Ran FA, Hsu PD, Wright J, Agarwala V, Scott DA, Zhang F (2013) Genome engineering using the CRISPR-Cas9 system. Nat Protoc 8(11):2281–2308

Rana MM, Takamatsu T, Baslam M, Kaneko K, Itoh K, Harada N, Sugiyama T, Ohnishi T, Kinoshita T, Takagi H, Mitsui T (2019) Salt tolerance improvement in rice through efficient SNP marker-assisted selection coupled with speed-breeding. Intf Mol 20(10):2585

Raney JA (2012) Transcriptome analysis of drought induced stress in *Chenopodium quinoa.* Theses and Dissertations, p 3915. https://scholarsarchive.byu.edu/etd/3915

Septiningsih EM, Pamplona AM, Sanchez DL, Neeraja CN, Vergara GV, Heuer S, Ismail AM, Mackill DJ (2009) Development of submergence-tolerant rice cultivars: the Sub1 locus and beyond. Ann Bot 103(2):151–160

Seren Ü, Vilhjálmsson BJ, Horton MW, Meng D, Forai P, Huang YS, Long Q, Segura V, Nordborg M (2012) GWAPP: a web application for genome-wide association mapping in *Arabidopsis*. Plant Cell 24(12):4793–4805

Shamshad M, Sharma A (2018) The usage of genomic selection strategy in plant breeding. In: Next generation plant breeding. InTech, Rijeka, p 93. https://doi.org/10.5772/intechopen.76247

Shan Q, Wang Y, Li J, Gao C (2014) Genome editing in rice and wheat using the CRISPR/Cas system. Nat Protoc 9:2395

Shi J, Gao H, Wang H, Lafitte HR, Archibald RL, Yang M, Hakimi SM, Mo H, Habben JE (2017) ARGOS 8 variants generated by CRISPR-Cas9 improve maize grain yield under field drought stress conditions. Plant Biotechnol J 15:207–216

Siangliw JL, Jongdee B, Pantuwan G, Toojinda T (2007) Developing KDML105 backcross introgression lines using marker-assisted selection for QTLs associated with drought tolerance in rice. Sci Asia 33:207–214

Skol AD, Scott L, Abecasis GR, Boehnke M (2006) Joint analysis is more efficient than replication-based analysis for two-stage genome-wide association studies. Nat Genet 38(2):209–213

Soyk S, Müller NA, Park SJ, Schmalenbach I, Jiang K, Hayama R, Zhang L, Van Eck J, Jiménez-Gómez JM, Lippman ZB (2017) Variation in the flowering gene SELF PRUNING 5G promotes day-neutrality and early yield in tomato. Nat Genet 49(1):162–168

Sprenger H, Erban A, Seddig S, Rudack K, Thalhammer A, Le MQ et al (2018) Metabolite and transcript markers for the prediction of potato drought tolerance. Plant Biotechnol J 16(4):939–950

Stam P (1993) Construction of integrated genetic linkage maps by means of a new computer package: join map. Plant J 3(5):739–744

Steele KA, Price AH, Shashidhar HE, Witcombe JR (2006) Marker-assisted selection to introgress rice QTLs controlling root traits into an Indian upland rice variety. Theor Appl Genet 112(2):208–221

Steiner B, Buerstmayr M, Michel S, Schweiger W, Lemmens M, Buerstmayr H (2017) Breeding strategies and advances in line selection for fusarium head blight resistance in wheat. Trop Plant Pathol 42(3):165–174

Svitashev S, Young JK, Schwartz C, Gao H, Falco SC, Cigan AM (2015) Targeted mutagenesis, precise gene editing, and site-specific gene insertion in maize using Cas9 and guide RNA. Plant Physiol 169:931–945

Tashkandi M, Ali Z, Aljedaani F, Shami A, Mahfouz MM (2018) Engineering resistance against tomato yellow leaf curl virus via the CRISPR/Cas9 system in tomato. Plant Signal Behav 13: e1525996

Tautz D (1989) Hypervariability of simple sequences as a general source for polymorphic DNA markers. Nucleic Acids Res 17(16):6463–6471

Thomson MJ (2014) High-throughput SNP genotyping to accelerate crop improvement. Plant Breed Biotechnol 2(3):195–212

Thottathil GP, Jayasekaran K, Othman AS (2016) Sequencing crop genomes: a gateway to improve tropical agriculture. Trop Life Sci Res 27(1):93

Tripathi JN (2019) CRISPR/Cas9 editing of endogenous banana streak virus in the B genome of *Musa* spp. overcomes a major challenge in banana breeding. Commun Biol 2:46

Utz HF, Melchinger AE (1996) PLABQTL: a program for composite interval mapping of QTL. J Agric Genomics 2:1–6

van Ooijen JW, Maliepaard C (1996) MapQTL version 3.0: software for the calculation of QTL positions on genetic maps. Proceedings of the 4th plant genome conference, San Diego, pp 316. http://www.intl-ag.org/4/abstracts/p316.html

Vos P, Hogers R, Bleeker M, Reijans M, Van De Lee T, Hornes M, Friters A, Pot J, Paleman J, Kuiper M, Zabeau M (1995) AFLP: a new technique for DNA fingerprinting. Nucleic Acids Res 23(21):4407–4414

Wang FJ, Wang CL, Liu PQ, Lei CL, Hao W, Gao Y, Liu YG, Zhao KJ (2016) Enhanced rice blast resistance by CRISPR/Cas9-targeted mutagenesis of the erf transcription factor gene OsERF922. PLoS One 11:e0154027

Wang J, Zhou Z, Zhang Z, Li H, Liu D, Zhang Q, Bradbury PJ, Buckler ES, Zhang Z (2018) Expanding the BLUP alphabet for genomic prediction adaptable to the genetic architectures of complex traits. Heredity 121:648

Wang S, Basten CJ, Zeng ZB (2005) Windows QTL cartographer 2.5. Department of Statistics, North Carolina State University, Raleigh

Wang T, Zhang H, Zhu H (2019) CRISPR technology is revolutionizing the improvement of tomato and other fruit crops. Hortic Res 6:77. https://doi.org/10.1038/s41438-019-0159-x

Waziri A, Kumar P, Purty R (2016) Saltol QTL and their role in salinity tolerance in rice. Austin J Biotechnol Bioeng 3(3):1067

Welsh J, Mcclelland M (1990) Fingerprinting genomes using PCR with arbitrary primers. Nucleic Acids Res 18(24):7213–7218

Wu Y, Bhat PR, Close TJ, Lonardi S (2008b) Efficient and accurate construction of genetic linkage maps from the minimum spanning tree of a graph. PLoS Genet 4(10):e1000212

Wu Y, Close TJ, Lonardi S (2008a) The accurate construction of consensus genetic maps. Comput Syst Bioinfo Conf 7:285–296

Xie K, Yang Y (2013) RNA-guided genome editing in plants using a CRISPR–Cas system. Mol Plant 6:1975–1983

Xu Y, Li P, Yang Z, Xu C (2017) Genetic mapping of quantitative trait loci in crops. Crop J 5(2):175–184

Ye X, Zhang S, Li S, Wang J, Chen H, Wang K, Lin Z, Wei Y, Du L, Yan Y (2019) Improvement of three commercial spring wheat varieties for powdery mildew resistance by marker-assisted selection. Crop Prot 125:104889

Yin Y et al (2018) BZR1 transcription factor regulates heat stress tolerance through FERONIA receptor-like kinase-mediated reactive oxygen species signaling in tomato. Plant Cell Physiol 59:2239–2254

Zhang A, Liu Y, Wang F, Li T, Chen Z, Kong D, Bi J, Zhang F, Luo X, Wang J, Tang J (2019) Enhanced rice salinity tolerance via CRISPR/Cas9-targeted mutagenesis of the OsRR22 gene. Mol Breed 39(3):47

Zhang X, Wang J, Huang J, Lan H, Wang C, Yin C, Wu Y, Tang H, Qian Q, Li Jet al. (2012) Rare allele of OsPPKL1 associated with grain length causes extra-large grain and a significant yield increase in rice. Proc Natl Acad Sci U S A 109:21534–21539

Zhang Y, Bai Y, Wu G, Zou S, Chen Y, Gao C, Tang D (2017) Simultaneous modification of three homoeologs of ta EDR 1 by genome editing enhances powdery mildew resistance in wheat. Plant J 91:714–724

Zhou H, He M, Li J, Chen L, Huang Z, Zheng S, Zhu L, Ni E, Jiang D, Zhao B, Zhuang C (2016) Development of commercial thermo-sensitive genic male sterile rice accelerates hybrid rice breeding using the CRISPR/Cas9-mediated TMS5 editing system. Sci Rep 6(1):1–12

Transgenic Plants: A Tool to Increase Crop Productivity Under Stress Environment

4

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Abstract

Being static, the plants are exposed to different kinds of external factors. Many external factors negatively influence the plant metabolism and physiology which cause stress. Stress is such a condition mainly created by external factors in which metabolism of cell is adversely regulated, so that normal functioning of the cell is disrupted. These external factors contributing to stress may be biotic or abiotic and their interaction with plant leads to compromised productivity. The cell machinery that attempts to combat such situation involves genes like reactive oxygen species detoxifying genes, protein producing genes, osmoprotectant enhancer genes, heat shock protein synthesis genes, transcription factors, and so on. These have been isolated from different plants, native to the localities having harsh environmental conditions (like abiotic stresses) and depict adequate potential to impart tolerance to such adverse conditions. Many such genes are effectively transferred to diverse agricultural plant cells, where their fruitful expression enabled the crops to endure/ mitigate/ tolerate abiotic stresses like

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drought, salinity, etc., including herbicides as well as heavy metals. This chapter provides an overview of transgenic strategies/approaches in the plants for imparting resistance/tolerance to environmental stress conditions and thereby enhancing crop productivity under such environmental limitation.

Keywords

Crops · Stress · Tolerance · Transgenic plant

4.1 Introduction

Era of crop improvement can be divided into two phases. The classical or conventional era, with limitations of genetic barrier and the modern era, with theoretically all barriers abolished. The main concern about the hindering of crop improvement by conventional breeding has been slender explored genetic variability along with some natural barriers. Some techniques like the mutational breeding as well as somaclonal variation were used to increase the existing genetic variability, but the success is less predictable in long term. Onset of recombinant DNA technology, transformation strategies, and regeneration protocols together contributed towards evolution of new era dominated by transgenic research (Pandey et al. 2018). This genetic engineering as well as tissue culture led tools has great potential for providing effective breeding alternatives in crop improvement aspects. As a process in genetic engineering, the potential genes from a living organism may be brought to a desired crop plant that can show an appropriate expression. Therefore, genetic engineering of crop plants has gained much more interest as a productive field for creating novel varieties mainly because of its success in abolishing genetic barrier in trait transfer. Conventional breeding method exploits the whole organism. On the other hand, new breeding technologies work at cellular and molecular level and remain focused around gene of interest. Approaches like genetic engineering, gene transformation as well as protoplast fusion facilitate to overtake sexual reproduction. Also, these approaches enable us to transfer desirable gene between completely isolated and otherwise incompatible organisms.

The conventional breeding strategy is mainly based on the sexual reproduction for transferring genetic materials to introduce a desirable trait like drought resistant, salinity resistant, etc., in a particular organism (such as agricultural plants). Nowadays, some gene transfer methods are explored to enhance the stress acclimatization/adaptation trait of agricultural plants. The shifted genes can encode enzymes needed towards the formation of osmoprotectants or modification of membrane lipids, detoxification enzyme, stress-inducible transcription factors and so on. The genes involved in stress tolerance can be identified by QTL mapping and then such genes can be incorporated into the genetic system of the desirable cultivar with the help of appropriate genetic engineering and hybridization tools. Apart from this, there are some contemporary as well as modern molecular methods like CRISPR/Cas9 and RNA interference, which may help as regulators in stress tolerance. Since reactive

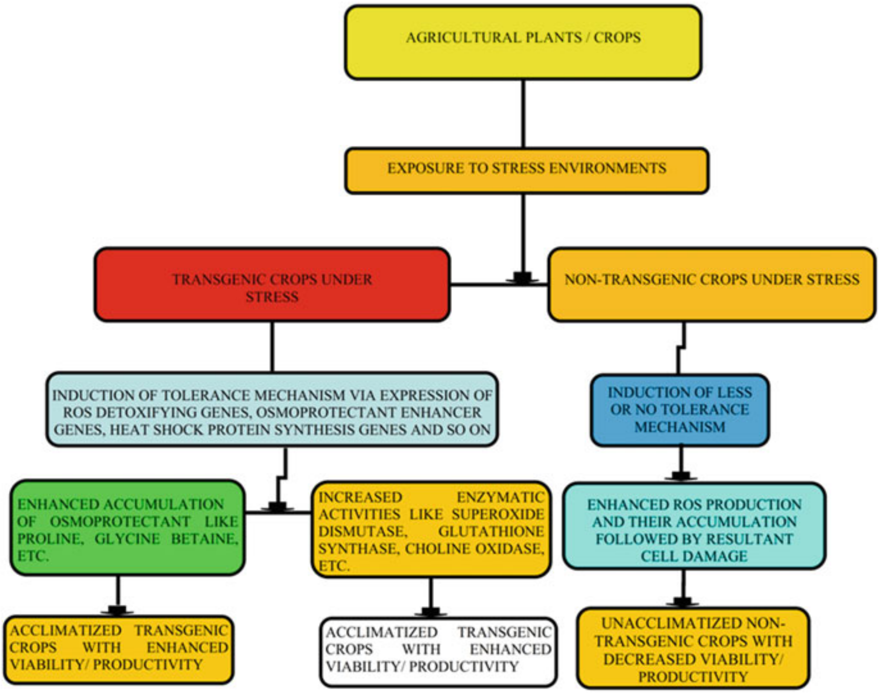

Fig. 4.1 Induction of tolerance/acclimatization mechanism in transgenic crops for overcoming environmental stresses

oxygen species (ROS) are formed in environmental stress conditions that cause severe toxicity towards cellular enzymatic and macromolecular systems, many models have been developed to combat their effect by scavenging the ROS through enzymatic or nonenzymatic antioxidants (Al-Khayri et al. 2021). Many transgenic improvements technologies have also been developed towards abiotic stress endurance/acclimatization via detoxification approach. Some recombinant plants overexpressing enzymes like superoxide dismutase, glutathione peroxidase and so on have been attempted (Zhu et al. 1999). There are several types of genes, which have been on target for production of transgenic plants like ROS detoxifying genes, protein producing genes, osmoprotectant enhancer genes, late embryogenesis abundant (LEA) genes related to lipid biosynthesis, heat shock protein synthesis genes, regulatory genes, transcription factors, signal transduction genes (Fig. 4.1). Additionally, different techniques such as locus mapping, quantitative trait, marker-assisted breeding and introgression can be explored to boost the stress tolerance. This chapter presents a summary on the genetically modified plants with enhanced resistance towards different abiotic stresses and thereby enhancing crop productivity under stress environment.

4.2 Transgenic Strategies for Enhancing Crop Productivity in Stress Environment

Various methods for transgenic approach are being utilized to regulate molecular mechanisms towards abiotic stress resistance (Table 4.1) along with genes responsible for stress, the transcription factors as well as signaling pathways. Considering this, the transgenic agricultural plants with enhanced resistance to different abiotic stresses can be studied under the following headings:

4.2.1 Drought Resistant Transgenic Crops

Scarcity of water which leads to dysregulation of plant physiology and exhibits reduced growth and development has been a major area of concern for plant biologist. Many morphological, biochemical and developmental anomalies have been observed under drought condition in plants (Al-Khayri et al. 2021). Drought influences the absorption of Ca^{2+} through pods as well as N_2 fixation in groundnut in which the photosynthetic activity is also decreased. Several genes isolated from different plant systems were introduced in recombinant wheat to acquire stress tolerance. Such genes can be categorized into following two classes: (1) The genes responsible for cell fortification together with osmoprotectants, detoxification, etc. and (2) The genes related to transcription factors as well as signaling molecules (Vendruscolo et al. 2007). Amongst numerous abiotic stresses, the drought stress is found to adversely influence the wheat crop and thereby causing 29% decrease in its yield (Daryanto et al. 2016; Khan et al. 2019). Considering this, many attempts have been made globally by the researchers to introduce the drought stress tolerance in crops including wheat, with the objective to boost crop yield. For instance, the expression of dehydration-responsive element binding gene (*DREB1a* gene) in recombinant wheat plants displayed substantial endurance towards drought stress over wild type (Pellegrineschi et al. 2004). As well, rice plants overexpressing OsDREB genes result in increased drought resistance (Chen et al. 2008). Further, it was observed that recombinant wheat as well as barley plants expressing the homeodomain-leucine zipper I (*HD-Zip I*) transcription factors resulted in better tolerance/acclimatization towards drought. It is another side of coin that such recombinant plants also revealed issues like drop in biomass/productivity (Kovalchuk et al. 2016; Yang et al. 2018). Apart from this, the expression of *Arabidopsis* CBF1 in tomato plants revealed improved endurance towards drought stress (Hsieh et al. 2002). The chickpea crop, which is the second most extensively grown pulse depicted 40–50% decline in its production per annum owing to drought stress. Recombinant chickpea plants expressing the dehydration-responsive element binding protein 1A of *Arabidopsis thaliana* (*AtDREB1a* gene) were shown to develop enhanced drought tolerance/acclimatization through altering osmotic adjustment, greater chlorophyll preservation capability and so on with associated mechanism. Such drought tolerance/acclimatization in recombinant chickpea plants led to enhanced production of seed over control (Das et al. 2021). The better drought

Table 4.1 Adverse stress environment tolerant transgenic crops raising hope for enhancing crop productivity

Types of transgenic crop	Types of stress condition	Remarks	References
Transgenic potato/tobacco plants with Cu/Zn superoxide dismutase (*SOD*) gene	Cold	Improvement against cold stress	Perl et al. (1993)
Transgenic tobacco plants with chloroplastic GS2	Light	Improvement in adaptation/ acclimatization under light stress, i.e., higher light intensity	Kozaki and Takeba (1996)
Transgenic *Arabidopsis* plants with *codA* gene	Light	Decreasing the injury caused by photo-oxidation and hence better adaptation under light stress	Alia et al. (1999)
Transgenic tobacco plants with *Arabidopsis* proline dehydrogenase gene	Salinity	Enhancement in proline accumulation as well as increased osmotic pressure followed by salinity tolerance/acclimatization	Kuznetsov et al. (1999)
Transgenic *Arabidopsis* plants with choline oxidase (*codA*) gene	Cold	Improvement against cold stress	Sakamoto et al. (2000)
Transgenic rice plants with *OsGS2*	Salinity	Enhancement in tolerance towards salt stress	Hoshida et al. (2000)
Transgenic tomato plants with *Arabidopsis* CBF1	Drought	Improvement against drought stress	Hsieh et al. (2002)
Transgenic *Arabidopsis* plants with CBF1	Cold	Enhancement in freezing tolerance	Jaglo-Ottosen et al. (1998)
Transgenic wheat plants with *DREB1a* gene	Drought	Enhancement in drought tolerance	Pellegrineschi et al. (2004)
Transgenic tobacco plants with *Arabidopsis* DREB1A gene and stress-inducible rd29A promoter	Drought/ cold	Enhancement in drought and cold tolerance	Kasuga et al. (2004)
Transgenic wheat plants	Glyphosate (herbicide)	Enhancement in glyphosate herbicide resistance/tolerance	Ortiz et al. (2007)
Transgenic rice plants with *OsDREB* genes	Drought	Enhancement in drought tolerance	Chen et al. (2008)
Transgenic turf and forage grass with DREB1A transcription factor	Cold	Enhancement in tolerance against cold	James et al. (2008)
Transgenic rice plants with *OsGS1;1*	Heavy metal-cadmium Cd triggered oxidative bursts	Mitigation of oxidative stress responses	Lee et al. (2013)

(continued)

Table 4.1 (continued)

Types of transgenic crop	Types of stress condition	Remarks	References
Transgenic barley plants with wheat transcription factor TaHDZipI-2	Cold	Regulates cold tolerance and so on	Kovalchuk et al. (2016)
Transgenic peanut plants with *Arabidopsis thaliana AtDREB1a* gene	Drought	Enhancement in drought tolerance	Noor et al. (2018)
Transgenic rice plants supplemented with *OsGS1;1* as well as *OsGS2*	Salinity/ drought	Enhancement in salinity/ drought tolerance	James et al. (2018)
Transgenic wheat plants with transcription factor TaHDZipI-5	Drought	Enhancement in drought tolerance	Yang et al. (2018)
Transgenic soybeans plants	Drought	Enhancement in drought tolerance	Bergau (2019)
Transgenic chickpea plants with *Arabidopsis thaliana AtDREB1a* gene	Drought	Enhancement in drought tolerance	Das et al. (2021)

endurance/acclimatization of the AtDREB1A recombinant plants like chickpea, pea nut is accomplished through enhancing the relative water content, sugar and so on over non-recombinant plants (Noor et al. 2018). Also, the expression of *AtDREB1a* gene in recombinant peanut imparted endurance under soil moisture deficit stress (Sarkar et al. 2016). Intriguingly, the first biotechnologically developed plant ever to arrive the market with enhanced drought endurance/acclimatization was developed by Verdeca under the trademark of HB4® Drought Tolerance Soybeans (Bergau 2019).

4.2.2 Herbicides Resistant Transgenic Crops

Herbicides are pesticides exploited to eliminate the unwanted plants like grasses as well as weeds. However, use of such pesticides in agriculture fields may affect the growth, development as well as productivity of desired crops, which are in close vicinity. Considering this, one approach that allows us to overcome the adverse effect of herbicides on crops is to develop herbicide tolerant crop plants. The first fruitful herbicide tolerant recombinant wheat plants were attempted through microprojectile bombardment of regenerable embryonic callus (Vasil et al. 1992). Likewise, the first approved recombinant wheat against glyphosate herbicide resistance was produced by Monsanto (Ortiz et al. 2007). As well, recombinant maize plants were developed that overexpresses ZmNF-YB2, thereby exhibited enhanced growth and development subjected to drought stress (Nelson et al. 2007). Apart from this, the glutamine synthetase (GS) that plays an important function in nitrogen metabolism of higher plants is found to be substantially regulated in distinct abiotic stresses. In this context, James et al. (2018) studied the impact of simultaneous overexpression of the rice cytosolic GS1 (*OsGS1*;*1*) as well as chloroplastic GS2 (*OsGS2*) genes in recombinant rice towards its endurance/adaptation under abiotic stresses as well as the broad-spectrum herbicide glufosinate (phosphinothricin is active ingredient) whose target enzyme was GS. The genetically modified rice plants retained considerably enhanced fresh weight, chlorophyll molecules and so on over wild variety including null segregant controls upon exposure to osmotic/salinity stress. The contemporaneous overexpression of *OsGS1;1/OsGS2* in recombinant rice plants caused enhanced formation of proline, which in addition also exhibited reduction in seepage of electrolyte with smaller malondialdehyde (MDA) upon exposure to stress environments. The genetically modified rice plants at the reproductive stage also revealed substantially improved photosynthesis with agronomical performance when exposed to drought/salinity stress over wild variety as well as null segregant controls. The grain setting levels of the recombinant rice plant systems at the reproductive stage with drought stress (64.6 ± 4.7%) as well as salinity stress (58.2 ± 4.5%) were substantially greater over controls. This leads to enhance crop productivities in aforementioned stress environments. Initial assessment also showed that the genetically modified plants gained enhanced acclimatization towards methyl viologen triggered photo-oxidative burst. Further, the study conducted by James et al. (2018) reveals that the simultaneous overexpression of *OsGS1*;*1* as well as *OsGS2* isoforms in rice improved the physiological acclimatization with agronomical performance in hostile abiotic stress environments. Nevertheless, the transgenic rice plants also exhibited the reduced acclimatization towards the glufosinate. The phosphinothricin (PPT) is found to depict the structural analog of the substrate (glutamate) of GS. Consequently, PPT binds to the glutamate pocket of the GS, thereby blocking the same substrate association with GS (Gill and Eisenberg, 2001). The PPT mediated deactivation of GS enzyme results in the accumulation of NH_3 in the cells of plants together with the prevention of photosynthesis as well as amino acid formation that finally kill the plants (Donn and Köcher 2002). Some other investigations revealed that transgenic overexpression of GS results in acclimatization of plants (like poplar and rice) when exposed to PPT (Pascual et al. 2008; Cai et al. 2009). Likewise, the simultaneous overexpression of pea's cytosolic GS1 as well as chloroplastic GS2 in recombinant wheat and rice has been found to trigger adaptation exposed to PPT (Huang et al. 2005; Sun et al. 2005).

4.2.3 Light Resistant Transgenic Crops

Transgenic approach has also been attempted to impart tolerance/acclimatization against intensity of light beyond the tolerance window. It was found that genetically modified tobacco plants that over-express the chloroplastic GS2 developed improved adaptation/acclimatization under light stress, i.e., higher light intensity (Kozaki and Takeba 1996). This tolerance was achieved owing to the overexpressed

GS2 that resulted in enhanced re-assimilation of photorespiratory ammonia, thereby facilitating improved safeguard of photosynthetic apparatus/photosynthesis via decreasing the injury caused by photo-oxidation. Likewise, the expression of the *coaA* gene accountable for encoding a bacterial choline oxidase in recombinant *Arabidopsis* plants has been depicted to enhance resistance under light stress (Alia et al. 1999). These studies revealed that transgenic approaches enabled us to develop promising recombinant agricultural plants with enhanced resistance to higher light intensity and thereby enhancing crop productivity under such stress environment.

4.2.4 Heavy Metals Resistant Transgenic Crops

Heavy metals like Cd, Hg and so on are extremely toxic to metal-susceptible enzymes, which cause growth impediment as well as death of cells. In this context, the *PvSR2* gene isolated from the bean cDNA library through differential screening has been expressed particularly in the environmental condition of heavy-metal stress. Such stress condition led to encoding of a new heavy-metal stress responsive protein molecule (Huang et al. 1997). Similarly, the expression of *PvSR2* gene in recombinant bacterial species found to develop tolerance against $CdCl_2$ supplementation (Zhang et al. 2001). It was found that overexpression of *OsGS1;1* in recombinant rice led to improved endurance/adaptation to Cd triggered oxidative burst (stress) via the adjustment of oxidative stress responses (Lee et al. 2013). These studies are clearly indicating that endurance/adaptation of agricultural crops against toxic heavy metals can be achieved through genetic engineering.

4.2.5 Salinity Resistant Transgenic Crops

The transgenic approach also enables us to develop salinity resistant transgenic crops, thereby not only improving the growth and development of agricultural plants but also the productivity. For instance, the genetically modified rice plants which overexpresses the chloroplastic *OsGS2* gene showed improved salinity endurance/adaptation (Hoshida et al. 2000). Similarly, *Arabidopsis thaliana* that overexpresses dehydrin DHN-5 was found to reveal improved endurance under salinity (Brini et al. 2007). Under abiotic stresses, there occurs membrane lipid peroxidation because of increased ROS activity as well as consequent membrane leakage. Such phenomenon ultimately led to extensive harm to cells of plants and thereby promoting cell death. Nonetheless, the contemporaneous overexpression of *OsGS1;1* as well as *OsGS2* in recombinant rice resulted in substantially lesser oxidative bursts together with lower electrolyte leakage over control rice plants when exposed to drought as well as salinity stresses (James et al. 2018). However, expression of fragment of proline dehydrogenase gene from *Arabidopsis* in SR1, tobacco (*Nicotiana tabacum*) plant transformants resulted in enhanced proline accumulation and increased osmotic pressure followed by salinity tolerance/acclimatization. The defensive role of proline is believed to link with its capability to undergo interaction with biomolecules and thereby maintaining their native structure as well as functional activities (Kuznetsov et al. 1999).

4.2.6 Cold Resistant Transgenic Crops

The genetic basis of abiotic stress resistance is established in many studies. Resistance against chilling and frost conditions are not exceptions to it. Transgenic potato and tobacco plants with overexpressed Cu/Zn superoxide dismutase (*SOD*) gene in chloroplasts were shown to have an improved photosynthesis stress induced by very low temperature (Perl et al. 1993; Sen Gupta et al. 1993). *Arabidopsis* plants transformed with choline oxidase (*codA*) gene were found to be more chilling stress tolerant over untransformed plants (Sakamoto et al. 2000). Kasuga et al. (2004) reported the high tolerance of transgenic tobacco plants against chilling stress. Chilling stress tolerance was found to be associated with centromere-binding factor 1 (CBF-1) protein's overexpression (Jaglo-Ottosen et al. 1998). James et al. (2008) reported that xeric *Hordeum spontaneum* L. sourced dehydration-responsive element binding protein (DREB1A) transcription factor expression in turf and forage grass (*Paspalum notatum* Flügge) resulted in an increased abiotic stress tolerance.

4.3 Limitations of Transgenic Agricultural Plants

There are many roadblocks for the effective implementation of strategies towards development and cultivation of transgenic plants, e.g., operational constraints, requirements of large monetary investments, lack of skilled professionals, issues with solation and characterization of small number of genes, lack of trust of end user on genetically modified food, regulatory and ethical-legal issues, environmental and ecological issues and so on (Pandey et al. 2018). All these issues pose greater difficulties in developing countries over developed ones. If developing nations want to implement this technology, then such nations have to not only depend on the developed countries but also spend a large revenue for the same purpose due to the involvement of commercial companies. The situation is further complexed by the fact that transgenic approach is beneficial only in case of single gene traits. Genome position effect is a major challenge faced by genetic engineering professionals. The position of integration of the transgene can affect the regulation of its expression. Sometimes, multiple copies of the transgene can become inserted in the genome and stops its expression. In other instances, a transgene inserted in vicinity to another gene can for unpredictable and undesired phenotypes. A successful and stable integration of a transgene results in its long-term expression. This demands that a single copy is inserted only at a specific locus, which is not affected by the presence of adjacent sequence elements. One of the most successful applications of transgenic technology is the development of Bt cotton crop in which insect plants are transformed for insect resistance. Recent evidence indicates possibilities of development of resistance in insects, against Cry proteins (proteins responsible for insect resistance in plants), to different but significant degrees after variable number of generations. The Cry protein resistant insects pose serious difficulties for farmers in terms of sustainability of crops and economic losses. Particularly, the farmers of poorer nations are affected the most as they are small land holders with limited backup of resources and purchasing power needed for transgenic crop seed acquisition. Economic and political status along with agriculture and loan policies also influences the implementation of transgenic agriculture. Sino-Indian conditions are a good example of it in countries like China, even the small farmers have gained and improved their production due to cheaper seeds and other resources (Jain 2010), while in other neighbouring countries the situation is not so good. Another limitation for the transgenic approach for crop improvement is the absence of competent transformation and regeneration techniques for monocots. Since monocots are the major cereal crops of the world, this technical problem of plant genetic engineering is of utmost importance and needs to be explored with great efforts.

4.4 New Technologies Overcoming Limitations of Transgenic Approach

The discovery of clustered regularly interspaced short palindromic repeats (CRISPR) Cas 9 mediated plant transformation methods has created high hopes as this is a very effective tool for gene editing (Kausch et al., 2019). Recently, scientists have achieved success in application of morphogenic regulator elements BABYBOOM (*BBM*) and WUSCHEL (*WUS*) for their usage as adjuvants for transformation (Lowe et al. 2016). The conventionally used plant transformation methods are the biolistic and *Agrobacterium* mediated based. However, another novel method has been reported in which carbon nanotubes are used for targeted gene delivery (Demirer et al. 2019). This method allowed only transient transformation in leaves and protoplasts. An advantage of using this method is its genotype independence. With CRISPR/Cas9 gene editing stable transgene integration can be achieved. Gene editing is done stably in the target cells with Cas9 and gRNA transient expression (Zhang et al. 2016). The most important advantages associated with CRISPR/Cas9 gene edition method are that the desired changes are present in the first generation itself and there is no need to separate the CRISPR elements. This is especially beneficial in case of crops, which are resistant to crossing. In spite of these advancements, only few biotechnologically modified varieties of crops for improved resistance against drought are available, e.g., DroughtGard® maize, Verdeca's HB4 soybean and wheat, and Indonesian Perkebunan Nusantara's NXI-4 T sugarcane (Nuccio et al. 2018).

4.5 Conclusion and Future Directions

Stress tolerance in plants is mediated by several mechanisms, which include regulation of osmoprotectants like amino acids, amines, sugars, sugar alcohols, etc. Therefore, the genes encoding these osmoprotectants become important for identifying the mechanism of stress tolerance. Special osmoprotectants are accumulated naturally in organisms dwelling in stressed environments. However, majority of crops are not able to produce these osmoprotectants. Abiotic stress tolerance is best achieved by osmoregulation. For this to happen, the genes responsible for osmoregulation could be triggered from stressed environmental conditions. So, if osmolytes can be engineered or over expressed, stress tolerance can be enhanced in crop plants. Moreover, targeting of many sugar alcohols has been carried out to engineer overproduction of compatible solutes. This resulted in better protection of membrane components and protein complexes under stressed conditions. The general approach towards capacity building for stress tolerance in crop plants is by commissioning and activating the well characterized and cloned transcription factors and stress genes. Transgenic approach for these improvements is most effective for improving stress tolerance when regulation of many genes is targeted over the involvement of single gene. Assessment of the stress tolerance against a particular abiotic stress in exclusion as well as in comparison with the tolerance after gene manipulation is also very important. The use of genetic engineering in increasing stress tolerant should negligibly affect the yield and other metabolic processes. Therefore, these aspects should be evaluated well in advance before implementation of this technology. Even considerable technological advances, there are still some gaps present in our understanding of the usage of this high-end technology in terms of effects over variable time duration. Therefore, to successfully achieve the goal of effective stress tolerance enhancement in crop plants, we need an approach with a combination of the aspects of metabolism, physiology, gene expression and morphogenesis under stressed environment. These approaches need a thoroughly understanding the intricate working of the plant physiology under various abiotic stress environmental conditions. Only after this background information available in hand, one can select the most appropriate genetic element as the target for plant transformation.

References

Alia KY, Sakamoto A, Nonaka H, Hayashi H, Pardhasaradhi P, Chen THH, Norio M (1999) Enhanced tolerance to light stress of transgenic *Arabidopsis* plants that express the *coaA* gene for a bacterial choline oxidase. Plant Mol Biol 40:279–288

Al-Khayri JM, Ansari MI, Singh AK (2021) Nanobiotechnology: mitigation of abiotic stress in plants, 1st edn. Springer, Cham, pp 1–593

Bergau J (2019) Verdeca introduces HB4® drought tolerant soybeans to growers at Argentina's Expoagro. https://www.businesswire.com https://www.businesswire.com/news/home/20190326005300/en/Verdeca-Introduces-HB4%C2%AE-Drought-Tolerant-Soybeans-Growers, Arcadia Biosciences. Accessed 26 Apr 2019

Brini F, Hanin M, Lumbreras V, Amara I, Khoudi H, Hassairi A, Pages M, Masmoudi K (2007) Overexpression of wheat dehydrin DHN-5 enhances tolerance to salt and osmotic stress in *Arabidopsis thaliana*. Plant Cell Rep 26:2017–2026

Cai H, Zhou Y, Xiao J, Li X, Zhang Q, Lian X (2009) Overexpressed glutamine synthetase gene modifies nitrogen metabolism and abiotic stress responses in rice. Plant Cell Rep 28:527–537

Chen JQ, Meng XP, Zhang Y, Xia M, Wang XP (2008) Over-expression of OsDREB genes lead to enhanced drought tolerance in rice. Biotechnol Lett 30:2191–2198

Daryanto S, Wang L, Jacinthe PA (2016) Global synthesis of drought effects on maize and wheat production. PLoS One 11(5):e0156362

Das A, Basu PS, Kumar M, Ansari J, Shukla A, Thakur S, Singh P, Datta S, Chaturvedi SK, Sheshshayee MS, Bansal KC, Singh NP (2021) Transgenic chickpea (*Cicer arietinum* L.) harbouring AtDREB1a are physiologically better adapted to water deficit. BMC Plant Biol 21(1):39

Demirer GS, Zhang H, Matos JL, Goh NS, Cunningham FJ, Sung Y, Chang R, Aditham AJ, Chio L, Cho MJ, Staskawicz B, Landry MP (2019) High aspect ratio nanomaterials enable delivery of functional genetic material without DNA integration in mature plants. Nat Nanotechnol 14(5):456–464

Donn G, Köcher H (2002) Inhibitors of glutamine synthetase. In: Böger P, Wakabayashi K, Hirai K (eds) Herbicide classes in development. Springer, Berlin, Heidelberg, pp 87–101

Gill HS, Eisenberg D (2001) The crystal structure of phosphinothricin in the active site of glutamine synthetase illuminates the mechanism of enzymatic inhibition. Biochemistry 40:1903–1912

Hoshida H, Tanaka Y, Hibino T, Hayashi Y, Tanaka A, Takabe T, Takabe T (2000) Enhanced tolerance to salt stress in transgenic rice that overexpresses chloroplast glutamine synthetase. Plant Mol Biol 43(1):103–111

Hsieh TH, Lee JT, Charng YY, Chan MT (2002) Tomato plants ectopically expressing *Arabidopsis* CBF1 show enhanced resistance to water deficit stress. Plant Physiol 130:618–626

Huang L, Gitschier J (1997) A novel gene involved in zinc transport is deficient in the lethal milk mouse. Nat Genet 17(3):292–297

Huang QM, Liu WH, Sun H, Deng X, Su J (2005) *Agrobacterium tumefaciens* mediated transgenic wheat plants with glutamine synthetases confer tolerance to herbicide (in Chinese). J Plant Ecol 29:338–344

Jaglo-Ottosen KR, Gilmour SJ, Zarka DG, Schabenberger O, Thomashow MF (1998) *Arabidopsis* CBF1 overexpression induces COR genes and enhances freezing tolerance. Science 280:104–106

Jain SM (2010) Mutagenesis in crop improvement under the climate change. Romanian Biotechnol Lett 15(2):89–106

James D, Borphukan B, Fartyal D, Ram B, Singh J, Manna M, Sheri V, Panditi V, Yadav R, Achary VMM, Reddy MK (2018) Concurrent overexpression of *OsGS1;1* and *OsGS2* genes in transgenic rice (*Oryza sativa* L.): impact on tolerance to abiotic stresses. Front Plant Sci 21(9):786

James VA, Neibaur I, Altpeter F (2008) Stress inducible expression of the DREB1A transcription factor from xeric, *Hordeum spontaneum* L. in turf and forage grass (*Paspalum notatum* Flugge) enhances abiotic stress tolerance. Transgenic Res 17:93–104

Kasuga M, Miura S, Shinozaki K, Yamaguchi-Shinozaki K (2004) A combination of the *Arabidopsis* DREB1A gene and stress-inducible rd29A promoter improved drought- and low temperature stress tolerance in tobacco by gene transfer. Plant Cell Physiol 45:346–350

Kausch AP, Nelson-Vasilchik K, Hague J, Mookkan M, Quemada H, Dellaporta S, Fragoso C, Zhang ZJ (2019) Edit at will: genotype independent plant transformation in the era of advanced genomics and genome editing. Plant Sci 281:186–205

Khan S, Anwar S, Yu S, Sun M, Yang Z, Gao Z-Q (2019) Development of drought-tolerant transgenic wheat: achievements and limitations. Int J Mol Sci 20(13):3350

Kovalchuk N, Chew W, Sornaraj P, Borisjuk N, Yang N, Singh R, Bazanova N, Shavrukov Y, Guendel A, Munz E, Borisjuk L, Langridge P, Hrmova M, Lopato S (2016) The homeodomain transcription factor TaHDZipI-2 from wheat regulates frost tolerance, flowering time and spike development in transgenic barley. New Phytol 211(2):671–687

Kozaki A, Takeba G (1996) Photorespiration protects C_3 plants from photooxidation. Nature 384: 557–560

Kuznetsov VV, Shevyakova NI (1999) Proline during stress: biological role, metabolism, and regulation. Fiziol Rastenii 1999:321–336

Lee HJ, Abdula SE, Jang DW, Park SH, Yoon UH, Jung YJ, Kang KK, Nou IS, Cho YG (2013) Overexpression of the glutamine synthetase gene modulates oxidative stress response in rice after exposure to cadmium stress. Plant Cell Rep 32(10):1521–1529

Lowe K, Wu E, Wang N, Hoerster G, Hastings C, Cho MJ, Scelonge C, Lenderts B, Chamberlin M, Cushatt J, Wang L, Ryan L, Khan T, Yiu JC, Hua W, Yu M, Banh J, Bao Z, Brink K, Igo E, Rudrappa B, Shamseer PM, Bruce W, Newman L, Shen B, Zheng P, Bidney D, Falco C, Register J, Zhao ZY, Xu D, Jones T, Kamm WG (2016) Morphogenic regulators baby boom and Wuschel improve monocot transformation. Plant Cell 28(9):1998–2015

Nelson DD, Repetti PP, Adams TT, Creelman RR, Wu J, Warner DD, Anstrom DD, Bensen RR, Castiglioni PP, Donnarummo MG, Hinchey BS, Khumimoto RW, Maszle DR, Canales RD, Krolikowski KA, Dotson SB, Gutterson N, Ratcliffe OJ, Heard JE (2007) Plant nuclear factor Y (NF-Y) B subunits confer drought tolerance and lead to improved corn yields on water-limited acres. Proc Natl Acad Sci USA 104(42):16450–16455

Noor S, Ali S, Ali GM (2018) Comparative study of transgenic (DREB1A) and non-transgenic wheat lines on relative water content, sugar, proline and chlorophyll under drought and salt stresses. Sarhad J Agric 34:986–993

Nuccio ML, Paul M, Bate NJ, Cohn J, Cutler SR (2018) Where are the drought tolerant crops? An assessment of more than two decades of plant biotechnology effort in crop improvement. Plant Sci 273:110–119

Ortiz R, Iwanaga M, Reynolds M, Huixia W, Crouch JH (2007) Overview on crop genetic engineering for drought-prone environments. J SAT Agric Res 4:1–30

Pandey B, Tiwari RK, Kumar A (2018) Expanding the global horizon of engineered crops: miles ahead to go. Sci Res Essays 13(10):105–110

Pascual MB, Jing ZP, Kirby EG, Cánovas FM, Gallardo F (2008) Response of transgenic poplar overexpressing cytosolic glutamine synthetase to phosphinothricin. Phytochemistry 69:382–389

Pellegrineschi A, Reynolds M, Pacheco M, Brito RM, Almeraya R, Yamaguchi-Shinozaki K, Hoisington D (2004) Stress-induced expression in wheat of the *Arabidopsis thaliana* DREB1A gene delays water stress symptoms under greenhouse conditions. Genome 47:493–500

Perl A, Perl-Treves R, Galili S, Aviv D, Shalgi E, Malkin S, Galun E (1993) Enhanced oxidative stress defense in transgenic potato expressing tomato cu, Zn superoxide dismutases. Theor Appl Genet 85:568–576

Sakamoto A, Valverde R, Alia CTH, Murata N (2000) Transformation of *Arabidopsis* with the *codA* gene for choline oxidase enhances freezing tolerance of plants. Plant J 22:449–453

Sarkar T, Thankappan R, Kumar A, Mishra GP, Dobaria JR (2016) Stress inducible expression ofAtDREB1A transcription factor in transgenic peanut (*Arachis hypogea* L.) conferred tolerance to soil-moisture deficit stress. Front Plant Sci 7:935

Sen Gupta A, Heinen JL, Holady AS, Burke JJ, Allen RD (1993) Increased resistance to oxidative stress in transgenic plants that over-express chloroplastic cu/Zn superoxide dismutase. Proc Natl Acad Sci USA 90:1629–1633

Sun H, Huang Q, Su J (2005) Overexpression of glutamine synthetases confers transgenic rice herbicide resistance high technology letters. ECOJ 11(1):75–79

Vasil V, Castillo AA, Fromm ME, Vasil IK (1992) Herbicide resistant fertile transgenic wheat plants obtained by microprojectile bombardment of regenerable embryogenic callus. Nat Biotechnol 10(6):667–674

Vendruscolo ECG, Schuster I, Pileggi M, Scapim CC, Molinari HBC, Marur CC, Vieira LGE (2007) Stress-induced synthesis of proline confers tolerance to water deficit in transgenic wheat. J Plant Physiol 164:1367–1376

Yang Y, Luang S, Harris J, Riboni M, Li Y, Bazanova N, Hrmova M, Haefele S, Kovalchuk N, Lopato S (2018) Overexpression of the class I homeodomain transcription factor TaHDZipI-5 increases drought and frost tolerance in transgenic wheat. Plant Biotechnol J 16:1227–1240

Zhang Y, Liang Z, Zong Y, Wang Y, Liu J, Chen K, Qiu JL, Gao C (2016) Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nat Commun 7:12617

Zhang YX, Chai TY, Zhao WM (2001) Cloning and expression analysis of the heavy-metal responsive gene PvSR2 from bean. Plant Sci 161(4):783–790

Zhu L, Tang GS, Hazen SP, Kim HS, Ward RW (1999) RFLP-based genetic diversity and its development in Shaanxi wheat lines. Acta Bot Boreali Occident Sin 19:13

Breeding Efforts for Crop Productivity in Abiotic Stress Environment

5

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Abstract

In the present state, human activities coupled with simultaneous exploitation of the earth's resources have resulted in newer challenges that surface day-by-day. In a response to overcome the after-effects, new methods are being developed to address these challenges in an effective manner. Considering the projection that the world population will rise by 1.8 billion by the upcoming 2030 which will directly increase the expected food demand by 50% (www.popcouncil.org). As

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per FAO, if the world's population tally even touches the projected mark, the global food production in developing countries should also observe a parallel growth of two-fold. Irrespective of thinking about the future feeding at present, the focus is also given on reducing the overall losses in food productivity due to the cumulative effects of different abiotic stresses. However, at a present situation of 2020, when the availability of staple foods needs to be dramatically increased to meet the needs of a rising human population; abiotic stresses (drought, salinity, high-temperature, cold) and climatic changes have established as severe threats to global crop production. All these together have pressurized the agriculture's responsibility for preserving the environment and climate change parallelly. In this regard only, increasing plant resistance to various abiotic stresses is one of the top-priority goals for scientific community. This has been done with many, new breeding programs that have reoriented the breeding capabilities in the recent years. Therefore, in the present chapter, the primary focus is on highlighting the latest achievements and discoveries used in breeding for the treatment of abiotic stress. In a relay, the book chapter initiates from new physiological concepts and breeding methods followed by discussing modern molecular biological approaches aimed at creating improved abiotic stress-resistant varieties.

Keywords

Abiotic stress · Physiological response · Crop productivity · Molecular breeding · Marker-assisted selection · GWAS · Genetic engineering

5.1 Introduction

In their physical environment, both plants and animals face various stresses and undergo many types of changes in a response to tackle. Animals employ various techniques to avoid these changes, however, the plants fail to directly avoid due to their sedentary growth habit. Therefore, to survive in their fluctuating external environment, plants rely on regulation of their internal pathways (Xie et al. 2019). As a result, the environment does not affect plant's growth or development up to that extent.

As per the classification, the components of fluctuating external environment can be divided into two types such as non-biological (abiotic) and biological (biotic) stresses (Sardhara et al. 2018). Out of both, the abiotic stresses (due to inanimate factors) significantly cause more physical damage to the plants. Interestingly, Mehta et al. (2020) elucidated that all abiotic stresses are interlinked and usually affect the water affinity or ion levels in a plant at various levels (ranging from sub-cellular to whole plant level). This influences certain indefinite reactions that lead to several molecular, biochemical, physiological, and morphological changes (Barlow et al. 2015; Salehi-Lisar and Bakhshayeshan-Agdam 2016; Becklin et al. 2016; Khan et al. 2017; Jan et al. 2017; Zandalinas et al. 2018). These severe environmental stresses primarily arose due to water scarcity, salt stress, nutritional imbalance (accompanying mineral deficiency and toxicity) as well as extreme temperatures (Hirayama et al. 2010; Fahad et al. 2017). For example, 45% of the world's agricultural land is often found under low rainfall, which is home to 38% of the global population, Simultaneously, about 6% of mapped area of the world is prone to salinization that account up to more than 3,106 km^2 (Volkov et al. 2015). Furthermore, 19.5% of agricultural irrigated land is classified as saline. Furthermore, about 1% of the world's arable land decreases annually due to increase in salinity that ultimately results in fewer or no yield (Flowers et al. 2004; Gupta et al. 2020). In addition to salinity, water scarcity also affects plants during their growth and development. According to the World Soil Resources Report 2000 by Food and Agriculture Organization of the United Nations (FAO), the world's land area exposed to cold, drought, and salinity account up to 57%, 64%, and 6%, respectively. With persistent climate changes and human-induced environmental degradation in the present era, these physical stresses pose a significant risk to food security worldwide (Espeland and Kettenring 2018; Zandalinas et al. 2018; Singh et al. 2018a, b; Raza et al. 2019). For example, Zhao et al. (2017) study the effects of climate change showed that the yield of wheat, rice, soybean, and maize decreased by 6%, 3.2%, 3.1%, and 7.4%, respectively (Zhao et al. 2017). Thus, understanding crop response to particular abiotic stresses has become a most crucial part of crop research to ensure food security (Hirayama et al. 2010; Richardson et al. 2018).

To supply crops in a significant amount to the present humongous population, improving crop cultivation is of utmost important for filling the gap between food production and consumption and minimizing the losses due to increasing stresses. To withstand and adjust too many abiotic stresses, the varieties are being developed by using traditional as well as modern plant breeding approaches for a very long time. In this regard, knowledge of abiotic stresses (causes, perception, effects) as well as certain wild plant species is being used to increase stress tolerance.

5.2 Plants and Impact of Abiotic Stress Environment

Plant development and productivity are mainly affected by abiotic stresses that affect plants at three important plant developmental stages: vegetative growth, pre-anthesis flowering, and the terminal phase (Fahad et al. 2017; Shavrukov et al. 2017). Plant’s physiological responses to stresses like drought include leaf wilting, leaf shedding, reduced leaf area, and reduced water loss (Fghire et al. 2015). Under the stress of drought, crop development greatly alleviates the problem of extreme water use in agriculture. In addition, it also causes disruption of water movement (turgor pressure) in higher plants from the xylem to neighboring stretching cells and inhibits cell elongation. Furthermore, the decrease in plant height, leaf area, and yield is the result of drought stress due to mitosis, cell elongation, and growth disruption (Fahad et al. 2017). In a response, plants show resistance to abiotic stress either by the mechanism of avoidance or tolerance. The harmful effects of stress can be reduced by osmotic adjustment, which promotes the solute's active accumulation in the cytoplasm to maintain the water equilibrium of cells (Shanker et al. 2016; Masouleh et al. 2019).

Low temperatures also greatly affect the survival and geographical distribution of plants (Zhang et al. 2020a, b). Large yield losses due to slower plant growth and reduced yield are mainly caused by cold stress (Browse et al. 2001; Ritonga et al. 2020). At physiological level, dehydration of cells/tissues, crystallization of cell water, increase in water viscosity, free radicals as well as electrolyte, decrease in membrane conductivity and hydroactive stomatal closure are few of the changes that occur due to cold stress (Pearce et al. 2001; Kuromori et al. 2018; Dong et al. 2018a, b; Wang et al. 2020a, b, c). All these changes reduce plant development and yield ultimately at low temperature.

The yield of cereal crops is also more affected by high temperature as if the temperature exceeds 35°C, it destroys the important enzyme of photosynthesis (RuBisCo) and ultimately inhibits photosynthesis (Hatfield and Prueger 2015; Pereira 2016; Tkemaladze et al. 2016; Zargar et al. 2017; Morales et al. 2020; Bharti et al. 2021). In cereal crops, flower initiation and inflorescence are severely impressed by water stress. Likewise, during the development period of flowers in cereals, they become sterile when the temperature rises to 30°C. Similarly, fertilization and anthesis in rice are mostly hindered by drought stress. Water scarcity reduces seed setting and harvests index up to 60%. In *Zea mays*, Gong et al. investigated that antioxidant enzymes are negatively affected by high temperatures. The yield of maize, sorghum, and barley is also affected by heat stress (Dawood et al. 2020). It was found out that the combined effect of both drought and high temperature is more harmful than individual stress (Wang et al. 2004). On *Leymus chinensis*, Xu and Zhou (2006) applied high-temperature conditions and found that photosystem II (PSII) function is reduced (Xu et al. 2006). In rice and wheat, a shortage of water during the meiotic phase leads to a 35–75% reduction in seed set (Saini and Aspinall 1983: Sheoran and Saini 1996). According to research studies related to climate change, the yield of wheat has decreased by 6% (Abhinandan et al. 2018). Challinor and his colleagues reported that in variable climates, crop yields decrease when the temperature is higher during the grain-filling phase (Challinor et al. 2007). As per one source, it is estimated that by 2080 climate change will reduce agricultural production by 25.7% worldwide, and especially corn growing in Mexican region (Hellin et al. 2014). The climate data of the ECHAM6 line for the North German Plains was studied for two different periods 1981–2010 and 2041–2070 and concluded that water availability is necessary to maintain winter wheat yields (Svoboda et al. 2015).

In case of drought, all development stages of wheat are affected, however, reproduction and grain formation are most affected (Pradhan et al. 2012; Pereira 2016). Mild drought stress leads to a reduction in yield from 1% to 30% during post-anthesis in wheat, while its prolonged stay on flower and grain formation reduces yield by up to 92% (Araus et al. 2002; De Oliveira et al. 2013). The productivity of leguminous crops has also declined significantly due to drought stress. In mash bean (*Vigna mungo* L.), drought stress during the flowering and reproductive phase leads to 31%–57% and 26% yield reduction, respectively (Baroowa and Gogoi 2014). Drought stress significantly affects soybean production and causes a 42% drop in its productivity during the grain-filling phase (Maleki et al. 2013). Legumes are also highly sensitive to drought stress at vegetative and reproductive stages and eventually result in production loss (Nadeem et al. 2019). Wang et al. (2020a) in his studies reported the strong yield loss of soybean in its filling stage and production loss in maize in different growth stages due to drought stress.

The gene expression, metabolic pathways, and physiology of plants vary in different climatic stresses (Fig. 5.1). Despite much research, only a few sensors with ability to perceive any type of changes in their environment have been identified so far (Zhu 2016). Under stress conditions, transcription factors, stress-responsive proteins, solutes, hormones, and antioxidant cellular signals of plant cells or tissues undergo variable expression (Dinneny et al. 2008; Liu and Howell 2010; Verma et al. 2016; Rymaszewski et al. 2017; Menezes-Silva et al. 2017; Kurepin et al. 2017; Klay et al. 2018; Kuromori et al. 2018; Carvalho and Amancio 2018; Wu et al. 2017). At secondary level, these abiotic stresses cause both oxidative and osmotic stresses that ultimately break down cell membranes and inhibit plant characteristics (Nasim et al. 2017; Hasanuzzaman et al. 2020). Simultaneously, ROS interferes with the synthesis of nucleic acids, proteins, lipids, and carbohydrates as well as leads to cell apoptosis (Vincent et al. 2007; Ahmad et al. 2018; Martinez et al. 2018).

As per present, an important task of current agricultural research is to develop climate-resilient crop cultivars under environmental changes and to know their responses. It is being achieved by applying recent genomics technologies to strengthen climate-smart agriculture by minimizing the inevitable effects of climate change on agricultural production (Scheben et al. 2016; Abhinandan et al. 2018; De Pinto et al. 2020).

5.3 Breeding Approaches to Combat Stress environment

For a long time, dynamic plant breeding approaches provide a potentially guaranteed way to food security under a drastic environment as they make plants more resistant and escapable in stressful climates (Blum 2018). The long list of approaches primarily include QTL mapping, marker-assisted selection (MAS), genome-wide linked studies (GWAS), genome selection, and editing that are being used to produce abiotic stress-tolerant crop varieties (Abdelrahman et al. 2017; Boopathi et al. 2020). Table 5.1 illustrates the recent breeding progress for abiotic stress tolerance.

These approaches completely rely on genetic distances, genetic similarities, polymorphism, assortment, inbreeding, recombination, (homologous and non-homologous) and evaluation to achieve plant completeness (Raza et al. 2018a, b; Bohra et al. 2019; Rodenburg et al. 2018; Bohra et al. 2020). Apart from this, landraces are important sources for genetic analysis. A broad genetic-based wheat landrace, as recorded in the data bank, contains stress-resistant cultivars to survive in stressful environments (Lopes et al. 2015). Table 5.2 summarizes the recent successful examples of breeding for abiotic stress tolerance.

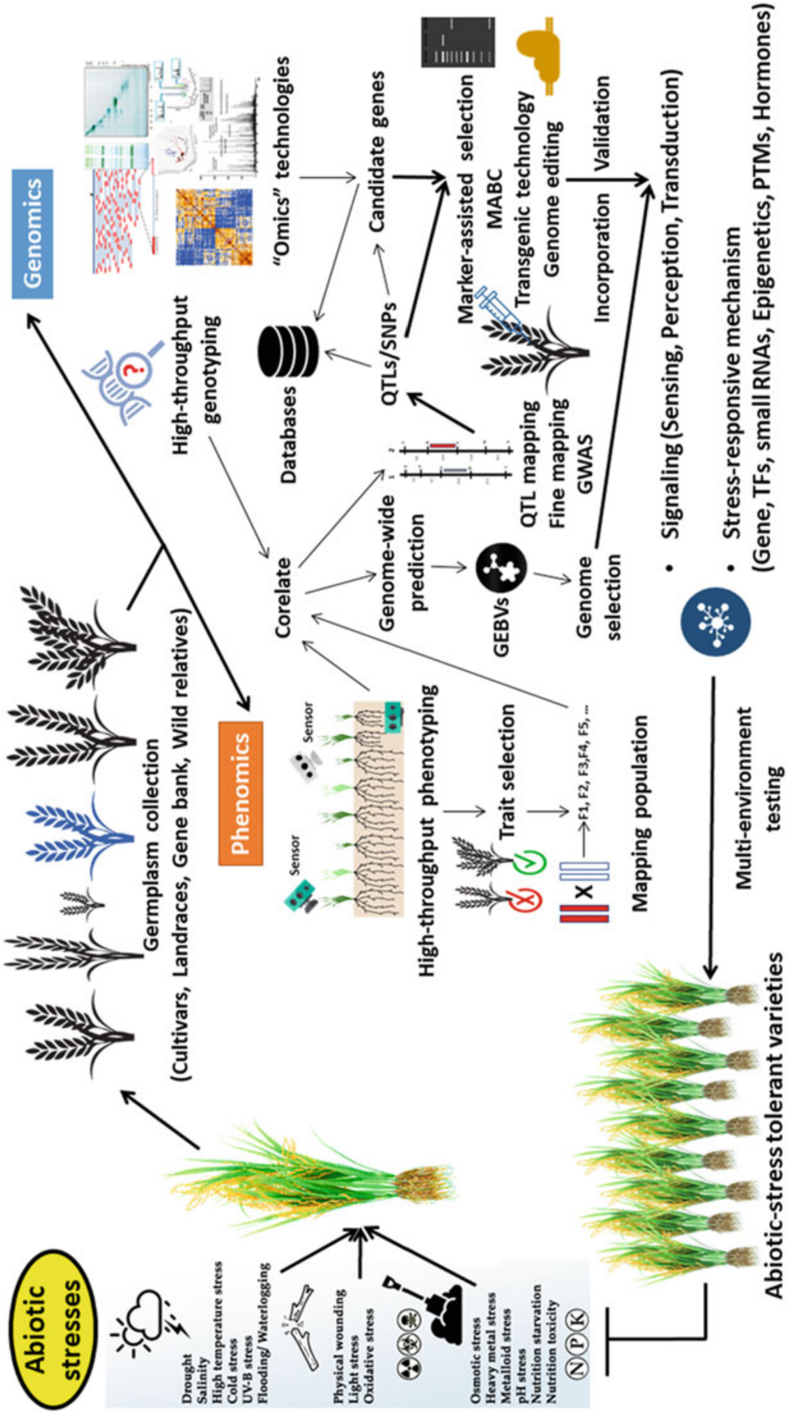

Fig. 5.1 Advances in omics approach for abiotic stress tolerance in crops

Table 5.1. List of recent breeding progress for abiotic stress tolerance

Name of crops	Type of stress	Traits	Major QTLs/gene/TF/hormone	Breeding methods/approach	References
Barley	Drought	Drought tolerance	QDT.TxFr.2H	DH population; QTL mapping	Fan et al. (2015)
			QDT.TxFr.5H		
		Relative water content	QRMO.TxFr.2H		
		Proline content under drought tolerance	QPC-D.TxFr.3H		
	Salinity	Salinity tolerance	QST.TxFr.7H	DH population; QTL mapping	Fan et al. (2015)
		Proline content under salinity tolerance	QPC-S.TxFr.3H		
	Salinity and waterlogging	Salinity tolerance under drained condition	QSlsd.YG.1H, QSlsd.YG.2H, QSlsd.YG.5H	DH population/QTL mapping	Ma et al. (2015)
		Salinity tolerance Waterlogged Conditions	QSlsw.YG.2H, QSlsw.YG.5H		
	Waterlogging	Aerenchyma formation	–	DH population/QTL mapping	Zhang et al. (2016)
		Root porosity	–		
		After 7 days waterlogging	–		
		Waterlogging tolerance	–		
		Aerenchyma formation	QTL-AER	DH population/QTL mapping	
		Waterlogging tolerance	QTL-WL-4H QTL-WL-6H QTL-WL-7H		
	ROS Formation under Hypoxia	O2•−in mature zone	QSO.TxNn.2H	DH population/QTL mapping	Gill et al. (2019)
		H_2O_2 in elongation zone	QSO.TxNn.2H		

(continued)

Table 5.1. (continued)

Name of crops	Type of stress	Traits	Major QTLs/gene/TF/hormone	Breeding methods/approach	References
	Salinity	Salinity tolerance at germination	L1H018492689, C1H556900757, L7H212035410, D7H085710245	QTN/Association mapping	Mwando et al. (2020)
Maize	Heat	Susceptibility index, Adjusted dry yield	QHSI:DYA	Segregating populations/QTL Mapping	Frey et al. (2016)
		Heat susceptibility index, Female flowering	QHSI:FF		
		Heat susceptibility index, Male flowering	QHSI:MF		
		Principal component	QPC		
		Leaf length	QHSI:LLa, QHSI:LLb	Six segregating populations derived from pairwise crosses/QTL Mapping	Inghelandt et al. (2019)
		Plant height	QHSI:PH		
		Leaf scorching	QHSI:SC		
		Leaf greenness	QHSI:SD		
		Leaf growth rate	QHSI:LR		
	Salinity	Root Length	qRLS1	DH Population/QTL mapping	Luo et al. (2019)
		Shoot length	qSLS1-2		
		Full length	qFLS1-2		
		Root fresh weight	qRFS1		
		Shoot fresh weight	qSFS1		
		Full fresh weight	qFFS1		
		Full dry weight	qFDS1		
		Root length	qRLR1		
		Full length	qFLR1		

		Shoot length	qSLR1-1		
		Root fresh weight	qRFR1		
		Shoot fresh weight	qSFR1-1		
		Full fresh weight	qFFR1		
		Plant height under normal condition	qNPH4, qNPH5, qNPH8, qNPH9–2	DH population/QTL mapping	Luo et al. (2017)
		Plant height under salt stress	qSPH1, qSPH 5–1, qSPH5–2		
		Plant height-based salt tolerance index	qPHI1, qPHI3, qPHI4, qPHI9, qPHI10		
		Salt tolerance associated genes	SAG4, SAG6	Natural association populations/ GWAS	Luo et al. (2019)
		Salt tolerance related traits	QSkc7, qRL2s, qRRDWS		
	Oxidative Stress	O_3-induced leaf damage	QTL	NIL population/QTL mapping	Sorgini et al. (2019)
	Nitrogen deficiency	Early vigor and leaf senescence	QTLSEN	DH population/QTL mapping	Liu et al. (2020)
	Drought	Ear height-to-plant height ratio	qEHPH-Ch.1-1	Two F 2: 3 populations/QTL mapping	Zhao et al. (2018)
			qEHPH-Ch.3-1		
			qEHPH-Ch.6-1,		
			qEHPH-J6-2		
			qEHPH-Ch.8-1		
		Grain weight	qGW-Ch.1-1		
			qGW-Ch.1-2,		
			qGW-J1-1		
			qGW-Ch.2-1,		
			qGW-J2-1		
			qGW-J2-2,		
			qGW-Ch.4-1		
			qGW-Ch.6-1,		

(continued)

Table 5.1. (continued)

Name of crops	Type of stress	Traits	Major QTLs/gene/TF/hormone	Breeding methods/approach	References
			qGW-J6-1		
			qGW-Ch.8-1,		
			qGW-J8-1		
			qGW-Ch.8-1		
			qGW-Ch.9-1		
		Kernel ratio	qKR-Ch.1-1		
			qKR-Ch.1-2		
			qKR-J1-1		
			qKR-Ch.3-1		
			qKR-Ch.6-1,		
			qKR-J6-1		
			qKR-J8-1,		
			qKR-Ch.8-1		
	Heavy Metal	Cadmium accumulation	qLCd2, qLCd5, qLCd7, qLCd8, qLCd9	IBMSyn10 DH population/QTL Identification by GWAS	Zhao et al. (2018)
	Cold	Leaf rolling degree	LRD	Testcrossing association mapping population and F2:3 population/GWAS, QTL Mapping	Yan et al. (2017)
		Water content in shoots and leaves	WCS		
		Ratio of root-to-shoot	RRS		
		Soluble sugar content	SSC		
Wheat	Drought	RLWL	QRL.nust-3A QRL.nust-4D QRL.nust-7B	RIL/QTL mapping	Onyemaobi et al. (2018)

		Fresh shoot weight	QSL.nust-3A QSL.nust-4A QSL.nust-7B QSL.nust-7D		
		Fresh root weight well watered	QFRW.nust-3B QFRW.nust-7A QFRW.nust-7B		
		Fresh shoot weight well watered	QFSW.nust-6D QFSW.nust-7B		
		Dry shoot weight water-limited	QDSW.nust-3D		
		Plant above ground biomass (DW)	36 (MTA under non stress)	93 Diverse bread wheat genotypes/ GWAS	Qaseem et al. (2019)
		Grain yield (GY)	23(MTA under non stress)		
		Tillers per plant and	22 (MTA under stress)		
		Stress tolerance index	19(MTA under stress)		
		Leaf area	1(MTA under stress)		
		Stress tolerance index	QSTI_S2.NIAB-7Att	RIL population/QTL mapping	Rehman Arif et al. (2020)
		Mean productivity	QMP_S2.NIAB-3B.2x		
		Stress tolerance	QST_S2.NIAB-5Ahh		
		Drought resistance index	QDRI_S1.NIAB-5Ahh		
		Grain weight per primary tiller	QGWt.adr-2D	Diverse 315 spring type accessions of bread wheat; RIL/GWAS, QTL	Schmidt et al. (2020)
		Grain weight per plant	QGWp.adr-2D		
		Days-to-heading	4 (MTA under DS);4 (MTA under NS)	93 diverse bread wheat genotypes/GWAS	Mwadzingeni et al. (2017)
		Plant height	2 (MTA under DS);6 (MTA under NS)		
		Spike length	13 (MTA under DS);8 (MTA under NS)		

(continued)

Table 5.1. (continued)

Name of crops	Type of stress	Traits	Major QTLs/gene/TF/hormone	Breeding methods/approach	References
		Days-to-maturity	1 (MTA under NS)		
		Spikelets per spike	8 (MTA under DS);7 (MTA under NS)		
		Kernels per spike	2 (MTA under DS);8 (MTA under NS)		
		1000 Seed weight	1 (MTA under NS)		
		Grain yield	1(MTA under NS)		
	Heat	TS (Timely sown)_ grain weight/spike	Qtgwas.iiwbr-2A, Qtgwas.iiwbr-6D.1, Qtgwas.iiwbr-6D.2	RIL population/QTL mapping	Bhusal et al. (2017)
		LS (Late sown)_ grain weight/ spike	Qgwas.iiwbr-2A		
		HIS (Heat susceptibility index)_ grain weight/spike	Qgws.iiwbr-2A		
		TS_ grain number/spike	Qgns.iiwbr-2A, Qtgns.iiwbr-6D		
		LS_ grain number/spike	Qgns.iiwbr-2A, Qlgns.iiwbr-2A		
		HSI_ grain number/spike	Qgns.iiwbr-2A		
		TS_thousand grain weight	Qtgw.iiwbr-2A		
		HIS_thousand grain weight	Qtgw.iiwbr-2A		
		Grain weight per primary tiller;	QGWt.ara-1A.6, QGWt.ara-3D.1,	Diverse 315 spring type accessions of bread wheat; RIL/GWAS, QTL	Schmidt et al. (2020)

			QGWt.ara-6B.7, QGWt.ara-6D.2, QGWt.ara-7A.1, QGWt.ara-7B.1		
		Grain weight per plant	QGWp.ara-6B.3, QGWp.ara-6D, QGWp.ara-7B		
	Drought and heat	Grain weight per primary tiller;	QGWt.adh-3A, QGWt.ara-3B.3, QGWt.ara-4A.1, QGWt.ara-5B.6, QGWt.ara-6A.1, QGWt.ara-6A.3, QGWt.ara-6B.6, QGWt.ara-7B.6	Diverse 315 spring type accessions of bread wheat; RIL/GWAS, QTL	Schmidt et al. (2020)
		Grain weight per plant	QGWp.ara-4A, QGWp.ara-6A, QGWp.adh-3, QGWp.adh-3B.1, QGWp.adh-3B.2, QGWp.adh-5B, QGWp.adh-6B		
Rice	Salinity	Salt tolerance at germination	OsNRT2.2	Gene identification/Association study	Shi et al. (2017)
		Seed germination and seedling establishment under salinity stress	qSE3	Map based cloning	He et al. (2019)
		Salt injury score	qSES2, qSES4	200 F4 lines developed by SSD method/QTL mapping	Pang et al. (2017)

(continued)

Table 5.1. (continued)

Name of crops	Type of stress	Traits	Major QTLs/gene/TF/hormone	Breeding methods/approach	References
		Genes associated with grain yield and related traits under saline stress conditions	MYB6, GAMYB, HKT1;4, CTR3, SUT1, LOC_Os02g49700, LOC_Os03g28300	708 rice accessions/GWAS	Liu et al. (2019)
	Alkali stress	Alkali Tolerance	qAT11	Combined linkage mapping and a genome-wide association study (GWAS)	Li et al. (2020)
			LOC_Os11g37300 LOC_Os11g37320 LOC_Os11g37390		
	Heat	Root length under heat stress	rlht5.1	RIL population/QTL mapping	Kilasi et al. (2018)
		Root length under heat stress as per cent of control	rlpc1.1, rlpc2.1, rlpc3.1, rlpc4.1		
		Shoot length under heat stress	slht3.1, slht4.1, slht6.1		
		Shoot length under heat stress as per cent of control	slpc2.1, slpc4.1, slpc5.1, slpc6.1, slpc10.2, slpc10.3		
	Drought	Physio-morphological plant	9QTLs	Two sets of RIL population/QTL mapping	Prince et al. (2015)
		Production traits	24QTLs		
		Grain yield (Stable QTLs)	qDTY 1.1, qDTY 3.3, qDTY 6.3	Two BC1F3 mapping populations/ QTL Mapping	Yadav et al. (2019)
		Grain yield under severe stress	qDTY 1.3, qDTY 4.3, qDTY 4.4		
		DTF (Stable QTLs)	qDTF 3.3, qDTF 6.3		
		Mean days to flowering under moderate stress	qDTF 1.2, qDTF 7.1, qDTF 8.1		
		Plant height under moderate stress	qPH 1.2, qPH 1.3, qPH 5.1		

		Days to flowering	qDTF3.01, qDTF11.08	RIL population/QTL mapping	Bhattarai and Subudhi (2018)
		Plant height	qPH1.07, qPH1.38, qPH3.32 qPH5.24, qPH9.14		
		Leaf rolling score	qLRS1.37, qLRS7.07, qLRS12.17		
		Plant dry matter content (%)	qDM1.07 qDM3.33		
		Spikelet fertility	qSF1.38, qSF6.23, qSF7.0.4, qSF11.19		
		Grain yield under stress	qGY1.42		
		Yield index	qYI1.42, qYI12.03		
		Harvest index (%	qHI1.37, qHI6.25		
		Visual drought tolerance	qVDT2, qVDT6, qVDT11	DH population/QTL mapping	Kim et al. (2017)
		Relative water content	RWC11		
		Grain yield	80 MTA	Natural population/Association mapping	Swamy et al. (2017)
		Plant height			
		Days to flowering			
	Low Nitrogen	Grain yield under low nitrogen	qGY1	Three sets of trait-specific introgression lines (ILs)/ segregation distortion approach and GWAS	Mwadzingeni et al. (2017)
		Panicle number per plant under low nitrogen	qPN1, qPN2		
		Thousand grain weight under low nitrogen	qTGW3		
		Seed fertility under low nitrogen	qSF8		
		Panicle number per plant under normal nitrogen	qPN2		
	Cold	Spikelet fertility (%) under cold water	qCT3.12, qCT6.7, qCT9.6	BC2 CT introgression lines (ILs) generated from five random BC2F4 populations/QTL	Liang et al. (2018)
		Percent seed set under cold water treatment	qPSST6	Bulked-segregant analysis (BSA)	

(continued)

Table 5.1. (continued)

Name of crops	Type of stress	Traits	Major QTLs/gene/TF/hormone	Breeding methods/approach	References
		Candidate genes for cold tolerance	LOC_Os01g55510, LOC_Os01g55350, LOC_Os01g55560	Indica rice varieties/GWAS	Zhang et al. (2018)
	Arsenic toxicity stress	Relative chlorophyll content	qRChlo1	Early backcross breeding population/ QTL mapping	Murugaiyan et al. (2019)
		Arsenic content root	qAsR8.1, qAsR8.2		
		Arsenic content shoot	qAsS2, qAsS5.1, qAsS5.2, qAsS6, qAsS9.1, qAsS9.2		
	Heavy metal toxicity (Fe, Zn)	Shoot ion concentration	qSFe2, qSFe5, qSFe6	222 indica rice accessions/GWAS	Zhang et al. (2017a, b, c)
		Toxicity tolerance	qSdw3a, qSdw3b, qSdw12, qSFe5, qSZn5		
	Anaerobic germination	Tolerance to anaerobic germination	qAG7.1, qAG7.2 , qAG7.3, qAG3	F2:3 mapping population/ QTLmapping	Baltazar et al. (2019)

Table 5.2 List of recent successful examples of breeding for abiotic stress tolerance

Name of crops	Name of target variety	Donor variety	Major QTLs/ gene/TF/ hormone	Target trait	Target stress	References
Rice	Swarna-Sub1	IR 86918-B-305 (N 22/IR 64)	qDTY1.1,	Grain yield under drought	Drought	Singh et al. (2016)
		IR 81896-B-B-195 (IRRI 132/2*Swarna)	qDTY2.1,			
			qDTY3.1			
		IR 86931-B-6 (N 22/Swarna)	qDTY3.2,			
		IR 90019-17-159-B (IR 79971-B-102-B -B/ 3*Vandana)	qDTY12.1			
	Samba Mahsuri-Sub1	IR 86918-B-305 (N 22/IR 64)	qDTY1.1			
		IR 81896-B-B-195 (IRRI 132/2*Swarna)	qDTY2.1			
		IR 87728-367-B-B (IR77298-5-6-18/IR 64)	qDTY2.2			
		IR 81896-B-B-195 (IRRI 132/2*Swarna)	qDTY3.1			
		IR 86931-B-6 (N 22/Swarna)	qDTY3.2			
	IR 64-Sub1	IR 86918-B-305 (N 22/IR 64)	qDTY1.1			
		IR 87728-367-B-B (IR77298-5-6-18/IR 64)	qDTY2.2			
		IR 81896-B-B-195 (IRRI 132/2*Swarna)	qDTY3.1			
		Ranchi IR87728-59-B-B (Aday sel/IR64)	qDTY9.1			
	MR219 (Malaysian rice cultivar)	IR77298-14-1-2-10	qDTY 2.2			Shamsudin et al. (2016a)
		IR81896-B-B-195	qDTY 3.1			
		IR84984-83-15-18-B	qDTY 12.1			

(continued)

Table 5.2 (continued)

Name of crops	Name of target variety	Donor variety	Major QTLs/gene/TF/hormone	Target trait	Target stress	References
	MRQ74 (Malaysian rice cultivar)	IR77298-14-1-2-10	qDTY 2.2			Shamsudin et al. (2016b)
		IR81896-B-B-195	qDTY 3.1			
		IR84984-83-15-18-B	qDTY 12.1			
	Sabitri	IR 77298-5-6-18/2	qDTY3.2			Dixit et al. (2017b)
		IR 74371-46-1-1/2	qDTY12.1			
	Swarna	IR96321–1447-561-B-1	qDTY1.1 qDTY3.1			Dixit et al. (2020)
	ADT 39	CR1009-Sub1	Sub1	Submergence tolerance	Submergence	Singh et al. (2016)
	ADT 46	Swarna-Sub1				
	Bahadur					
	HUR 105	IR64-Sub1				
	MTU 1075	Swarna-Sub1				
	Pooja					
	Pratikshya					
	Rajendra Mahsuri					
	Ranjit					
	Sarjoo 52	IR64-Sub1				
	Swarna sub1	MER-20	Sub1locus			Donde et al. (2017)
	Swarna-Sub1	Jyothi	Sub1locus			John and Shylaraj (2017)
	TDK1-Sub1	IR55419–04	qDTY3.1, qDTY6.1, qDTY6.2	Grain yield under drought and submergence tolerance	Drought and submergence	Dixit et al. (2017a)
	Swarna	IR 91659-54-35	qDTY1.1			

		IR 81896-B-B-195	qDTY2.1 +qDTY3.1			
		Swarna-Sub1	Sub1			
	Improved Lalat	FR13A	Sub1	Submergence and salt tolerance	Submergence and salinity	Das and Rao (2015)
		FL478	Saltol			
	Rassi	FL478	Saltol	Salt tolerance	Salinity	Bimpong et al. (2016)
	Pusa Basmati1	FL478	Saltol locus			
	Bengal	Pokkali	qDWT7.17			De Leon et al. (2017)
	IR64	FL478	Saltol locus			Ho et al. (2016)
	BRRI Dhan49	FL478	Saltol locus			Hoque et al. (2015)
	Novator	IR61920-3B-22-2-1	Saltol locus			Usatov et al. (2015)
	Improved White Ponni	Nagina 22	qHTSF1.1, qHTSF4.1			Vivitha et al. (2017)
	OM5939, AS996, IR66, Gayabyeo and IKO547	N22 and Dular, IR66	QTL			Lang et al. (2015)
	ADT45	FL478 (Pokkali/IR29)	Saltol			Singh et al. (2016)
	CR 1009					
	Gayatri					
	MTU 1010					
	PR 114					
	Pusa 44					

(continued)

Table 5.2 (continued)

Name of crops	Name of target variety	Donor variety	Major QTLs/ gene/TF/ hormone	Target trait	Target stress	References
	Sarjoo 52					
	Pusa Basmati 1121 (PB1121)	FL478	Saltol locus			Babu et al. (2017)
	Pusa Basmati 1509 (PB 1509)	FL478	Saltol locus			Yadav et al. (2020)
Wheat	Inbar and Uzan	Wild emmer (acc. G18-16)	GY-S for grain yield (1BL)	Grain yield	Drought	Merchuk-Ovnat et al. (2016)
	Inbar and Uzan		GY and HI (2BS)	Grain yield and harvest index		
	BarNir, Zahir, and Inbar		SpDM-d and TotDM-d (7AS)	Spike dry matter and total dry matter		
	Inbar		GY-d, SpDM, and HI (7BS)	Grain yield under drought, spike dry matter, and harvest index		
	Kumpa-INIA	CAR3911	TaALMT1 (4DL)	Aluminum tolerance	Aluminum	Soto-Cerda et al. (2015)

The potential mechanism of abiotic stress tolerance and increased production in crop plants is induced by various abiotic environmental factors such as drought, water lodging, nutrient deficiency, oxidative stress, salinity, temperature, and heavy metal toxicity (arsenic, cadmium, zinc, lead, etc.). *Plants face* oxidative stress when exposed to *heavy metals* and show cellular damage acting as major threat for agriculture and a big hurdle in ensuring food security to current and future generation. Plants surfaced to abiotic stress displays enhanced levels of ROS (reactive oxygen species), proved to be toxic and reactive and affect the various physiological phenomenon like biosynthesis of chlorophyll, photosynthesis, antioxidant enzyme activities, and metabolism of carbohydrate, protein, and lipids. Transgenic breeding in various crops like wheat and rice offers a suitable alternative to conventional breeding to achieve plant genetic improvements (Table 5.2). Rice varieties like Swarna-Sub1, Samba Mahsuri-Sub1, IR 64-Sub1, MRQ74 (Malaysian rice cultivar), Sabitri, etc. were recently being modified using QTL mapping studies and the target genes were elucidated by exploring the physiology and epistatic mechanisms of QTL. The QTLs qDTY 1.1, qDTY 2.1, qDTY 3.1, qDTY 3.2, and qDTY 3.1 were identified, which significantly influence the grain yield under drought stress. Wheat varieties like Inbar, Uzan, BarNir, and Zahir demonstrated the major QTLs/ Gene/ TF/Hormone like GY-S, GY, HI (2BS), SpDM-d, TotDM-d(7AS), and HI that remarkably affected the grain yield under drought, spike dry matter, and harvest index (Table 5.2).

5.3.1 QTL Breeding and Marker-Assisted Selection

Since the inception of twenty-first century, molecular markers are being used to study population genomics to detect novel diversity patterns and to find gene expression for important ecological traits (Keurentjes et al. 2008; Di Vittori et al. 2019). For gaining success in molecular breeding, screening of elite germplasm, and pyramiding multiple traits in many crops, molecular markers have been combined with genomics approaches (Bevan and Waugh 2007; Roy et al. 2011; Dormatey et al. 2020). Based on the data available for environmental extremes, quantitative trait loci (QTL) mapping and DNA fingerprinting lead to screening of elite germplasm (Kole et al. 2015). For abiotic stress conditions, crop cultivar with good adaptability can be developed by QTL dissection of yield-associated traits (Collins et al. 2008). A variety of wheat "Rippers" have been successfully developed by QTL mapping that can survive Colorado's drought conditions without affecting the yield and quality of its grain (Haley et al. 2007). Drought-related QTLs in bread wheat (*Triticum beautivum* L.) and durum wheat (*Triticum turgidum* L.) were identified by marker-assisted selection studies (Merchuk-Ovnat et al. 2016). Two barley cultivars that were independent in response to drought stress were selected and QTL mapping was performed in double haploids for the malt character (Kochevenko et al. 2018). Target genes were elucidated by QTL mapping studies, exploring the physiology and epistatic mechanisms of QTL, most recently. Three QTLs qDTY 6.2, qDTY 6.1, and qDTY 3.1 were identified, which significantly influence the grain yield under drought stress. Three QTLs on the bread wheat genome: 7D, 7B, and 2B are predicted to be resistant to high-temperature conditions (Scheben et al. 2016). The QTL mapping study performed by Tahmasebi et al. (2016) on recombinant inbred lines (RIL) of wheat under different stress conditions showed a 19.6% variation in grain yield. This study showed that molecular markers have been used to detect unique allelic variation in wheat, increasing cultivars' ability to tolerate drought (Tahmasebi et al. 2016). Amalgamation of DNA markers with QTL mapping in wheat demonstrates a distinct design of stress tolerance genes on particular chromosomal loci and used in genetic variation analysis (Younis et al. 2020). Wen et al. (2019) in his study demonstrated that the rapid identification of candidate genes within major QTLs for a composite trait of interest by replacing the fine-mapping process is achieved in tomato by combining the conventional QTL mapping, QTL-seq analysis and RNA-seq (Fig. 5.1). Figure 5.1 demonstrates the synchronization of phenomics and genomics technological advances in abiotic stress in crops.

Marker-selected selection (MAS) is an important part of current agricultural research which is being used to speed up breeding programs for crop improvement (Da Silva Dias et al. 2015). This is because it based on relating the phenotyping data with genotyping of DNA marker (Mehta et al. 2019). A large number of DNA polymorphisms, particularly the identification of SNP markers and the discovery of genomic variants, have been facilitated by the introduction of precise sequencing tools (D’Agostino and Tripodi 2017). Wainaina et al. (2018) through marker-assisted selection reported QTLs as a useful tool to develop the cold-tolerant varieties highly productive in high altitude areas. The genetic architecture of reproductive stage drought tolerance in wheat was determined by using a correlated trait and correlated marker effect model (Dolferus et al. 2019). Similarly a protocol for assessing cold tolerance of New Rice of Africa (NERICA) is reported during reproductive growth stages by Samejima et al. (2020).

5.3.2 Genome-Wide Association Studies (GWAS)

Allelic variants associated with specific traits in different crop varieties can be identified by a potential technique, genome-wide association studies (GWAS), in which all their genetic variants can be studied (Manolio 2010; O’Connor et al. 2020). Based on GWAS design, genotyping tools, statistical models, and result interpretation, this approach reveals the association between SNPs and characters (Bush and Moore 2012). GWAS technology has been developed to detect the process of genetic resistance against climate stress in crop plants (Mousavi-Derazmahalleh et al. 2018) and extensively applied for drought tolerance (Thoen et al. 2017), salt tolerance (Wan et al. 2017), and heat tolerance (Lafarge et al. 2017). Verslues et al. (2014) conducted a GWAS study with a reverse genetic approach for profiling of proline-accumulating genes against drought stress in *Arabidopsis thaliana*. Reverse genetics approaches have identified several pro-accumulated proline proteins such as the universal stress protein a domain protein, the AMADS box protein, the thioredoxin, the ribosomal protein RPL24A, the protein phosphatase 2 subunit A3, and the mitochondrial protease LON1 (Verslues et al. 2014). Several resistance genes controlling abiotic stress have been reported in *Aegilops tauschii* (Ashraf 2009). A total of 373 different varieties of *A. tauschii* were characterized by Qin et al. (2016) for thirteen traits associated with drought stress. For the study of phenotypic behavior via GWAS, 7185 SNPs were designed and mixed linear models and general linear models were analyzed to find the link of SNPs with phenotypic traits (Qin et al. 2016). Salt tolerant QTLs were mapped onto genomic regions of chromosomes 1, 4, 6, and 7. "Saltol" is a novel QTL mapped to chromosome-1, which was found to be associated with salt stress tolerance in the seedling stage (Kumar et al. 2015).

To analyze the effect of heat stress on anthesis in rice, genotyping for spikelet sterility (SPKST), and panic micronutrient via haplotype regression, single marker regression, and co-fitting of all markers, was done in 167 varieties by GWDS (Lafarge et al. 2017). Stress-tolerant genes in *Sorghum bicolor* associated with heat and cold stress was reported by Chopra et al. (2017). Thirty SNPs associated with cold stress at the stage of seedling development were identified in *Sorghum*, which is also associated with anthocyanin expression and carbohydrate metabolism. Another 12 SNPs regulated by ion transport and sugar metabolism genes were reported to heat stress in the seedling stage of sorghum (Chopra et al. 2017). Leaf firing and blotching traits were observed in *Sorghum bicolor* that are associated with heat tolerance at the vegetative growth phase (Chen et al. 2017). Ethiopian sorghum successfully contributed to the characterization of genes and alleles controlling agronomic traits by identifying important traits for molecular breeding (Girma et al. 2019). Wang et al. (2020a) demonstrated lodging tolerant grain sorghum by using large-scale genome-wide association study proposing important role of carbon remobilization.

5.3.3 Genomic Selection (GS) for Crop Improvement

Nowadays, genomic selection (GS) is the most exciting technique to accelerate crop improvement and breeding programs using molecular marker polymorphisms and high throughput phenotyping, which include evaluation and characterization of germplasm, polygenic trait improvement, and elite breeding line development (Kumar et al. 2018; Singh et al. 2019; Allier et al. 2020).

By applying the linear mixed model to the G × E model, the first statistical design was proposed by Burguno et al. (2020). A method of modeling the relationship between markers and an enhanced environmental dimension combination that integrates with each other (G × E) was suggested by Jarquin et al. (2014). Phenotypic regression of the GBLUP type model proposed by Lopez-Cruz et al. is used for estimation of the marker × environment (M × E) interaction (Lopez-Cruz et al. 2015). For genomic predictions, a modern multi-environment model based on the Bayesian model was proposed by Cuevas et al. Higher significance rates and superior genomic predictions of the G × E model compared to other models, reported by the CIMMYT data bank following the application of these models on four wheat and one maize cultivars (Cuevas et al. 2017).

With 29 genomic selections, wheat is the most studied crop. Diversity Array Technology (DArT), single nucleotide polymorphism (SNP), and genotyping by sequencing (GBS) is used in GS, of which DArT is the most promising maker. For cereal breeding, research has shown that GS can be put to great use (Rutkoski et al. 2017). The ability of wheat germplasm to adapt to climate change is explained by widely developed designs of genomic selection (GS) (Dong et al. 2018a, b). Using a high throughput phenomics approach, 1000 wheat cultivars were investigated for heat and drought stress in CIMMYT (Crain et al. 2018). The automated high throughput system, or similar equipment, can likely accelerate progress in plant breeding and potentially assist in rapid development of superior varieties in wheat, which would in turn impact global food security (Zhang et al. 2018). Kim et al. (2020) quantified the physiological responses of plants to drought by evaluating WUE and TR using Drought Spotter that assisted in the characterization of the actual drought resistance in the mutants. Wani et al. (2020) decipher the recent advances in genomics assisted breeding for drought stress tolerance in major cereals.

5.3.4 Genetic Engineering

Biotechnology is a powerful approach to human welfare through genetic modification of the genome (Kulkarni et al. 2020). Genetics-encouraging data can be collected and used to serve the purpose of generating tolerance for various environmental stresses such as drought, heat, cold, and salinity (Sandhu et al. 2019a, b; Anamika et al. 2019). The characteristics associated with various stresses can be improved through the engineering of stress-responsive TFs and can be used for the development of climate-smart crop cultivars (Reynolds et al. 2015; Van Esse et al. 2020). Transgenic plants developed for climatic stress have shown significant resistance compared to non-transgenic (Shah et al. 2016; Nejat et al. 2017; Ullah et al. 2018; Jha et al. 2019; Rai et al. 2020).

Several plant-specific transcription factors (TFs) such as AP2/ERFBP (Riechmann et al. 1998; Licausi et al. 2010) have been identified. DREB and ERF are two main subfamilies of the AP2/ERFBP TFs family that have been extensively investigated for their response extensively under abiotic stresses (Licausi et al. 2010). DREB TFs regulate various stress conditions such as water scarcity and cold (Stockinger et al. 1997) with reports coming from various plant species (Agarwal et al. 2006; Lata and Prasad 2011; Mizoi et al. 2012; Wang et al. 2018; Ma et al. 2019; Niu et al. 2020). DREB1 and DREB2 have been studied in rice and *Arabidopsis* and have reported their regulatory function for cold stress, drought, high temperature, and salinity stress, respectively (Liu et al. 1998; Sakuma et al. 2002; Lucas et al. 2011; Yoon et al. 2020). Transgenic *Arabidopsis* plants have been developed to endure salinity, drought, and cold stress using DREB1 (Gilmour et al. 1998; Jaglo-Ottosen et al. 1998). Similarly, the DREB gene was also incorporated to develop transgenic crop varieties for resistance to abiotic stress

(Jaglo et al. 2001; Hsieh et al. 2002; Kasuga et al. 2004; Ito et al. 2006; Qin et al. 2007; Sarkar et al. 2019; Niu et al. 2020; Latha et al. 2018). Similarly, transgenic plants have been developed for salt and drought tolerance by over-expression of the GDDREB2 gene, which was isolated from soybean (Chen et al. 2007). Transgenic rice has been successfully developed for drought and salinity resistance by over-expressing the OsDREB2A gene (Mallikarjuna et al. 2011).

Next to AP2, ERF TFs subfamily is also considered to be responsible for the regulation of stress tolerance genes in plants (Hao et al. 1998; Liang et al. 2008). Transgenic tobacco and wheat developed from over-expression of the ERF3 gene have been shown to have greater tolerance to various abiotic stresses (Zhang et al. 2009; Zhu et al. 2014; Tolosa et al. 2020).

Another large family of TFs is the myeloblastosis oncogenes (MYB) TFs that regulate various physiological and biochemical pathways such as the cell cycle, hormone biosynthesis, and metabolism, including transduction signaling under biotic and abiotic stress (Ambawat et al. 2013; Baldoni et al. 2015; Li et al. 2015). Transgenic *Arabidopsis* has been developed by using *At*MYB61, *At*MYB60, and *At*MYB44 *At*MYB96 to increase drought resistance through stomatal regulation (Cominelli et al. 2005; Liang et al. 2005; Jung et al. 2008; Seo et al. 2009, 2011). *Gm*MYB76 gene over-expressed in *Arabidopsis* successfully enhanced salinity and freezing tolerance (Liao et al. 2008). Similarly, apple and tomato transgenic plants were developed by introducing *Md*MYB121 for increasing drought and salt tolerance from apple (Cao et al. 2013).

Similarly, in wheat, tolerance to drought stress was incorporated by transformation of the TPIMP1 gene (Liu et al. 2020; Zhang et al. 2012). Furthermore, several transgenic plants were produced by over-expressing several WRKY genes to increase tolerance to climate change (Wu et al. 2009; Zhou et al. 2008; Li et al. 2013; He et al. 2016; Fan et al. 2016; Javed et al. 2020).

NACs are also a large family of TFs, which play important roles in cell division, floral development, and stress-responsive regulation against environmental stresses (Nuruzzaman et al. 2010; Shiriga et al. 2014; Banerjee and Roychoudhury 2015; Nuruzzaman et al. 2013). Several NAC genes have been identified for stress tolerance and expressed in various plants (Jiang and Deyholos 2006; Hu et al. 2006; Fang et al. 2008; Zheng et al. 2009; Lu et al. 2013; Sun et al. 2018a, b; Schmockel et al. 2019; Yuan et al. 2020).

5.3.5 Genome Editing Strategies

Traditional plant breeding is an important and basic science of plant research that develops the elite and high-yielding cultivars of cultivated as well as domesticated crop species. However, extensive exploitation of crops has led to increased vulnerability of crops to many biotic and abiotic stresses along with a continued reduction in genetic diversity of various crop varieties (Flint-Garcia et al. 2013; Abdelrahman et al. 2018a, b). Since the year 2013, genome editing (GE) has emerged as a notable tool for developing climate-smart cultivars for crop improvement through sequence-specific nucleases (Liu et al. 2013; Taranto et al. 2018; Ahmar et al. 2020). This can be supported by the fact that in the past year of 2020, a noble prize was awarded to the developers of same technique.

Crop germplasm is essentially necessary to engineer gene pools with novel genome alterations to improve elite crop varieties with their increased capacity to produce stable and high yields under climate change (Kamburova et al. 2017). Overall, genome editing uses site-specific endonucleases, including zinc-finger nucleases (ZFNs), transcription activator-like effectors nucleases (TALENs), and CRISPR-Cas9 (Zhu et al. 2017). The CRISPR/Cas9 system is dawn as the most effective GE approach, being, rapid, economical, accurate and enables multiple site-specific editing within the genome compared to ZEN and TALEN (Abdelrahman et al. 2018a, b; Mahmood et al. 2020).

As per classification, CRISPR/Cas9 is a recent genome editing tool that arises from the defense mechanisms of bacteria triggered organization against invading viruses (Mousavi-Derazmahalleh et al. 2018; Hussain et al. 2018; Lino et al. 2018). The genome produced by this modern genome editing tool contains mutations and knock-downs in candidate genes for single nucleotides (Larochelle 2018). The CRISPR/Cas9 technique is transforming into an "environment friendly tool" for developing non-transgenic plants with edited genomes to solve problems related to food security under climate change (Khurshid et al. 2017; Haque et al. 2018).

The triple mutant in rice was produced by employing CRISPR/Cas9 technology where the size of the wheat seed was increased by knockdown of the *Ta*GW2 gene, a negative regulator of the seed size (Wang et al. 2018). The CRISPR/Cas9 technique has been also used to develop the non-transgenic cultivar of wheat with low gluten content (Sanchez-Leon et al. 2018). In another study, tomato mutant lines were developed from CRISPR/Cas9, indicating high concentrations of proline, malondialdehyde, and H_2O_2 while being susceptible to oxidative stress in drought conditions. In another study, the importance of the *Sl*MAPK3 gene for drought tolerance was highlighted by engineering this gene for enhancing drought tolerance (Wang et al. 2017). To produce parthenocarpic fruits in response to high temperatures, the *Sl*AGL6 gene was knocked down using the CRISPR/Cas9 system (Klap et al. 2017). Furthermore, Japonica rice was studied for Osan3 gene knockout (Shen et al. 2017) and a mutant rice lines having OsANN3 gene for cold tolerance (Shen et al. 2017). Using the CRISPR/Cas9 technique, herbicide tolerance was also developed by knocking down the PmCDA1 gene in rice mutant lines (Shimatani et al. 2017). In current times CRISPR/Cas9 is a revolutionary research field in fundamental as well as applied sciences (Mehta et al. 2020). CRISPR/Cas9 is a strong genome editing tool which has been successfully displayed in rice, maize, wheat, and barley to achieve desirable traits (Ansari et al. 2020).

5.4 Conclusions and Future Thrusts

Most of the crop losses are due to abiotic stresses, which cause even more than 50 %. From a number of research findings, it is clear that these abiotic stresses have devastating impact on plant growth, growth, physiology, and productivity. Over the last century, conventional plant breeding has played an important role in improving resistance to abiotic stresses. However, it takes more time to develop/hybrid varieties that withstand abiotic stress. As a result, varieties/lines/hybrids of crops are being developed with increased tolerance to drought, salinity, heat, heat and nutrient deficiencies, by using traditional, molecular breeding, and biotechnological tools.

Combining knowledge of traditional breeding and marker-assisted breeding makes it easier and more effective to increase tolerance using crop genotypic data to increase and maintain productivity. Plant breeders of the future will need a mix of knowledge, skills, and experience in plant breeding, genetics, genomics, statistics, experimental design, genetic diversity, and management of germplasm to be effective. With better adaptation to stresses, breeding approaches will help grow climate-resistant crops. Genome-wide association studies (GWAS), genomic selection (GS) with high throughput phenotyping and genotyping are of great importance for crop improvement in the face of climate change. In the future, to combat climate change, we must create "sustainable super crops" with amalgamation of GS, GWAS, and CRISPR/Cas9 mediated genome editing.

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References

Abdelrahman M, Al-Sadi AM, Pour-Aboughadareh A, Burritt DJ, Tran L-SP (2018a) Genome editing using CRISPR/Cas9–targeted mutagenesis: An opportunity for yield improvements of crop plants grown under environmental stresses. Plant Physiol Biochem 131:31–36

Abdelrahman M, El-Sayed M, Sato S, Hirakawa H, Ito S-I, Tanaka K, Mine Y, Sugiyama N, Suzuki M, Yamauchi N (2017) RNA-sequencing-based transcriptome and biochemical analyses of steroidal saponin pathway in a complete set of *Allium fistulosum—A. cepa* monosomic addition lines. PLoS One 12:e0181784

Abdelrahman M, Jogaiah S, Burritt DJ, Tran LSP (2018b) Legume genetic resources and transcriptome dynamics under abiotic stress conditions. Plant Cell Environ 41:1972–1983

Abhinandan K, Skori L, Stanic M, Hickerson NM, Jamshed M, Samuel MA (2018) Abiotic stress signaling in wheat—an inclusive overview of hormonal interactions during abiotic stress responses in wheat. Front Plant Sci 9:734

Agarwal M, Hao Y, Kapoor A, Dong C-H, Fujii H, Zheng X, Zhu J-K (2006) A R2R3 type MYB transcription factor is involved in the cold regulation of CBF genes and in acquired freezing tolerance. J Biol Chem 281:37636–37645

Ahmad Z, Anjum S, Waraich EA, Ayub MA, Ahmad T, Tariq RMS, Ahmad R, Iqbal MA (2018) Growth, physiology, and biochemical activities of plant responses with foliar potassium application under drought stress—a review. J Plant Nutr 41:1734–1743

Ahmar S, Saeed S, Khan MHU, Ullah Khan S, Mora-Poblete F, Kamran M, Faheem A, Maqsood A, Rauf M, Saleem S et al (2020) A revolution toward gene-editing technology and its application to crop improvement. Int J Mol Sci 21:5665

Allier A, Teyssèdre S, Lehermeier C et al (2020) Optimized breeding strategies to harness genetic resources with different performance levels. BMC Genomics 21:349. https://doi.org/10.1186/s12864-020-6756-0

Ambawat S, Sharma P, Yadav NR, Yadav RC (2013) MYB transcription factor genes as regulators for plant responses: an overview. Physiol Mol Biol Plants 19:307–321

Anamika, Mehta S, Singh B, Patra A, Islam MA (2019) Databases: a weapon from the arsenal of bioinformatics for plant abiotic stress research. In: Recent approaches in Omics for plant resilience to climate change. Springer, Cham, pp 135–169

Ansari WA, Chandanshive SU, Bhatt V, Nadaf AB, Vats S, Katara JL, Sonah H, Deshmukh R (2020) Genome editing in cereals: approaches, applications and challenges. Int J Mol Sci 21: 4040

Araus J, Slafer G, Reynolds M, Royo C (2002) Plant breeding and drought in C3 cereals: what should we breed for? Ann Bot 89:925–940

Ashraf M (2009) Biotechnological approach of improving plant salt tolerance using antioxidants as markers. Biotechnol Adv 27:84–93

Babu NN, Krishnan SG, Vinod KK, Krishnamurthy SL, Singh VK, Singh MP, Singh R, Ellur RK, Rai V, Bollinedi H, Bhowmick PK, Yadav AK, Nagarajan M, Singh NK, Prabhu KV, Singh AK (2017) Marker aided incorporation of *Saltol*, a major QTL associated with seedling stage salt tolerance, into *Oryza sativa* 'Pusa Basmati 1121'. Front Plant Sci *8*:41

Baldoni E, Genga A, Cominelli E (2015) Plant MYB transcription factors: Their role in drought response mechanisms. Int J Mol Sci 16:15811–15851

Baltazar MD, Ignacio J, Thomson MJ, Ismail AM, Mendioro MS, Septiningsih EM (2019) QTL mapping for tolerance to anaerobic germination in rice from IR64 and the *aus* landrace Kharsu 80A. Breed Sci 69(2):227–233

Banerjee A, Roychoudhury A (2015) WRKY proteins: signaling and regulation of expression during abiotic stress responses. Sci World J 2015:1–17

Barlow K, Christy B, O'leary G, Riffkin P, Nuttall J (2015) Simulating the impact of extreme heat and frost events on wheat crop production: a review. Field Crop Res 171:109–119

Baroowa B, Gogoi N (2014) Biochemical changes in black gram and green gram genotypes after imposition of drought stress. J Food Legum 27:350–353

Becklin KM, Anderson JT, Gerhart LM, Wadgymar SM, Wessinger CA, Ward JK (2016) Examining plant physiological responses to climate change through an evolutionary lens. Plant Physiol 172:635–664

Bevan M, Waugh R (2007) Applying plant genomics to crop improvement. BioMed Central, London

Bharti J, Sahil M, Ahmad S, Singh B, Padhy AK, Srivastava N, Pandey V (2021) Mitogen-activated protein kinase, plants and heat stress. In: Husen A (ed) Resilient environment and plant potential. Springer, Cham

Bhattarai U, Subudhi PK (2018) Genetic analysis of yield and agronomic traits under reproductive-stage drought stress in rice using a high-resolution linkage map. Gene *669*:69–76

Bhusal N, Sarial AK, Sharma P, Sareen S (2017) Mapping QTLs for grain yield components in wheat under heat stress. PLoS One *12*(12):e0189594

Bimpong IK, Manneh B, Sock M, Diaw F, Amoah N, Ismail AM, Gregorio G, Singh RK, Wopereis M (2016) Improving salt tolerance of lowland rice cultivar 'Rassi' through marker-aided backcross breeding in West Africa. Plant Sci *242*:288–299

Blum A (2018) Plant breeding for stress environments: 0. CRC Press, Boca Raton

Bohra A, Bharadwaj C, Radhakrishnan T, Singh NP, Varshney RK (2019) Translational genomics and molecular breeding for enhancing precision and efficiency in crop improvement programs: some examples in legumes. Indian J Genet Plant Breed 79:227–240

Bohra A, Saxena KB, Varshney RK, Saxena RK (2020) Genomics-assisted breeding for pigeon pea improvement. Theor Appl Genet 133:1721–1737

Boopathi NM (2020) Marker-assisted selection (MAS). In: Genetic mapping and marker assisted selection. Springer, Singapore, pp 343–388. https://doi.org/10.1007/978-981-15-2949-8_9

Browse J, Xin Z (2001) Temperature sensing and cold acclimation. Curr Opin Plant Biol 4(3): 241–246

Burgueño J, Crossa J, Cotes JM, Vicente FS, Das B (2020) Prediction assessment of linear mixed models for multi-environment trials. Crop Sci 51:944–954

Bush WS, Moore JH (2012) Genome-wide association studies. PLoS One 8:e1002822

Cao Z-H, Zhang S-Z, Wang R-K, Zhang R-F, Hao Y-J (2013) Genome wide analysis of the apple MYB transcription factor family allows the identification of MdoMYB121 gene confering abiotic stress tolerance in plants. PLoS One 8:e69955

Carvalho LC, Amâncio S (2018) Cutting the Gordian Knot of abiotic stress in grapevine: From the test tube to climate change adaptation. Physiol Plant 165:330

Challinor A, Wheeler T, Craufurd P, Ferro C, Stephenson D (2007) Adaptation of crops to climate change through genotypic responses to mean and extreme temperatures. Agric Ecosyst Environ 119:190–204

Chen J, Chopra R, Hayes C, Morris G, Marla S, Burke J, Xin Z, Burow G (2017) Genome-wide association study of developing leaves' heat tolerance during vegetative growth stages in a sorghum association panel. Plant. Genome 10:1–15

Chen M, Wang Q-Y, Cheng X-G, Xu Z-S, Li L-C, Ye X-G, Xia L-Q, Ma Y-Z (2007) GmDREB2, a soybean DRE-binding transcription factor, conferred drought and high-salt tolerance in transgenic plants. Biochem Biophys Res Commun 353:299–293

Chopra R, Burow G, Burke JJ, Gladman N, Xin Z (2017) Genome-wide association analysis of seedling traits in diverse Sorghum germplasm under thermal stress. BMC Plant Biol 17:12

Collins NC, Tardieu F, Tuberosa R (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand? Plant Physiol 147:469–486

Cominelli E, Galbiati M, Vavasseur A, Conti L, Sala T, Vuylsteke M, Leonhardt N, Dellaporta SL, Tonelli C (2005) A guard-cell-specific MYB transcription factor regulates stomatal movements and plant drought tolerance. Curr Biol 15:1196–1200

Crain J, Mondal S, Rutkoski J, Singh RP, Poland J (2018) Combining high-throughput phenotyping and genomic information to increase prediction and selection accuracy in wheat breeding. Plant Genome 11:1–14

Cuevas J, Crossa J, Montesinos-López OA, Burgueño J, Pérez-Rodríguez P, de los Campos G (2017) Bayesian genomic prediction with genotype× environment interaction kernel models. G3: Genes Genom Genet 7:41–53

D'Agostino N, Tripodi P (2017) NGS-based genotyping, high-throughput phenotyping and genome-wide association studies laid the foundations for next-generation breeding in horticultural crops. Diversity 9:38

Da Silva Dias JC (2015) Biodiversity and plant breeding as tools for harmony between modern agriculture production and the environment. In: Molecular approaches to genetic diversity. InTech, London

Das G, Rao GJN (2015) Molecular marker assisted gene stacking for biotic and abiotic stress resistance genes in an elite rice cultivar. Front Plant Sci 6:698

Dawood MFA, Moursi YS, Amro A, Baenziger PS, Sallam A (2020) Investigation of heat-induced changes in the grain yield and grains metabolites, with molecular insights on the candidate genes in barley. Agronomy 10:1730

De Leon TB, Linscombe S, Subudhi PK (2017) Identification and validation of QTL for seedling salinity tolerance in introgression lines of a salt tolerant rice landrace 'Pokkali'. PLoS One 12(4):e0175361

De Oliveira ED, Bramley H, Siddique KH, Henty S, Berger J, Palta JA (2013) Can elevated CO_2 combined with high temperature ameliorate the effect of terminal drought in wheat? Funct Plant Biol 40:160–171

De Pinto A, Cenacchi N, Kwon H-Y, Koo J, Dunston S (2020) Climate smart agriculture and global food-crop production. PLoS One 15:6. https://doi.org/10.1371/journal.pone.0231764

Di Vittori V, Gioia T, Rodriguez M, Bellucci E, Bitocchi E, Nanni L, Attene G, Rau D, Papa R (2019) Convergent evolution of the seed shattering trait. Gen 10:68

Dinneny JR, Long TA, Wang JY, Jung JW, Mace D, Pointer S, Barron C, Brady SM, Schiefelbein J, Benfey PN (2008) Cell identity mediates the response of *Arabidopsis* roots to abiotic stress. Science 320:942–945

Dixit S, Singh A, Sandhu N, Bhandari A, Vikram P, Kumar A (2017a) Combining drought and submergence tolerance in rice: marker-assisted breeding and QTL combination effects. Molec Breed 37(12):143

Dixit S, Singh UM, Singh AK, Alam S, Venkateshwarlu C, Nachimuthu VV, Yadav S et al (2020) Marker assisted forward breeding to combine multiple biotic-abiotic stress resistance/tolerance in rice. Rice 13(1):29

Dixit S, Yadaw RB, Mishra KK, Kumar A (2017b) Marker-assisted breeding to develop the drought-tolerant version of Sabitri, a popular variety from Nepal. Euphytica 213:184

Dolferus R, Thavamanikumar S, Sangma H, Kleven S, Wallace X, Forrest K, Rebetzke G, Hayden M, Borg L, Smith A et al (2019) Determining the genetic architecture of reproductive stage drought tolerance in wheat using a correlated trait and correlated marker effect model. Genes Genomes Genet 9:473–489

Donde R, Mukherjee M, Barik M, SKY B, Padhi B, Mahadani P, Behera L, Swain P, Sahu K, Singh N, Czechowski T, Graham I, SR MC, Singh ON, Dash SK (2017) Marker-assisted introgression of drought tolerance from wild ancestors into popular Indian rice varieties using a 7K infinium SNP array. Can J Biotech 1:205

Dong H, Bai L, Chang J, Song C-P (2018a) Chloroplast protein PLGG1 is involved in abscisic acid-regulated lateral root development and stomatal movement in *Arabidopsis*. Biochem Biophys Res Commun 495:280–285

Dong H, Wang R, Yuan Y, Anderson J, Pumphrey M, Zhang Z, Chen J (2018b) Evaluation of the potential for genomic selection to improve spring wheat resistance to Fusarium head blight in the Pacific Northwest. Front Plant Sci 9:911

Dormatey R, Sun C, Ali K, Coulter JA, Bi Z, Bai J (2020) Gene pyramiding for sustainable crop improvement against biotic and abiotic stresses. Agronomy 10:1255

Espeland EK, Kettenring KM (2018) Strategic plant choices can alleviate climate change impacts: a review. J Environ Manage 222:316–324

Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A et al (2017) Crop production under drought and heat stress: plant responses and management options. Front Plant Sci 29:8

Fan Q, Song A, Jiang J, Zhang T, Sun H, Wang Y, Chen S, Chen F (2016) CmWRKY1 enhances the dehydration tolerance of chrysanthemum through the regulation of ABA-associated genes. PLoS One 11:e0150572

Fan Y, Shabala S, Ma Y, Xu R, Zhou M (2015) Using QTL mapping to investigate the relationships between abiotic stress tolerance (drought and salinity) and agronomic and physiological traits. BMC Genomics 16(1):43

Fang Y, You J, Xie K, Xie W, Xiong L (2008) Systematic sequence analysis and identification of tissue-specificor stress-responsive genes of NAC transcription factor family in rice. Mol Genet Genomics 280:547–563

Fghire R, Anaya F, Ali OI, Benlhabib O, Ragab R, Wahbi S (2015) Physiological and photosynthetic response of quinoa to drought stress. Chilean J Agric Res 75(2):174–183

Flint-Garcia SA (2013) Genetics and consequences of crop domestication. J Agric Food Chem 61:8267–8276

Flowers TJ (2004) Improving crop salt tolerance. J Exp Bot 55(396):307–319

Frey FP, Presterl T, Lecoq P, Orlik A, Stich B (2016) First steps to understand heat tolerance of temperate maize at adult stage: identification of QTL across multiple environments with connected segregating populations. Theor Appl Genet 129:945–961

Gill MB, Zeng F, Shabala L, Zhang G, Yu M, Demidchik V, Shabala S, Zhou M (2019) Identification of QTL related to ROS formation under hypoxia and their association with waterlogging and salt tolerance in barley. Int J Mol Sci 20(3):699

Gilmour SJ, Zarka DG, Stockinger EJ, Salazar MP, Houghton JM, Thomashow MF (1998) Low temperature regulation of the *Arabidopsis* CBF family of AP2 transcriptional activators as an early step in cold-induced COR gene expression. Plant J 16:433–442

Girma G, Nida H, Seyoum A, Mekonen M, Nega A, Lule D, Dessalegn K, Bekele A, Gebreyohannes A, Adeyanju A, Tirfessa A, Ayana G, Taddese T, Mekbib F, Belete K, Tesso T, Ejeta G, Mengiste T (2019) A large-scale genome-wide association analyses of Ethiopian Sorghum Landrace collection reveal loci associated with important traits. Front Plant Sci 10:691

Gupta S, Schillaci M, Walker R (2020) Alleviation of salinity stress in plants by endophytic plant-fungal symbiosis: current knowledge, perspectives and future directions. Plant and Soil. https://doi.org/10.1007/s11104-020-04618-w

Haley SD, Johnson JJ, Peairs FB, Quick JS, Stromberger JA, Clayshulte SR, Butler JD, Rudolph JB, Seabourn BW, Bai G (2007) Registration of ‘Ripper’ wheat. J Plant Regist 1:1–6

Hao D, Ohme-Takagi M, Sarai A (1998) Unique mode of GCC box recognition by the DNA-binding domain of ethylene-responsive element-binding factor (ERF domain) in plant. J Biol Chem 273:26857–26861

Haque E, Taniguchi H, Hassan MM, Bhowmik P, Karim MR, Smiech M, Zhao K, Rahman M, Islam T (2018) Application of CRISPR/Cas9 genome editing technology for the improvement of crops cultivated in tropical climates: recent progress, prospects, and challenges. Front Plant Sci 9:617

Hasanuzzaman M, Bhuyan MB, Zulfiqar F, Raza A, Mohsin SM, Mahmud JA, Fujita M, Fotopoulos V (2020) Reactive oxygen species and antioxidant defense in plants under abiotic stress: revisiting the crucial role of a universal defense regulator. Antioxidants 9:681

Hatfield JL, Prueger JH (2015) Temperature extremes: Effect on plant growth and development. Weather Clim Extrem 10:4–10

He G-H, Xu J-Y, Wang Y-X, Liu J-M, Li P-S, Chen M, Ma Y-Z, Xu Z-S (2016) Drought-responsive WRKY transcription factor genes TaWRKY1 and TaWRKY33 from wheat confer drought and/or heat resistance in *Arabidopsis*. BMC Plant Biol 16:116

He Y, Yang B, He Y, Zhan C, Cheng Y, Zhang J, Zhang H, Cheng J, Wang Z (2019) A quantitative trait locus, qSE3, promotes seed germination and seedling establishment under salinity stress in rice. Plant Sci 97(6):1089–1104

Hellin J, Mauricio B, Sarah H (2014) Maize landraces and adaptation to climate change in Mexico. J Crop Improve 28:484–501. https://doi.org/10.1080/15427528.20

Hirayama T, Shinozaki K (2010) Research on plant abiotic stress responses in the post-genome era: Past, present and future. Plant J 61(6):1041–1052

Ho VT, Thomson MJ, Ismail AM (2016) Development of salt tolerant IR64 near isogenic lines through marker-assisted breeding. J Crop Sci Biotech 19(5):373–381

Hoque ABMZ, Haque MA, Sarker MRA, Rahman MA (2015) Marker-assisted introgression of *Saltol locus* into genetic background of BRRI Dhan-49. Int J Biosci 6:71–80

Hsieh T-H, Lee J-T, Yang P-T, Chiu L-H, Charng Y-Y, Wang Y-C, Chan M-T (2002) Heterology expression of the *Arabidopsis* C-repeat/dehydration response element binding factor 1 gene confers elevated tolerance to chilling and oxidative stresses in transgenic tomato. Plant Physiol 129:1086–1094

Hu H, Dai M, Yao J, Xiao B, Li X, Zhang Q, Xiong L (2006) Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. Proc Natl Acad Sci USA 103:12987–12992

Hussain B, Lucas SJ, Budak H (2018) CRISPR/Cas9 in plants: at play in the genome and at work for crop improvement. Brief Funct Genomics 17:319–328

Inghelandt DV, Frey FP, Ries D, Stich B (2019) QTL mapping and genome-wide prediction of heat tolerance in multiple connected populations of temperate maize. Sci Rep 9(1):14418

Ito Y, Katsura K, Maruyama K, Taji T, Kobayashi M, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2006) Functional analysis of rice DREB1/CBF-type transcription factors involved in cold-responsive gene expression in transgenic rice. Plant Cell Physiol 47:141–153

Jaglo KR, Kleff S, Amundsen KL, Zhang X, Haake V, Zhang JZ, Deits T, Thomashow MF (2001) Components of the *Arabidopsis* C-repeat/dehydration-responsive element binding factor cold-response pathway are conserved in *Brassica napus* and other plant species. Plant Physiol 127: 910–917

Jaglo-Ottosen KR, Gilmour SJ, Zarka DG, Schabenberger O, Thomashow MF (1998) *Arabidopsis* CBF1overexpression induces COR genes and enhances freezing tolerance. Science 280:104–106

Jan SA, Bibi N, Shinwari ZK, Rabbani MA, Ullah S, Qadir A, Khan N (2017) Impact of salt, drought, heat and frost stresses on morpho-biochemical and physiological properties of *Brassica* species: an updated review. J Rural Dev Agric 2:1–10

Jarquín D, Crossa J, Lacaze X, Du Cheyron P, Daucourt J, Lorgeou J, Piraux F, Guerreiro L, Pérez P, Calus M (2014) A reaction norm model for genomic selection using high-dimensional genomic and environmental data. Theor Appl Genet 127:595–607

Javed T, Shabbir R, Ali A, Afzal I, Zaheer U, Gao S-J (2020) Transcription factors in plant stress responses: challenges and potential for sugarcane improvement. Plan Theory 9:491

Jha S (2019) Transgenic approaches for enhancement of salinity stress tolerance in plants. In: Molecular approaches in plant biology and environmental challenges. Springer, Singapore, pp 265–322. https://doi.org/10.1007/978-981-15-0690-1_14

Jiang Y, Deyholos MK (2006) Comprehensive transcriptional profiling of NaCl-stressed *Arabidopsis* roots reveals novel classes of responsive genes. BMC Plant Biol 6:25

John D, Shylaraj KS (2017) Introgression of Sub1 QTL into an elite rice (*Oryza sativa* L.) variety Jyothi through marker assisted backcross breeding. J Trop Agric *55*(1):1–11

Jung C, Seo JS, Han SW, Koo YJ, Kim CH, Song SI, Nahm BH, Do Choi Y, Cheong J-J (2008) Overexpression of AtMYB44 enhances stomatal closure to confer abiotic stress tolerance in transgenic *Arabidopsis*. Plant Physiol 146:623–635

Kamburova VS, Nikitina EV, Shermatov SE, Buriev ZT, Kumpatla SP, Emani C, Abdurakhmonov IY (2017) Genome editing in plants: an overview of tools and applications. Int J Agron 2017:1–15

Kasuga M, Miura S, Shinozaki K, Yamaguchi-Shinozaki K (2004) A combination of the *Arabidopsis* DREB1Agene and stress-inducible rd29A promoter improved drought-and low-temperature stress tolerance in tobacco by gene transfer. Plant Cell Physiol 45:346–350

Keurentjes JJ, Koornneef M, Vreugdenhil D (2008) Quantitative genetics in the age of omics. Curr Opin Plant Biol 11:123–128

Khan A, Ali M, Siddiqui SU, Jatoi SA, Jan SA, Khan N, Ghafoor A (2017) Effect of various temperatures and duration on deterioration of rice seeds. Science 36:79–83

Khurshid H, Jan SA, Shinwari ZK, Jamal M, Shah SH (2017) An era of CRISPR/Cas9 mediated plant genome editing. Curr Issues Mol Biol 26:47–54

Kilasi NL, Singh J, Vallejos CE, Ye C, Jagadish S, Kusolwa P, Rathinasabapathi B (2018) Heat stress tolerance in rice (*Oryza sativa* L.): identification of quantitative trait loci and candidate genes for seedling growth under heat stress. Front Plant Sci 9:1578

Kim SL, Kim N, Lee H et al (2020) High-throughput phenotyping platform for analyzing drought tolerance in rice. Planta 252:38. https://doi.org/10.1007/s00425-020-03436-9

Kim TH, Hur YJ, Han SI, Cho JH, Kim KM, Lee JH, Song YC, Kwon YU, Shin D (2017) Drought-tolerant QTL qVDT11 leads to stable tiller formation under drought stress conditions in rice. Plant Sci 256:131–138

Klap C, Bolger AM, Arazi T, Gupta SK, Shabtai S, Usadel B, Salts Y, Barg R (2017) Tomato facultative parthenocarpy results from SlAGAMOUS-LIKE 6 loss of function. Plant Biotechnol J 15:634

Klay I, Gouia S, Liu M, Mila I, Khoudi H, Bernadac A, Bouzayen M, Pirrello J (2018) Ethylene Response Factors (ERF) are differentially regulated by different abiotic stress types in tomato plants. Plant Sci 274:137–145

Kochevenko A, Jiang Y, Seiler C, Surdonja K, Kollers S, Reif JC, Korzun V, Graner A (2018) Identification of QTL hot spots for malting quality in two elite breeding lines with distinct tolerance to abiotic stress. BMC Plant Biol 18:106

Kole C, Muthamilarasan M, Henry R, Edwards D, Sharma R, Abberton M, Batley J, Bentley A, Blakeney M, Bryant J (2015) Application of genomics-assisted breeding for generation of climate resilient crops: progress and prospects. Front Plant Sci 6:563

Kulkarni M (2020) Benefits of genetic engineering for human welfare. J Genet Molecr Biol 4:5

Kumar S, Muthusamy SK, Mishra CN, Gupta V, Venkatesh K (2018) Importance of genomic selection in crop improvement and future prospects. In: Advanced molecular plant breeding: meeting the challenge of food security. CRC Press, Boca Raton, p 275

Kumar V, Singh A, Mithra SA, Krishnamurthy S, Parida SK, Jain S, Tiwari KK, Kumar P, Rao AR, Sharma S (2015) Genome-wide association mapping of salinity tolerance in rice (*Oryza sativa*). DNA Res 22:133–145

Kurepin LV, Ivanov AG, Zaman M, Pharis RP, Hurry V, Hüner NP (2017) Interaction of glycine betaine and plant hormones: protection of the photosynthetic apparatus during abiotic stress. In: Photosynthesis: structures, mechanisms, and applications. Springer, Berlin/Heidelberg, pp 185–202

Kuromori T, Seo M, Shinozaki K (2018) ABA transport and plant water stress responses. Trends Plant Sci 23:513–522

Lafarge T, Bueno C, Frouin J, Jacquin L, Courtois B, Ahmadi N (2017) Genome-wide association analysis for heat tolerance at flowering detected a large set of genes involved in adaptation to thermal and other stresses. PLoS One 12:e0171254

Lang NT, Ha PTT, Tru PC, Toan TB, Buu BC, Cho Y (2015) Breeding for heat tolerance rice based on marker-assisted backcrosing in Vietnam. Plant Breed Biotech 3(3):274–281

Larochelle S (2018) Genomics: CRISPR–Cas goes RNA. Nat Methods 15:312

Lata C, Prasad M (2011) Role of DREBs in regulation of abiotic stress responses in plants. J Exp Bot 62:4731–4748

Latha GM, Raman KV, Lima JM et al (2018) Genetic engineering of indica rice with AtDREB1A gene for enhanced abiotic stress tolerance. Plant Cell Tiss Org Cult 136:173–188. https://doi.org/10.1007/s11240-018-1505-7

Li C, Ng CK-Y, Fan L-M (2015) MYB transcription factors, active players in abiotic stress signaling. Environ Exp Bot 114:80–91

Li H, Gao Y, Xu H, Dai Y, Deng D, Chen J (2013) ZmWRKY33, a WRKY maize transcription factor conferring enhanced salt stress tolerances in *Arabidopsis*. Plant Growth Regul 70:207–216

Li X, Zheng H, Wu W, Liu H, Wang J, Jia Y, Li J, Yang L, Lei L, Zou D, Zhao H (2020) QTL mapping and candidate gene analysis for alkali tolerance in Japonica rice at the bud stage based on linkage mapping and genome-wide association study. Rice 13(1):48

Liang H, Lu Y, Liu H, Wang F, Xin Z, Zhang Z (2008) A novel activator-type ERF of *Thinopyrum intermedium*, TiERF1, positively regulates defence responses. J Exp Bot 59:3111–3120

Liang Y, Meng L, Lin X, Cui Y, Pang Y, Xu J, Li Z (2018) QTL and QTL networks for cold tolerance at the reproductive stage detected using selective introgression in rice. PLoS One 13(9):e0200846

Liang Y-K, Dubos C, Dodd IC, Holroyd GH, Hetherington AM, Campbell MM (2005) AtMYB61, an R2R3-MYB transcription factor controlling stomatal aperture in *Arabidopsis thaliana*. Curr Biol 15:1201–1206

Liao Y, Zou H-F, Wang H-W, Zhang W-K, Ma B, Zhang J-S, Chen S-Y (2008) Soybean GmMYB76, GmMYB92, and GmMYB177 genes confer stress tolerance in transgenic *Arabidopsis* plants. Cell Res 18:1047

Licausi F, Giorgi FM, Zenoni S, Osti F, Pezzotti M, Perata P (2010) Genomic and transcriptomic analysis of the AP2/ERF superfamily in *Vitis vinifera*. BMC Genomics 11:719

Lino CA, Harper JC, Carney JP, Timlin JA (2018) Delivering CRISPR: a review of the challenges and approaches. Drug Deliv 25:1234–1257

Liu C, Chen K, Zhao X, Wang X, Shen C, Zhu Y, Dai M, Qiu X, Yang R, Xing D, Pang Y, Xu J (2019) Identification of genes for salt tolerance and yield-related traits in rice plants grown hydroponically and under saline field conditions by genome-wide association study. Rice 12(1): 88

Liu J-X, Howell SH (2010) Endoplasmic reticulum protein quality control and its relationship to environmental stress responses in plants. Plant Cell 22:2930–2942

Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, Yamaguchi-Shinozaki K, Shinozaki K (1998) Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought- and low-temperature-responsive gene expression, respectively, in *Arabidopsis*. Plant Cell 10:1391–1406

Liu W, Yuan JS, Stewart CN Jr (2013) Advanced genetic tools for plant biotechnology. Nat Rev Genet 14:781

Liu X, Yuan Y, Martinez C, Babu R, Suarez EA, Zhang X, Trachsel S (2020) Identification of QTL for early vigor and leaf senescence across two tropical maize doubled haploid populations under nitrogen deficient conditions. Euphytica 216:3

Lopes MS, El-Basyoni I, Baenziger PS, Singh S, Royo C, Ozbek K, Aktas H, Ozer E, Ozdemir F, Manickavelu A (2015) Exploiting genetic diversity from landraces in wheat breeding for adaptation to climate change. J Exp Bot 66:3477–3486

Lopez-Cruz M, Crossa J, Bonnett D, Dreisigacker S, Poland J, Jannink J-L, Singh RP, Autrique E, de los Campos G (2015) Increased prediction accuracy in wheat breeding trials using a marker × environment interaction genomic selection model. G3: Genes Genom Genet 5:569–582

Lu M, Zhang D-F, Shi Y-S, Song Y-C, Wang T-Y, Li Y (2013) Expression of SbSNAC1, a NAC transcription factor from sorghum, confers drought tolerance to transgenic *Arabidopsis*. Plant Cell Tiss Org Cult 115:443–455

Lucas S, Durmaz E, Akpınar BA, Budak H (2011) The drought response displayed by a DRE-binding protein from *Triticum dicoccoides*. Plant Physiol Biochem 49:346–351

Luo M, Zhao Y, Zhang R, Xing J, Duan M, Li J, Wang N, Wang W, Zhang S, Chen Z, Zhang H, Shi Z, Song W, Zhao J (2017) Mapping of a major QTL for salt tolerance of mature field-grown maize plants based on SNP markers. BMC Plant Biol 17(1):140

Luo X, Wang B, Gao S, Zhang F, Terzaghi W, Dai M (2019) Genome-wide association study dissects the genetic bases of salt tolerance in maize seedlings. J Integr Plant Biol 61(6):658–674

Ma Q, Xia Z, Cai Z, Li L, Cheng Y, Liu J, Nian H (2019) GmWRKY16 enhances drought and salt tolerance through an ABA-mediated pathway in *Arabidopsis thaliana*. Front Plant Sci 9:9

Ma Y, Shabala S, Li C, Liu C, Zhang W, Zhou M (2015) Quantitative trait loci for salinity tolerance identified under drained and waterlogged conditions and their association with flowering time in barley (*Hordeum vulgare*. L). PLoS One 10(8):e0134822

Mahmood T, Khalid S, Abdullah M, Ahmed Z, Kausar M, Shah N, Ghafoor A, Du X, Shah MKN, Ghafoor A (2020) Insights into drought stress signaling in plants and the molecular genetic basis of cotton drought tolerance. Cell 9:105–135

Maleki A, Naderi A, Naseri R, Fathi A, Bahamin S, Maleki R (2013) Physiological performance of soybean cultivars under drought stress. Bull Environ Pharmacol Life Sci 2:38–44

Mallikarjuna G, Mallikarjuna K, Reddy M, Kaul T (2011) Expression of OsDREB2A transcription factor confers enhanced dehydration and salt stress tolerance in rice (*Oryza sativa* L.). Biotechnol Lett 33:1689–1697

Manolio TA (2010) Genome wide association studies and assessment of the risk of disease. N Engl J Med 363:166–176

Martinez V, Nieves-Cordones M, Lopez-Delacalle M, Rodenas R, Mestre TC, Garcia-Sanchez F, Rubio F, Nortes PA, Mittler R, Rivero RM (2018) Tolerance to stress combination in tomato plants: new insights in the protective role of melatonin. Molecules 23:535

Masouleh SSS, Aldine NJ, Sassine YN (2019) The role of organic solutes in the osmotic adjustment of chilling-stressed plants (vegetable, ornamental and crop plants). Ornam Hortic 25:434–442

Mehta S, James D, Reddy MK (2019) Omics technologies for abiotic stress tolerance in plants: current status and prospects. In: Recent approaches in omics for plant resilience to climate change. Springer, Cham, pp 1–34

Mehta S, Lal SK, Sahu KP, Venkatapuram AK, Kumar M, Sheri V, Varakumar P, Vishwakarma C, Yadav R, Jameel MR, Ali M, Achary VMM, Reddy MK (2020) CRISPR/Cas9-edited rice: a new frontier for sustainable agriculture. In: New frontiers in stress management for durable agriculture. Springer, Singapore, pp 427–458

Menezes-Silva PE, Sanglard LM, Ávila RT, Morais LE, Martins SC, Nobres P, Patreze CM, Ferreira MA, Araújo WL, Fernie AR (2017) Photosynthetic and metabolic acclimation to repeated drought events play key roles in drought tolerance in coffee. J Exp Bot 68:4309–4322

Merchuk-Ovnat L, Barak V, Fahima T, Ordon F, Lidzbarsky GA, Krugman T, Saranga Y (2016) Ancestral QTL alleles from wild emmer wheat improve drought resistance and productivity in modern wheat cultivars. Front Plant Sci 7:452

Mizoi J, Shinozaki K, Yamaguchi-Shinozaki K (2012) AP2/ERF family transcription factors in plant abiotic stress responses. Biochim Biophys Acta Gene Regul Mech 1819:86–96

Morales F, Ancín M, Fakhet D, González-Torralba J, Gámez AL, Seminario A, Soba D, Ben Mariem S, Garriga M, Aranjuelo I (2020) Photosynthetic metabolism under stressful growth conditions as a bases for crop breeding and yield improvement. Plan Theory 9:88

Mousavi-Derazmahalleh M, Bayer PE, Hane JK, Babu V, Nguyen HT, Nelson MN, Erskine W, Varshney RK, Papa R, Edwards D (2018) Adapting legume crops to climate change using genomic approaches. Plant Cell Environ 42:6–19

Murugaiyan V, Ali J, Mahender A, Aslam UM, Jewel ZA, Pang Y, Marfori-Nazarea CM, Wu LB, Frei M, Li Z (2019) Mapping of genomic regions associated with arsenic toxicity stress in a backcross breeding populations of rice (*Oryza sativa* L.). Rice 12(1):61

Mwadzingeni L, Shimelis H, Rees DJ, Tsilo TJ (2017) Genome-wide association analysis of agronomic traits in wheat under drought-stressed and non-stressed conditions. PLoS One 12(2):e0171692

Mwando E, Han Y, Angessa TT, Zhou G, Hill CB, Zhang XQ, Li C (2020) Genome-wide association study of salinity tolerance during germination in barley (*Hordeum vulgare* L.). Front Plant Sci 11:118

Nadeem M, Li J, Yahya M, Sher A, Ma C, Wang X, Qiu L (2019) Research progress and perspective on drought stress in legumes: a review. Int J Mol Sci 20:2541

Nasim S, Shabbir G, Ilyas M, Cheema NM, Shah MKN (2017) Contemplation of wheat genotypes for enhanced antioxidant enzyme activity. Pak J Bot 49:647–653

Nejat N, Mantri N (2017) Plant immune system: Crosstalk between responses to biotic and abiotic stresses the missing link in understanding plant defence. Curr Issues Mol Biol 23:1–16

Niu X, Luo T, Zhao H, Su Y, Li H (2020) Identification of wheat DREB genes and functional characterization of TaDREB3 in response to abiotic stresses. Gene 740:144514

Nuruzzaman M, Manimekalai R, Sharoni AM, Satoh K, Kondoh H, Ooka H, Kikuchi S (2010) Genome-wide analysis of NAC transcription factor family in rice. Gene 465:30–44

Nuruzzaman M, Sharoni AM, Kikuchi S (2013) Roles of NAC transcription factors in the regulation of biotic and abiotic stress responses in plants. Front Microbiol 4:248

O'Connor K, Hayes B, Hardner C et al (2020) Genome-wide association studies for yield component traits in a macadamia breeding population. BMC Genomics 21:199. https://doi.org/10.1186/s12864-020-6575-3

Onyemaobi I, Ayalew H, Liu H, Siddique K, Yan G (2018) Identification and validation of a major chromosome region for high grain number per spike under meiotic stage water stress in wheat (*Triticum aestivum* L.). PLoS One 13(3):e0194075

Pang Y, Chen K, Wang X, Wang W, Xu J, Ali J, Li Z (2017) Simultaneous improvement and genetic dissection of salt tolerance of rice (*Oryza sativa* L.) by designed QTL pyramiding. Front Plant Sci 8:1275

Pearce R (2001) Plant freezing and damage. Ann Bot 87(4):417–424

Pereira A (2016) Plant abiotic stress challenges from the changing environment. Front Plant Sci 7: 1123

Pradhan GP, Prasad PV, Fritz AK, Kirkham MB, Gill BS (2012) Effects of drought and high temperature stress on synthetic hexaploid wheat. Funct Plant Biol 39:190–198

Prince SJ, Beena R, Gomez SM, Senthivel S, Babu RC (2015) Mapping consistent rice (*Oryza sativa* L.) yield QTLs under drought stress in target rainfed environments. Rice 8(1):53

Qaseem MF, Qureshi R, Shaheen H, Shafqat N (2019) Genome-wide association analyses for yield and yield-related traits in bread wheat (*Triticum aestivum* L.) under pre-anthesis combined heat and drought stress in field conditions. PLoS One 14(3):e0213407

Qin F, Kakimoto M, Sakuma Y, Maruyama K, Osakabe Y, Tran LSP, Shinozaki K, Yamaguchi-Shinozaki K (2007) Regulation and functional analysis of ZmDREB2A in response to drought and heat stresses in *Zea mays* L. Plant J 50:54–69

Qin P, Lin Y, Hu Y, Liu K, Mao S, Li Z, Wang J, Liu Y, Wei Y, Zheng Y (2016) Genome-wide association study of drought-related resistance traits in *Aegilops tauschii*. Genet Mol Biol 39: 398–407

Rai KK, Rai AC (2020) Recent transgenic approaches for stress tolerance in crop plants. In: Roychowdhury R, Choudhury S, Hasanuzzaman M, Srivastava S (eds) Sustainable agriculture in the era of climate change. Springer, Cham. https://doi.org/10.1007/978-3-030-45669-6_23

Raza A, Mehmood SS, Ashraf F, Khan RSA (2018a) Genetic diversity analysis of *Brassica* species using PCR-based SSR markers. Gesunde Pflanzen 2018:1–7

Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, Xu J (2019) Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. Plan Theory 8:34

Raza A, Shaukat H, Ali Q, Habib M (2018b) Assessment of RAPD markers to analyse the genetic diversity among sunflower (*Helianthus annuus* L.) genotypes. Turk J Agric Food Sci Technol 6: 107–111

Rehman Arif MA, Attaria F, Shokat S, Akram S, Waheed MQ, Arif A, Börner A (2020) Mapping of QTLs associated with yield and yield related traits in durum wheat (*Triticum durum* Desf.) under irrigated and drought conditions. Int J Mol Sci 21(7):2372

Reynolds M, Tattaris M, Cossani CM, Ellis M, Yamaguchi-Shinozaki K, Saint Pierre C (2015) Exploring genetic resources to increase adaptation of wheat to climate change. In: Advances in wheat genetics: from genome to field. Springer, Berlin/Heidelberg, pp 355–368

Richardson KJ, Lewis KH, Krishnamurthy PK, Kent C, Wiltshire AJ, Hanlon HM (2018) Food security outcomes under a changing climate: impacts of mitigation and adaptation on vulnerability to food insecurity. Clim Change 147:327–341. https://doi.org/10.1007/s10584-018-2137-y

Riechmann JL, Meyerowitz EM (1998) The AP2/EREBP family of plant transcription factors. Biol Chem 379:633–646

Ritonga F, Chen SU (2020) Physiological and molecular mechanism involved in cold stress tolerance in plants. Plan Theory 9:560. https://doi.org/10.3390/plants9050560

Rodenburg RJ (2018) The functional genomics laboratory: functional validation of genetic variants. J Inherit Metab Dis 41:297–307

Roy SJ, Tucker EJ, Tester M (2011) Genetic analysis of abiotic stress tolerance in crops. Curr Opin Plant Biol 14:232–239

Rutkoski JE, Crain J, Poland J, Sorrells ME (2017) Genomic selection for small grain improvement. In: Genomic selection for crop improvement. Springer, Berlin/Heidelberg, pp 99–130

Rymaszewski W, Vile D, Bediee A, Dauzat M, Luchaire N, Kamrowska D, Granier C, Hennig J (2017) Stress-related gene expression reflects morphophysiological responses to water deficit. Plant Physiol 174:1913–1930

Saini HS, Sedgley M, Aspinall D (1983) Effect of heat stress during floral development on pollen tube growth and ovary anatomy in wheat (*Triticum aestivum* L.). Australian J Plant Physiol 10: 137–144

Sakuma Y, Liu Q, Dubouzet JG, Abe H, Shinozaki K, Yamaguchi-Shinozaki K (2002) DNA-binding specificity of the ERF/AP2 domain of *Arabidopsis* DREBs, transcription factors involved in dehydration- and cold-inducible gene expression. Biochem Biophys Res Commun 290:998–1009

Salehi-Lisar SY, Bakhshayeshan-Agdam H (2016) Drought stress in plants: causes, consequences, and tolerance. In: Drought stress tolerance in plants. Springer, Berlin/Heidelberg, pp 1–16

Samejima H, Kikuta M, Katura K, Menge D, Gichuhi E, Wainaina C, John K, Inukai Y, Yamauchi A, Makihara D (2020) A method for evaluating cold tolerance in rice during reproductive growth stages under natural low-temperature conditions in tropical highlands in Kenya. Plant Prod Sci 5:1–11. https://doi.org/10.1080/1343943X.2020.1777877

Sánchez-León S, Gil-Humanes J, Ozuna CV, Giménez MJ, Sousa C, Voytas DF, Barro F (2018) Low-gluten, nontransgenic wheat engineered with CRISPR/Cas9. Plant Biotechnol J 16:902–910

Sandhu N, Dixit S, Swamy B, Raman A, Kumar S, Singh SP, Yadaw RB, Singh ON, Reddy JN, Anandan A, Yadav S, Venkataeshwarllu C, Henry A, Verulkar S, Mandal NP, Ram T, Badri J, Vikram P, Kumar A (2019a) Marker assisted breeding to develop multiple stress tolerant varieties for flood and drought prone areas. Rice 12(1):8

Sandhu N, Dixit S, Swamy BPM, Raman A, Kumar S, Singh SP, Yadaw RB, Singh ON, Reddy JN, Anandan A (2019b) Marker assisted breeding to develop multiple stress tolerant varieties for flood and drought prone areas. Rice 12:8

Sardhara K, Mehta K (2018) Effects of abiotic and biotic stress on the plant. Acad J Bot Sci 1:5–9

Sarkar T, Thankappan R, Mishra G, Nawade B (2019) Advances in the development and use of DREB for improved abiotic stress tolerance in transgenic crop plants. Physiol Mol Biol Plants 25:68. https://doi.org/10.1007/s12298-019-00711-2

Scheben A, Yuan Y, Edwards D (2016) Advances in genomics for adapting crops to climate change. Curr Plant Biol 6:2–10

Schmidt J, Tricker PJ, Eckermann P, Kalambettu P, Garcia M, Fleury D (2020) Novel alleles for combined drought and heat stress tolerance in wheat. Front Plant Sci 10:1800

Schmöckel S, Alshareef N, Rey E, Khoury H, Tester M (2019) Genome wide identification of NAC transcription factors and their role in abiotic stress tolerance in *Chenopodium quinoa*. https://doi.org/10.1101/693093

Seo PJ, Lee SB, Suh MC, Park M-J, Go YS, Park C-M (2011) The MYB96 transcription factor regulates cuticular wax biosynthesis under drought conditions in *Arabidopsis*. Plant Cell 23: 1138

Seo PJ, Xiang F, Qiao M, Park J-Y, Lee YN, Kim S-G, Lee Y-H, Park WJ, Park C-M (2009) The MYB96 transcription factor mediates abscisic acid signaling during drought stress response in *Arabidopsis*. Plant Physiol 151:275–289

Shah SH, Ali S, Hussain Z, Jan SA, Ali GM (2016) Genetic improvement of tomato (*Solanum lycopersicum*) with AtDREB1A dene for cold stress tolerance using optimized agrobacterium-mediated transformation system. Int J Agric Biol 18:471–782

Shamsudin N, Swamy B, Ratnam W, Sta Cruz MT, Sandhu N, Raman AK, Kumar A (2016b) Pyramiding of drought yield QTLs into a high quality Malaysian rice cultivar MRQ74 improves yield under reproductive stage drought. Rice 9(1):21

Shamsudin NA, Swamy BP, Ratnam W, Sta Cruz MT, Raman A, Kumar A (2016a) Marker assisted pyramiding of drought yield QTLs into a popular Malaysian rice cultivar, MR219. BMC Genet 17:30

Shanker AK, Shanker C (2016) Abiotic and biotic stress in plants—recent advances and future perspectives. IntechOpen, Rijeka

Shavrukov Y, Kurishbayev A, Jatayev S, Shvidchenko V, Zotova L, Koekemoer F et al (2017) Early flowering as a drought escape mechanism in plants: how can it aid wheat production? Front Plant Sci 17:8

Shen C, Que Z, Xia Y, Tang N, Li D, He R, Cao M (2017) Knock out of the annexin gene OsAnn3 via CRISPR/Cas9-mediated genome editing decreased cold tolerance in rice. J Plant Biol 60: 539–547

Sheoran IS, Saini HS (1996) Drought induced male sterility in rice: changes in carbohydrate levels and enzyme activities associated with the inhibition of starch accumulation in pollen. Sex Plant Reprod 9:161–169

Shi Y, Gao L, Wu Z, Zhang X, Wang M, Zhang C, Zhang F, Zhou Y, Li Z (2017) Genome-wide association study of salt tolerance at the seed germination stage in rice. BMC Plant Biol 17(1):92

Shimatani Z, Kashojiya S, Takayama M, Terada R, Arazoe T, Ishii H, Teramura H, Yamamoto T, Komatsu H, Miura K (2017) Targeted base editing in rice and tomato using a CRISPR-Cas9 cytidine deaminase fusion. Nat Biotechnol 35:441

Shiriga K, Sharma R, Kumar K, Yadav SK, Hossain F, Thirunavukkarasu N (2014) Genome-wide identification and expression pattern of drought-responsive members of the NAC family in maize. Meta Gene 2:407–417

Singh K, Kumar S, Subramani R, Singh M, Gupta K (2019) Plant genetic resources management and pre-breeding in genomics era. Indian J Genet Plant Breed 5:79. https://doi.org/10.31742/IJGPB.79S.1.1

Singh P, Basu S, Kumar G (2018a) Polyamines metabolism: a way ahead for abiotic stress tolerance in crop plants. In: Biochemical, physiological and molecular avenues for combating abiotic stress tolerance in plants. Elsevier, Amsterdam, pp 39–55

Singh R, Singh Y, Xalaxo S, Verulkar S, Yadav N, Singh S, Singh N, Prasad K, Kondayya et al (2016) From QTL to variety-harnessing the benefits of QTLs for drought, flood and salt tolerance in mega rice varieties of India through a multi-institutional network. Plant Sci 242: 278–287

Singh VK, Singh BD, Kumar A, Maurya S, Krishnan SG, Vinod KK, Singh MP, Ellur RK, Bhowmick PK, Singh AK (2018b) Marker-assisted introgression of *Saltol* QTL enhances seedling stage salt tolerance in the rice variety "Pusa Basmati 1". Int J Genomics 2018:8319879

Sorgini CA, Barrios-Perez I, Brown PJ, Ainsworth EA (2019) Examining genetic variation in maize inbreds and mapping oxidative stress response QTL in B73-Mo17 nearly isogenic lines. Front Sustain Food Syst 3:51

Soto-Cerda BJ, Inostroza-Blancheteau C, Mathias M, Penaloza E, Zuñiga J, Muñoz G, Rengel Z, Salvo-Garrido H (2015) Marker-assisted breeding for *TaALMT1*, a major gene conferring aluminium tolerance to wheat. Biol Plant 59(1):83–91

Stockinger EJ, Gilmour SJ, Thomashow MF (1997) *Arabidopsis thaliana* CBF1 encodes an AP2 domain-containing transcriptional activator that binds to the C-repeat/DRE, a cis-acting DNA regulatory element that stimulates transcription in response to low temperature and water deficit. Proc Natl Acad Sci USA 94:1035–1040

Sun H, Hu M, Li J, Chen L, Li M, Zhang S, Zhang X, Yang X (2018b) Comprehensive analysis of NAC transcription factors uncovers their roles during fiber development and stress response in cotton. BMC Plant Biol 18:150. https://doi.org/10.1186/s12870-018-1367-5

Sun J, Yang L, Wang J, Liu H, Zheng H, Xie D, Zhang M, Feng M, Jia Y, Zhao H, Zou D (2018a) Identification of a cold-tolerant locus in rice (*Oryza sativa* L.) using bulked segregant analysis with a next-generation sequencing strategy. Rice 11(1):24

Svoboda N, Strer M, Hufnagel J (2015) Rainfed winter wheat cultivation in the North German Plain will be water limited under climate change until 2070. Environ Sci Eur 27:29

Swamy B, Shamsudin N, Rahman S, Mauleon R, Ratnam W, Sta Cruz MT, Kumar A (2017) Association mapping of yield and yield-related traits under reproductive stage drought stress in rice (*Oryza sativa* L.). Rice 10(1):21

Tahmasebi S, Heidari B, Pakniyat H, McIntyre CL (2016) Mapping QTLs associated with agronomic and physiological traits under terminal drought and heat stress conditions in wheat (*Triticum aestivum* L.). Genome 60:26–45

Taranto F, Nicolia A, Pavan S, De Vita P, D'Agostino N (2018) Biotechnological and digital revolution for climate-smart plant breeding. Agronomy 8:277

Thoen MP, Davila Olivas NH, Kloth KJ, Coolen S, Huang PP, Aarts MG, Bac-Molenaar JA, Bakker J, Bouwmeester HJ, Broekgaarden C (2017) Genetic architecture of plant stress resistance: multi-trait genome-wide association mapping. New Phytol 213:1346–1362

Tkemaladze GS, Makhashvili K (2016) Climate changes and photosynthesis. Ann Agric Sci 14: 119–126

Tolosa LN, Zhang Z (2020) The role of major transcription factors in solanaceous food crops under different stress conditions: current and future perspectives. Plan Theory 9:56

Ullah A, Hussain A, Shaban M, Khan AH, Alariqi M, Gul S, Jun Z, Lin S, Li J, Jin S, Munis MF (2018) Osmotin: a plant defense tool against biotic and abiotic stresses. Plant Physiol Biochem 123:149–159

Usatov AV, Alabushev AV, Kostylev PI, Azarin KV, Makarenko MS, Usatova OA (2015) Introgression the *Saltol* QTL into the elite rice variety of Russia by marker-assisted selection. Am J Agric Biol Sci 10:165–169

Van Esse HP, Reuber TL, van der Does D (2020) Genetic modification to improve disease resistance in crops. New Phytol 225:70–86

Verma V, Ravindran P, Kumar PP (2016) Plant hormone-mediated regulation of stress responses. BMC Plant Biol 16:86

Verslues PE, Lasky JR, Juenger TE, Liu T-W, Kumar MN (2014) Genome-wide association mapping combined with reverse genetics identifies new effectors of low water potential-induced proline accumulation in *Arabidopsis*. Plant Physiol 164:144–159

Vincent D, Ergül A, Bohlman MC, Tattersall EA, Tillett RL, Wheatley MD, Woolsey R, Quilici DR, Joets J, Schlauch K (2007) Proteomic analysis reveals differences between *Vitis vinifera* L. cv. Chardonnay and cv. Cabernet Sauvignon and their responses to water deficit and salinity. J Exp Bot 58:1873–1892

Vivitha P, Raveendran M, Vijayalakshmi D (2017) Introgression of QTLs controlling spikelet fertility maintains membrane integrity and grain yield in improved white Ponni derived progenies exposed to heat stress. Ric Sci 24(1):32–40

Volkov V (2015) Salinity tolerance in plants. Quantitative approach to ion transport starting from halophytes and stepping to genetic and protein engineering for manipulating ion fluxes. Front Plant Sci 27:6

Wainaina CM, Makihara D, Nakamura M, Ikeda A, Suzuki T, Mizukami Y, Nonoyama T, Doi K, Kikuta M, Samejima H et al (2018) Identification and validation of QTLs for cold tolerance at the booting stage and other agronomic traits in a rice cross of a Japanese tolerant variety, Hananomai, and a NERICA parent, WAB56-104. Plant Prod Sci 21:132–143

Wan H, Chen L, Guo J, Li Q, Wen J, Yi B, Ma C, Tu J, Fu T, Shen J (2017) Genome-wide association study reveals the genetic architecture underlying salt tolerance-related traits in rapeseed (*Brassica napus* L.). Front Plant Sci 8:593

Wang C, Linderholm HW, Song Y, Wang F, Liu Y, Tian J, Xu J, Song Y, Ren G (2020b) Impacts of drought on maize and soybean production in Northeast China during the past five decades. Int J Environ Res Public Health 17:2459

Wang F, Chen S, Liang D, Qu G-Z, Chen S, Zhao X (2020a) Transcriptomic analyses of *Pinus koraiensis* under different cold stresses. BMC Genome 21:1–14

Wang L, Chen L, Li R, Zhao R, Yang M, Sheng J, Shen L (2017) Reduced drought tolerance by CRISPR/Cas9-mediated SlMAPK3 mutagenesis in tomato plants. J Agric Food Chem 65:8674–8682

Wang W, Pan Q, He F, Akhunova A, Chao S, Trick H, Akhunov E (2018) Transgenerational CRISPR-Cas9 activity facilitates multiplex gene editing in allopolyploid wheat. CRISPR J 1: 65–74

Wang X, Mace E, Tao Y et al (2020c) Large-scale genome-wide association study reveals that drought-induced lodging in grain sorghum is associated with plant height and traits linked to carbon remobilisation. Theor Appl Genet 133:3201–3215. https://doi.org/10.1007/s00122-020-03665-2

Wang Y, Ying J, Kuzma M, Chalifoux M, Sample A, McArthur C et al (2004) Molecular tailoring of farnesylation for plant drought tolerance and yield protection. Plant J 43:413–424

Wani SH, Choudhary JR, Choudhary M, Rana M, Gosal SS (2020) Recent advances in genomics assisted breeding for drought stress tolerance in major cereals. J Cereal Res 12(1):1–12

Wen J, Jiang F, Weng Y, Sun M, Shi X, Zhou Y, Yu L, Wu Z (2019) Identification of heat-tolerance QTLs and high-temperature stress-responsive genes through conventional QTL mapping, QTLseq and RNA-seq in tomato. BMC Plant Biol 19:398

Wu X, Cai K, Zhang G, Zeng F (2017) Metabolite profiling of barley grains subjected to water stress: to explain the genotypic difference in drought-induced impacts on malting quality. Front Plant Sci 8:1547

Wu X, Shiroto Y, Kishitani S, Ito Y, Toriyama K (2009) Enhanced heat and drought tolerance in transgenic rice seedlings overexpressing OsWRKY11 under the control of HSP101 promoter. Plant Cell Rep 28:21–30

Xie X, He Z, Chen N, Tang Z, Wang Q, Cai Y (2019) The roles of environmental factors in regulation of oxidative stress in plant. Biomed Res Int 11:9732325. https://doi.org/10.1155/2019/9732325

Xu Z, Zhou G (2006) Combined effects of water stress and high temperature on photosynthesis, nitrogen metabolism and lipid peroxidation of a perennial grass *Leymus chinensis*. Planta 224: 1080–1090. https://doi.org/10.1007/s00425-006-0281-5

Yadav AK, Kumar A, Grover N, Ellur RK, Krishnan SG, Bollinedi H, Bhowmick PK, Vinod KK, Nagarajan M, Krishnamurthy SL, Singh AK (2020) Marker aided introgression of ‘Saltol’, a major QTL for seedling stage salinity tolerance into an elite Basmati rice variety 'Pusa Basmati 1509'. Sci Rep 10(1):13877

Yadav S, Sandhu N, Singh VK, Catolos M, Kumar A (2019) Genotyping-by-sequencing based QTL mapping for rice grain yield under reproductive stage drought stress tolerance. Sci Rep 9(1):14326

Yan J, Wu Y, Li W, Qin X, Wang Y, Yue B (2017) Genetic mapping with testcrossing associations and F2:3 populations reveals the importance of heterosis in chilling tolerance at maize seedling stage. Sci Rep 7(1):3232

Yoon Y, Seo DH, Shin H, Kim HJ, Kim CM, Jang G (2020) The role of stress-responsive transcription factors in modulating abiotic stress tolerance in plants. Agronomy 10:788

Younis A, Ramzan F, Ramzan Y, Zulfiqar F, Ahsan M, Lim K (2020) Molecular markers improve abiotic stress tolerance in crops: a review. Plan Theory 9:1347. https://doi.org/10.3390/plants9101374

Yuan C, Li C, Lu X, Zhao X, Yan C, Wang J, Sun Q, Shan S (2020) Comprehensive genomic characterization of NAC transcription factor family and their response to salt and drought stress in peanut. BMC Plant Biol 20:454. https://doi.org/10.1186/s12870-020-02678-9

Zandalinas SI, Mittler R, Balfagón D, Arbona V, Gómez-Cadenas A (2018) Plant adaptations to the combination of drought and ss. Physiol Plant 162:2–12

Zargar SM, Gupta N, Nazir M, Mahajan R, Malik FA, Sofi NR, Shikari AB, Salgotra R (2017) Impact of drought on photosynthesis: molecular perspective. Plant Gene 11:154–159

Zhang C, Pumphrey M, Zhou J, Zhang Q, Sankaran S (2020b) Development of an automated high-throughput phenotyping system for wheat evaluation in a controlled environment. Trans ASABE 62:61–74

Zhang G, Chen M, Li L, Xu Z, Chen X, Guo J, Ma Y (2009) Overexpression of the soybean GmERF3 gene, an AP2/ERF type transcription factor for increased tolerances to salt, drought, and diseases in transgenic tobacco. J Exp Bot 60:3781–3796

Zhang J, Chen K, Pang Y, Naveed SA, Zhao X, Wang X, Wang Y, Dingkuhn M, Pasuquin J, Li Z, Xu J (2017a) QTL mapping and candidate gene analysis of ferrous iron and zinc toxicity tolerance at seedling stage in rice by genome-wide association study. BMC Genomics 18(1):828

Zhang X, Fan Y, Shabala S, Koutoulis A, Shabala L, Johnson P, Hu H, Zhou M (2017c) A new major-effect QTL for waterlogging tolerance in wild barley (*H. spontaneum*). Theor Appl Genet 130(8):1559–1568

Zhang M, Ye J, Xu Q, Feng Y, Yuan X, Yu H, Wang Y, Wei X, Yang Y (2018) Genome-wide association study of cold tolerance of Chinese indica rice varieties at the bud burst stage. Plant Cell Rep 37(3):529–539

Zhang X, Wei H, Zhao Z, Liu J, Zhang Q, Zhang X, Gu W (2020a) The global potential distribution of invasive plants: *Anredera cordifolia* under climate change and human activity based on random forest models. Sustainability 12:1491

Zhang X, Zhou G, Shabala S, Koutoulis A, Shabala L, Johnson P, Li C, Zhou M (2016) Identification of aerenchyma formation-related QTL in barley that can be effective in breeding for waterlogging tolerance. Theor Appl Genet 129(6):1167–1177

Zhang Z, Liu X, Wang X, Zhou M, Zhou X, Ye X, Wei X (2012) An R2R3 MYB transcription factor in wheat, Ta PIMP 1, mediates host resistance to *Bipolaris sorokiniana* and drought stresses through regulation of defense -and stress-related genes. New Phytol 196:1155–1170

Zhao C, Liu B, Piao S, Wang X, Lobell DB, Huang Y, Huang M, Yao Y, Bassu S, Ciais P (2017) Temperature increase reduces global yields of major crops in four independent estimates. Proc Natl Acad Sci USA 114:9326–9331

Zhao X, Luo L, Cao Y, Liu Y, Li Y, Wu W, Lan Y, Jiang Y, Gao S, Zhang Z, Shen Y, Pan G, Lin H (2018) Genome-wide association analysis and QTL mapping reveal the genetic control of cadmium accumulation in maize leaf. BMC Genomics 19(1):91

Zheng X, Chen B, Lu G, Han B (2009) Overexpression of a NAC transcription factor enhances rice drought and salt tolerance. Biochem Biophys Res Commun 379:985–989

Zhou QY, Tian AG, Zou HF, Xie ZM, Lei G, Huang J, Wang CM, Wang HW, Zhang JS, Chen SY (2008) Soybean WRKY-type transcription factor genes, GmWRKY13, GmWRKY21, and GmWRKY54, confer differential tolerance to abiotic stresses in transgenic *Arabidopsis* plants. Plant Biotechnol J 6:486–503

Zhu C, Bortesi L, Baysal C, Twyman RM, Fischer R, Capell T, Schillberg S, Christou P (2017) Characteristics of genome editing mutations in cereal crops. Trends Plant Sci 22:38–52

Zhu J-K (2016) Abiotic stress signaling and responses in plants. Cell 167:313–324

Zhu X, Qi L, Liu X, Cai S, Xu H, Huang R, Li J, Wei X, Zhang Z (2014) The wheat ethylene response factor transcription factor pathogen-induced ERF1 mediates host responses to both the necrotrophic pathogen *Rhizoctonia cerealis* and freezing stresses. Plant Physiol 164:1499–1514

6

Changing Environment and Crop Plant Breeding

Ashutosh Kumar Mall, Varucha Misra, and A. D. Pathak

Abstract

Any crop exposed to stress environment is influenced by the weather aberrations. These aberrations generate abiotic stress conditions contributing to 60 to 80% changes in crop production and productivity. The problem of climate change is further augmenting these stresses causing much more reduction in crop yield. Variable and complex responses by the plant are generally seen under such conditions resulting in changes at physiological, biochemical, morphological, and molecular levels. The extent and impact of crop response under abiotic stress conditions are dependent on several factors. In general, avoidance, escape, and susceptibility are the three ways which crop under stress conditions adopts. These response mechanisms vary from plant to plant and genotype to genotype. Developing tolerant crop varieties having high productivity for stress conditions is the need of the prevailing climate-changing condition. The current breeding approaches are focusing on such physiological traits which impart tolerance to the plant. The recent advances in biotechnology have also advanced the breeder hand in developing tolerant varieties with a specific target trait for stress conditions which otherwise through conventional breeding efforts are more time taken. Crop response under stress environment and breeding approaches for enhancing crop productivity under abiotic conditions is briefly described in this chapter.

Keywords

Abiotic · Tolerance · Mechanism · Breeding · Biotechnology

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6.1 Introduction

Stress environment is a factor that is regulated externally whose response is the result of strain (Buddenhagen 1983). In the wide terminology definition, stress is a situation that originated due to the sudden environmental changes or blending of multi-stress situations. The abiotic stresses are known to produce from abnormal environmental stresses. These are the initial factors that restrain crop production and productivity (Padgham 2009; Grayson 2013). High and low temperatures, drought, salinity, alkaline, water logging, nutrient deficiency, and light intensity constitute abiotic stresses (Shrivastava et al. 2017; Misra et al. 2020a, b). This causes confinement in the growth and development of plants resulting in hampering of yield and production (Thompson 1975; Blum 1982a, b). Environmental stress is majorly affected by variations in climatic conditions. Due to alterations in weather conditions, 60–80% of the changes in crop growth environment were reported. The chief variables with respect to productivity are temperature and water availability to the plant (Thompson 1975; Blum 1982a, b). When the plant is grown under stress environment, at times their growth potential is altered. The metabolic processes involved in determining the growth and yield of plants are basically energy-dependent. The use and generation of ATP in the plant physiological activities under such a condition are performed by aerobic respiration (Jones and Qualset 1984). There are many reasons governing the nature and extent of the damage caused to the plant due to stress. These are quantity of stress and its time duration, physiological/ developmental age of the plant, type of genotype/variety used. These morphological traits are used by the breeder in the breeding programs while selecting the plant either for further improvement or for varietal release (Jones and Qualset 1984).

Plants exposed to stress environments show highly variable and complex responses involving changes in physiological and molecular (transcription stage) levels. The response behavior of the plant varies from exposure to solitary stress to multiple stresses. The variation is clearly seen in the stimulation of specific gene expressions (Raza et al. 2020). Activation of specific genes as a response to stress in plants is bestowed by natural capability. This is the reason behind the intricate research for multiple responses shown by the plant under stress environment with the presently available tools and techniques. There is a need for assessing the multiple stress in plants and their tolerance capability (Atkinson and Urwin 2012; Zhu 2016). In this stress perspective, breeding efforts either through conventional or modern technology play an important part. The genetic modification of plants to grow and produce an economic yield under the given environmental constraints remains the most viable solution to problems of environmental stress.

6.2 Crop Stress Resistance and Its Nature

Abiotic stress is defined as the alterations in physico-chemical traits caused due to the changes in the environment on the plant. When stress is severe, the plant shows prevention in flowering, stimulation in senescence, and other changes that result in plant death. These plants belong to the susceptible category while the ones having the lesser impact of the stress are termed as resistant. Stress resistance can be divided into three categories, i.e., avoidance, tolerance, and escape (Buddenhagen 1983). The escape strategy is adopted by plants like desert plants, ephemeral. In general, the ephemeral plants due to their short life cycle are known to have survival to abiotic stress conditions through stress avoidance mechanisms. In this method, the impact of stress on the plant is much reduced. In tolerance mechanism of plants, the plant is either resistant to one or multiple stresses by their ability to either adjust or acclimation. Adjustment/adaptation and acclimation are the two diverse methods of tolerance for particular stress. The stress adaptation in plants implies adaptation characteristics of the plant through their heritable traits. The acclimation implies the non-heritable traits which the plant develops gradually in its life cycle to survive/cope under abiotic stress condition (Khan et al. 2014). The stress response mechanism in plants is depicting in generalized manner in Fig. 6.1.

6.3 Response of Crop Plants to Environmental Stresses

Impact of stress environment on plant causes a series of changes in either their physiology or morphology. The severity depends on the stress condition, type, and duration (Mall et al. 2019). Leaf curling, wilting, senescence, chlorosis, adventitious root growth (Misra et al. 2020b) are some of the morphological changes under stress environments. Alteration in respiration, photosynthesis rate, thrashing of the integrity of cells, necrosis is some of the physiological changes under stress conditions. The morpho-physiological changes in the stress environment cause death of the susceptible plants. Hammond-Kosack (2000) reported that for specific stress, each plant responds differently by activating a particular response mechanism. This is so to avoid the injury that a plant may occur when exposed to stress environment. The plant response to the stress environment varies from reversible to irreversible manner. This response is known to be governed by factors like the duration of the stressor on the tissue/organ at which the stress affects. A good example is the transcriptional responses (tissue- or cell-specific) observed in plants under a stress environment which vary depending on the stress. Cramer et al. (2011) revealed that water deficit condition in the plant causes an impact on cell wall either enzymatically or non-enzymatically leading to restraining in plant growth. Raza et al. (2019a) found that water deficit and high temperatures are the two main abiotic stresses that are known to hamper the production and productivity of crops under field conditions.

6.4 Breeding for Crop Stress Resistance

Stress resistance breeding is a selective trait of such genotypes which easily overcomes the stress conditions. The morpho-physiological changes occurring during stress environments in plants help the breeder in understanding the insight of the stress impact on the plant. The adaptive mechanism by some plants towards stress

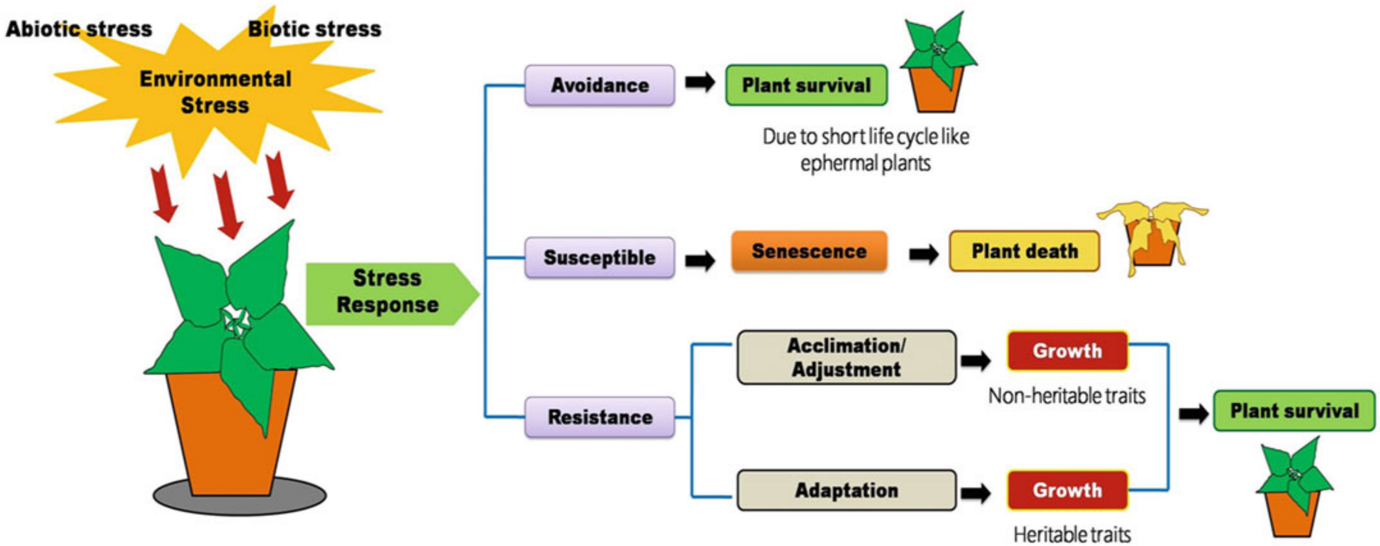

Fig. 6.1 Crop response mechanism in environmental stress conditions

environment may also bring forth by the breeders. The metabolic response of a plant in a stress environment can be analyzed either on the dysfunctions generated from the injuries caused by the stress or by the adaptive modifications that the plant undergoes (Jones and Qualset 1984). The breeding methodology for developing stress-tolerant genotype involves four steps. The first and foremost is the finding the particular features required in the plant for the particular environment. Evaluating those features in the plants is the second step. Heritable variation for the traits providing tolerance to the plant under stress environment is the next step. The last step involves the breeding plan for incorporation of these characters/traits into the desirable plant and in the required form (Jones and Qualset 1984).

6.4.1 Conventional Method of Breeding for Improving Plant Growth and Development

Breeding approaches in improving the plant performance, quality, diversity are based on the principle of genetics. It is a method where the crossing of the species having good characteristics is chosen as a parent and the progeny so developed will have better traits in comparison to the parent. Germplasm collection, screening, and identifying phenotypic characteristics of germplasm and its hybridization for improving the cultivars are the steps involved in conventional breeding method (Fehr 1987; Stoskopf et al. 1993). The plants showing best performance after breeding methods are known to be selected from the mixed plant population. After this the selected cultivars are stabilized for long time period. The cultivars are then tested for different environmental conditions for their performance and suitability (Bharadwaj 2016).

6.4.2 Identification of Target Traits for Abiotic Stress Tolerance Through Breeding

There are two means by which screening of target traits for abiotic stress tolerance may be performed, i.e., direct or indirect (Richards 1982). Direct selection involves two ways of selection, viz., selection for a particular trait like yield or sucrose content in plants under abiotic stress conditions and selection of such a profitable trait where the only minor reduction was observed in stress conditions. Advances in crop productivity improvement can be performed by selection of such traits which accelerates the end product. This is done either by a combination of unknown genes or genes dependent on a particular trait. The crossing of such traits should result in the production of superior phenotypes. The negative aspect of this method lies in the fact that genotypes so developed have a poor adaptation to the testing location. Indirect selection for target traits has been studied in many crops (Mussel and Staples 1979; Turner and Kramer 1980; Hanson and Hitz 1982; Graham and Patterson 1982). The traits seen in the indirect selection are proline, waxiness, glycine betaine, awns, survival, germination and growth, production of abscisic acid, etc. (Singh et al. 1973; Blum 1982a, b; Wyn Jones et al. 1977; Evans et al. 1972; Rush and Epstein 1981; Kingsbury and Epstein 1984; Quarrie 1980).

6.5 Advances in Crop Stress Tolerance Through Biotechnology

The development of defense mechanisms in plants to cope up with abiotic stresses is well known. In the prevailing time, the evaluation of the mechanism of plants under stress is gaining importance for the development of new genetically stress-tolerant varieties. Advances in biotechnological research such as fields of transcriptomics, genomics, and proteomics had paved a better option for developing stress-tolerant varieties in a much easier manner, besides knowing their defense mechanism (Liu et al. 2014). Raza et al. (2019b) had found the importance of molecular markers in genetically engineered crops where candidate genes were often associated with stress-related tolerant genes. The development of transgenic has been emerging out as a chief tool for crops adaptive to stress condition. The utilization of transgenic crops in fields has increased in the past some years. The initial step involved in this approach is the recognition of such genes which help as key regulators for various metabolic activities in plants exposed to stress condition (Ahmad et al. 2012). Tzfira et al. (2012) reported the importance and utilization of genome editing in providing the desired trait through selection or incorporation of genes tolerant to stress environment. A particular stress causes change in expression of a particular gene. This expression alteration further causes variation in perception of signal and its transduction. Consequently, alterations in transcriptional genes result in generation of a particular response that leads to improvement in stress tolerance of the crop. Microarray hybridization technique and suppression subtraction hybridization are some of the techniques used as a biotechnological tool for developing stress-tolerant genotypes (Ban and Moriguchi 2010). In water deficit stress condition, the difference in both sort of breeding approaches, i.e., conventional means and transgenic is significant for such stress environment. In transgenic several feasible advances have been developed. One such is genetic engineering of such genes responsible for crucial metabolic and defensive activities of plant (Wang et al. 2016). Identification of inducible genes through use of microarrays has been reported in many studies however their functioning as a reaction to stress and its tolerance is still not decoded (Hoth et al. 2002; Wang et al. 2016; Ahanger et al. 2017). Tuteja (2007) reported that under stress environment abscisic acid causes stomatal closure in crops. This result in genes responsive to stress condition to stimulate, however, their functioning is not yet known. CRISPR/Cas 9 is another biotechnological tool evolving as an effective technology for providing tolerance to plants under stress conditions. It involves gene modification, mutation, and gene analysis (Ahmad et al. 2021).

Understanding of the stress signaling pathways in plants exposed to such conditions is even becoming easier through advanced biotechnological techniques. This helps the breeder in developing genetically improved varieties for stress environment. The modern efforts in developing tolerant cultivars through genetics are also important for understanding the insight of genes controlling the tolerant

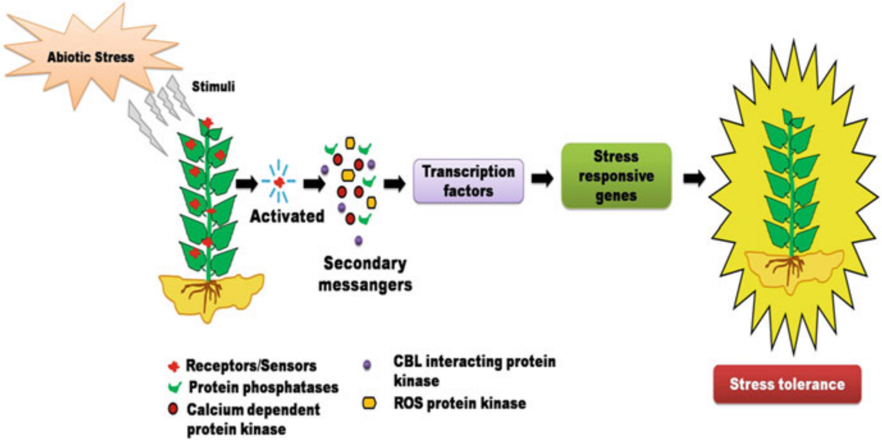

Fig. 6.2 Signaling pathway mechanism in plants exposed to stress environment. The extracellular stimuli are received by the plant through the presence of sensors and receptors present on the cell wall. The secondary messengers (inositol phosphate, sugar, reactive oxygen species (ROS), calcium ions (Ca^{2+}), cyclic nucleotides (cAMP and cGMP), and nitric oxide (NO)) are responsible for conversion of signals from extracellular to intracellular. Activation of these messengers transduce the signal

traits. Marker-assisted breeding, selection of genome and quantitative trait locus (QTL) mapping are some of these approaches that help the breeder in identifying and selecting high yielding genotypes/cultivars (Maphosa et al. 2020).

In general, signal perception, signal transduction, stress-responsive gene expression, concerning physiological processes, and metabolic reactions are the important part of the signaling pathway (Zhu 2016; Pérez-Clemente et al. 2013). For instance, several studies had reported the importance of signaling pathways involving mitogen-activated protein kinases (MAPKs) and calcium-dependent protein kinases (CDPKs) in plants under stress conditions (Simeunovic et al. 2016; Huang et al. 2012; Rayapuram et al. 2018). The signaling pathway in a generalized manner is depicted in Fig. 6.2.

6.6 Conclusion

Stress environment during plant growth and development strongly influences it. Abiotic stress is a threatening problem in plants that are economically important. The productivity and yield are greatly hampered by the sudden occurrence of such stress conditions. Developing tolerant stress varieties and cultivars is the need of the hour. Conventional breeding methods with advances in biotechnological tools help the breeders to identify such tolerant traits and their functioning in the plant under stress environment. These traits/genes were either incorporated or modified through the recent advanced techniques in the field of transcriptomics, proteomics, and genomics. The regulatory mechanism in plants under a stress environment for providing tolerance has always been a topic of interest for research for several decades. Testing of the validity of the theoretical results had led to novel approaches in understanding and elucidation of stress-induced modifications in plants. Screening, identification, and selection of particular genes responding to stress environment and its incorporation through breeding methods for the development of resistant genotypes/varieties are a long procedure involving high time consumption. Though developing stress-tolerant varieties is expensive through the use of biotechnological tools yet it is well-organized. The transgenic crops developed for the stress environment by this method are a good example.

References

Ahanger MA, Akram NA, Ashraf M, Alyemeni MN, Wijaya L, Ahmad P (2017) Plant responses to environmental stresses-from gene to biotechnology. AoB Plants 9:1–17

Ahmad M, Ali Q, Hafeez MM, Malik A (2021) Improvement for biotic and abiotic stress tolerance in crop plants. Biol Clin Sci Res J 2021:e004

Ahmad P, Ashraf M, Younis M, Hu X, Kumar A, Akram NA, Al-Qurainy F (2012) Role of transgenic plants in agriculture and biopharming. Biotechnol Adv 30:524–540

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

Ban Y, Moriguchi T (2010) Suppression subtractive hybridization as a tool to identify anthocyanin metabolism-related genes in apple skin. Methods Mol Biol 643:15–31

Bharadwaj DN (2016) Sustainable agriculture and plant breeding. In: Al-Khayri JM, Jain SM, Johnson DV (eds) Advances in plant breeding strategies: agronomic, abiotic and biotic stress traits. Springer, New York, pp 3–34

Blum A (1982a) Evidence for genetic variability in drought resistance and its implications in plant breeding. In: Drought resistance in crops with emphasis on rice. IRRI, Los Banos, pp 53–70

Blum JS (1982b) Plant productivity and environment. Science 218:433–448

Buddenhagen IW (1983) Breeding strategies for stress and disease resistance in developing countries. Annu Rev Phytopathol 21:385–409

Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K (2011) Effects of abiotic stress on plants: a systems biology perspective. BMC Plant Biol 11:163. https://doi.org/10.1186/1471-2229-11-163

Evans LT, Bingham J, Jackson P, Sutherland J (1972) Effect of awns and drought on the supply of photosynthate and its distribution within wheat ears. Ann Appl Biol 70:67–76

Fehr WR (1987) Principles of cultivar development. Vol. 1 theory and technique. In: Crop species. Macmillan, New York

Graham D, Patterson BD (1982) Responses of plants to low, nonfreezing temperatures: proteins, metabolism, and acclimation. Annu Rev Plant Physiol 33:347–372

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

Hammond-Kosack K (2000) Responses to plant pathogens. In: Biochemistry and molecular biology of plants. American Society of Plant Physiologists, Rockville, pp 1102–1109

Hanson AD, Hitz WD (1982) Metabolic responses of mesophytes to plant water deficits. Annu Rev Plant Physiol 33:163–203

Hoth S, Morgante M, Sanchez JM, Hanafey MK, Tingey SV, Chua NH (2002) Genome-wide gene expression profiling in *Arabidopsis thaliana* reveals new targets of abscisic acid and largely impaired gene regulation in the abi1-1 mutant. J Cell Sci 115:4891–4900

Huang G-T, Ma S-L, Bai L-P, Zhang L, Ma H, Jia P, Liu J, Zhong M, Guo Z-F (2012) Signal transduction during cold, salt, and drought stresses in plants. Mol Biol Rep 39:969–987

Jones RA, Qualset CO (1984) Breeding crops for environmental stress tolerance. In: Collins GB, Petolino JG (eds) Application of genetic engineering to crop improvement. Part of advances in agricultural biotechnology, vol 10. Springer, Berlin, pp 305–339

Khan PSSV, Nagamallaiah GV, Rao MD, Sergeant K, Hausman JF (2014) Abiotic stress tolerance in plants: insights from proteomics. In: Ahmad P (ed) Emerging technologies and management of crop stress tolerance, vol 2. Academic Press, Boston, pp 23–67

Kingsbury RW, Epstein E (1984) Selection for salt-resistant spring wheat. Crop Sci 24:310–315

Liu C, Mao B, Ou S, Wang W, Liu L, Wu Y, Chu C, Wang X (2014) OsbZIP71, a bZIP transcription factor, confers salinity and drought tolerance in rice. Plant Mol Biol 84:19–36

Mall AK, Varucha M, Ashwani K, Pathak AD (2019) Drought: status, losses and management in sugarcane crop. In: Bharti PK, Ray J (eds) Farm and development: technological perspectives. Discovery Publishing House, New Delhi, pp 165–187

Maphosa L, Richards MF, Norton SL, Ngyugen GN (2020) Breeding for abiotic stress adaptation in chickpea (*Cicer arietinum* L.): a comprehensive review. Crop Breed Genet Genom 2(4): e200015

Misra V, Solomon S, Hassan A, Allah EFE, Al-Arjani AF, Mall AK, Prajapati CP, Ansari MI (2020a) Minimization of post harvest sucrose losses in drought affected sugarcanes using chemical formulation. Saudi J Biol Sci 27(1):309–317

Misra V, Solomon S, Mall AK, Prajapati CP, Hassan A, Allah EFE, Ansari MI (2020b) Morphological assessment of water stressed sugarcane: a comparison of waterlogged and drought affected crop. Saudi J Biol Sci 27(5):1228–1236

Mussel H, Staples RS (1979) Stress physiology in crop plants. John Wiley and Sons, New York, p 501

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

Pérez-Clemente RM, Vives V, Zandalinas SI, López-Climent MF, Muñoz V, Gómez-Cadenas A (2013) Biotechnological approaches to study plant responses to stress. Biomed Res Int 2013: 654120

Quarrie SA (1980) Genotypic differences in leaf water potential, abscisic acid and proline concentration in spring wheat during drought stress. Ann Bot 46:383–394

Rayapuram N, Bigeard J, Alhoraibi H, Bonhomme L, Hesse AM, Vinh J, Hirt H, Pflieger D (2018) Quantitative phosphoproteomic analysis reveals shared and specific targets of *Arabidopsis* mitogen-activated protein kinases (MAPKs) MPK3, MPK4, and MPK6. Mol Cell Proteomics 17:61–80

Raza A, Mehmood SS, Shah T, Zou X, Yan L, Zhang X, Khan RS (2019b) Applications of molecular markers to develop resistance against abiotic stresses in wheat. In: Wheat production in changing environments. Springer, Singapore, pp 393–420

Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, Xu J (2019a) Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. Plan Theory 8:34

Raza A, Zhou X, Zhnag X (2020) Plant adaptation and tolerance to environmental stresses: mechanisms. In: Hasanuzzaman M (ed) Plant ecophysiology and adaptation under climate change: mechanism and perspectives. Springer, Singapore, pp 117–145

Richards RA (1982) Breeding and selecting for drought resistance in wheat. In: Drought resistance in crops with emphasis on rice. IRRI, Los Sanos, pp 303–316

Rush DW, Epstein E (1981) Comparative studies on the sodium, potassium, and chloride relations of a wild halophytic and a domestic salt-sensitive tomato species. Plant Physiol 68:1308–1313

Shrivastava AK, Pathak AD, Varucha M, Sangeeta S, Swapna M, Shukla SP (2017) Sugarcane crop: its tolerance towards abiotic stresses. In: Minas PS et al (eds) Abiotic stress management for resilient agriculture. Springer, Singapore, pp 375–397

Simeunovic A, Mair A, Wurzinger B, Teige M (2016) Know where your clients are: subcellular localization and targets of calcium-dependent protein kinases. J Exp Bot 67:3855–3872

Singh TN, Paleg LG, Aspinall D (1973) Stress metabolism. III Variations in response to water deficit in the barley plant. Aust J Biol Sci 26:65–76

Stoskopf NC, Tomes DT, Christie BR (1993) Plant breeding: theory and practice. Westview Press, Boulder

Thompson LM (1975) Weather variability, climatic change and grain production. Science 188:535–539

Turner NC, Kramer PJ (1980) Adaptation of plants to water and high temperature stress. Wiley, New York, p 482

Tuteja N (2007) Abscisic acid and abiotic stress signalling. Plant Signal Behav 2:135–138

Tzfira T, Weinthal D, Marton I, Zeevim V, Zuker A, Vainstein A (2012) Genome modifications in plant cells by custom-made restriction enzymes. Plant Biotechnol J 10:373–389

Wang H, Wang H, Shao H, Tang X (2016) Recent advances in utilizing transcription factors to improve plant abiotic stress tolerance by transgenic technology. Front Plant Sci 7:67. https://doi.org/10.3389/fpls.2016.00067

Wyn Jones RG, Storey R, Leigh RA, Ahmad N, Pollard A (1977) A hypothesis on cytoplasmic osmoregulation. In: Marre E, Ciferri O (eds) Regulation of cell membrane activities in plants. Elsevier, Amsterdam, pp 121–136

Zhu JK (2016) Abiotic stress signaling and responses in plants. Cell 167:313–324

Crop Plants, Abiotic Stress, Reactive Oxygen Species Production, Signaling, and Their Consequences

7

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Abstract

The utmost normally abiotic stress–triggered expression in plants involves the transcription factors activating stress responsive genes, thereby causing the formation of reactive oxygen species (ROS). ROS signaling pathways along with plant hormones act as key mediators culminating into activation of downstream metabolic routes and alterations at the physiological levels according to the altered environment. A critical amount of ROS is needed by plant systems for normal functioning of important physiological mechanisms. Furthermore, if exist at a higher than critical level, ROS may be lethal and devastating for the entire physiological response. Consequently, plant systems retain a threshold level of

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ROS by inherent antioxidant defense mechanisms comprising of enzymatic and nonenzymatic components. Usually, surplus ROS are neutralized by these antioxidants, but under stress, ROS formation is elevated, and antioxidant activity is lowered. Overall, the present chapter provides an overview on the ROS signaling together with their production, impact, and mitigation through antioxidant mechanisms in crops under adverse environments.

Keywords

Antioxidant mechanism · Crop plants · Growth and production · ROS signaling · Stress amelioration

7.1 Introduction

Abiotic stresses like salinity, drought, flooding, cold, freezing, etc., decreases crop growth, development, and production (Al-Khayri et al. 2021). Crop plants have shown many physiological and metabolic responses in alleviating the abiotic stresses. These responses are controlled by the instigation of gene networks/routes, which lead to higher tolerance/resistance. Stress induces the production of damaging by-products, which have negative impact on plants. Most frequently produced by-products are the reactive oxygen species (ROS) generated by reduction of oxygen, e.g., superoxide radicals, hydrogen peroxide, and so on (Jain et al. 2021; Sonkar et al. 2021a, b, c; Porwal et al. 2021). Cellular injury and death results due to the detrimental effects of oxygen radicals on the proteins and lipid constituents of cellular machinery. The organellar levels of ROS are low in optimal growth conditions, while under stress conditions, these levels are raised due to disorders in water potential of cells, upsetting cellular homeostasis. ROS homeostasis in the cell is accomplished by the equilibrium between its manufacture and rummaging. Growth circumstances are affected by acuteness, period of stress, and disturbed cellular balance. In plants, ROS-rummaging mechanisms exhibit a very critical defensive role against stress induced cellular damages. As a result, deciphering the mechanistic details of ROS production, signaling, and rummaging allows an important approach to augment the crop adaptability/tolerance toward abiotic stress environments. The ROS formation in plant systems under various stress conditions found to trigger downstream metabolic pathways (Chan et al. 2016). ROS result in serious impairment of proteins, DNA, and lipids due to its interaction with many metabolites and important enzymes, causing malfunctioning in the cell (Khan and Khan 2017). The production and balance of ROS are signaling dependent. ROS has a threshold limit for the normal functioning of plants, and a change in the levels of ROS production causes a change in the plant physiology. The steadiness in ROS production and accumulation is maintained by the efficient functioning of an intriguing indigenous defense system referred to as the antioxidant system contributed together by enzymatic and nonenzymatic antioxidants. Higher ROS production accompanied by lower levels of antioxidants causes oxidative stress leading to oxidative damages in terms of cellular membrane damage and hence metabolic anomalies. Proper mineral nutrition, among various agricultural management practices, contributes to sustained productivity (Ahanger et al. 2017). ROS is a key indicator of the acclimatization of plants to the abiotic stress in its surroundings. ROS not only plays a prime role as signal transducing molecules regulating various pathways of plant adaptation to stress but also contribute to the toxic byproducts due to changes in metabolism in response to stress. The pathways for ROS-producing and ROS-scavenging is well defined in every subcellular compartment in plants; variations exist in the ROS steady-state levels and redox state of every subcellular compartment at any time. This in turn suggests the separate regime of ROS levels at the varied subcellular compartments of the cell (Choudhury et al. 2017).

Some reports are accessible that signify the drastic impacts of salinization of soil sap on plant photosynthesis variedly due to stomatal closure (Munns and Tester 2008), chlorophyll malfunctioning (Jiang et al. 2012), deficiency of enzymatic proteins (Mittal et al. 2012), damages in membranes, and ultrastructure of chloroplast (Gengmao et al. 2015). Persistence of several stresses in our environment exhibits the main limitations in agricultural productivity. Unfavorable conditions promote the plants to under express their genetic yield potential. Water deficit stress is the chief stress among several stresses that affects crop growth negatively (Embiale et al. 2016; Getnet et al. 2015; Husen et al. 2014, 2017). It lowers the availability of nutrients to plant roots (Osakabe et al. 2014). The presence of mineral nutrients and phytohormones govern the accumulation of proline, which acts as an osmoprotectant against ROS formation (Per et al. 2017). It is the general behavior of ROS that occurs at basal levels along with the activity of enzymatic and nonenzymatic antioxidants in favorable situations. Nevertheless, both the ROS production and the activity of the antioxidant components increase under unfavorable environments (Schneider et al. 2019). The antioxidative defense system, thus, acts as a balancing system to counteract the effect of ROS. Nutrients availability and utilization efficiency affect the metabolic pathways mediated by ROS. Overaccumulation of Na^+ causes efflux of cytosolic K^+ and Ca^{2+} resulting in a discrepancy in homeostatic cellular environment, nutrient scarcity, oxidative stress, and retarded growth including cellular mortality (Ahanger and Agarwal 2017). Salt-stressed soils have enhanced levels of Na^+/K^+ and Na^+/Ca^{2+} ratios owing to overaccumulation of Na^+ in the soil microenvironment. Hence, a decrease in K^+ and Ca^{2+} uptakes cause reticence in normal cell functioning, cell membrane leakage or damage, and interrupted enzymatic activities (Quintero et al. 2007). Some additional stresses such as osmotic pressure and ionic toxicity along with oxidative stress also cause higher ROS production in cytosol, chloroplast, and mitochondria. Several studies report the reduction in plant productivity by triggering ionic and osmotic effects further causing reduced mineral uptake and changed assimilation (Ahanger and Agarwal 2017). This chapter provides an overview on ROS signaling, production, and after effects along with mitigation by antioxidant mechanisms under stress conditions.

7.2 ROS Production and Their Participation in Cell Signaling

ROS deactivates enzymatic activities in general and causes impairment to key cellular machinery. ROS governs the intactness in the structure of the biomolecules like protein, etc. and considered to be a key role player in ageing and cell death (Jacobson et al. 1996). Halliwell and Gutteridge (2015) explained ROS as moderately reduced or excited forms of atmospheric oxygen. The life span of ROS is in milli-, micro-, or nanoseconds as it frequently reacts with lipids, proteins, and so on, thereby harming in terms of detrimental products such as lipid peroxides. The damage induced by ROS in proteins causes declined enzyme activities, whereas in DNA might lead to mutagenesis and carcinogenesis (Shah et al. 2001). The surplus formation of ROS consequently causes the reticence of electron transport systems in chloroplast and mitochondria and metabolic dysfunction causing damage to cellular structures, thus contributing to premature senescence (Rogers and Munne-Bosch 2016). ROS are nevertheless, reported to play an advantageous function with respect to the stress signaling (Khan and Khan 2017). ROS is considered to be indispensable for plants existence and performs cellular functions like signaling and defense responses at basal levels (Schneider et al. 2019). ROS production mediates modification in genes expression and signal transduction routes, which signifying that cells develop a strategy to use ROS as a natural stimulus and signals to commence in stress-response programs. ROS signaling together with hormonal signaling networks transmits ecological variations as input to generate responses in plants to environmental stimuli (Mittler et al. 2011). ROS thus plays a role as secondary messengers by interfering with signal transduction pathways.

A complex signaling network evolved in plants, while sensing the ecological stimulus, might also cross talk. Stress signal transduction pathways are commenced with the capture of stimulus by receptors like phytochromes, histidine kinases, receptor-like kinases, and so on, further producing secondary signaling molecules like ROS, abscisic acid, and so on. Such secondary signaling molecules can change the level of intracellular Ca^{2+} and commence protein phosphorylation cascades, i.e., calcium-dependentprotein kinase. Drought and salinity are the environmental conditions manipulating cells chiefly via upsetting the ionic and osmotic equilibrium causing an events cascade in turn that further categorized into ionic and osmotic signaling pathways. Stress conditions in plants are manifested by signs of stress injury. Stress damage happens mainly by denaturation of cellular proteins/enzymes or ROS generation. Plants react to stress injury by initiating several detoxification processes like LEA/dehydrin-type gene's differential expression in addition to the formation of proteinases, etc. (Boguszewska and Zagdańska 2012).

7.3 Antioxidant Mechanism: ROS Scavenger

Increased amounts of ROS in cells cause injury to biomolecules, viz., proteins, amino acids, and lipids causing cellular mortality. Such damages in plant systems are overcome by the higher activity of both enzymatic and nonenzymatic antioxidants (Schneider et al. 2019). These can actively rummage ROS. Antioxidants are usually categorized into two groups: enzymatic and nonenzymatic antioxidants. Enzymatic antioxidants comprise of catalase (CAT), superoxide dismutase (SOD) (Sharma et al. 2016; Furukawa et al. 2017), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) (Lushchak 2014). The antioxidants categorized as nonenzymatic comprise glutathione (GSH) (Diaz-Vivancos et al. 2015), ascorbate (AsA) (Foyer 2017), carotenoids, tocopherols (Birben et al. 2012), etc. (Gupta et al. 2005). Antioxidant systems comprising both the above said categories of antioxidants play a key role in cellular defense in plants. ROS induction or by-products of oxidative stress cause protein oxidation through covalent interactions (Forrester et al. 2018). Protein oxidations are mostly irreversible with exception in case of amino acids with sulfur moieties (Ahmad et al. 2017). It is prevalent in all plants and is therefore used as an indicator for ROS or oxidative stress.

Induced activities of both the nonenzymatic and enzymatic antioxidants well mark the refinement in plants' capacity to withstand a huge range of abiotic stresses, therefore playing a critical role in plants survival, which now also illustrated by the approaches of genetic engineering (Birnie-Gauvin et al. 2017). Several enzymatic antioxidants like PrxR, GPX, and APX actively scavenge hydrogen peroxide (H_2O_2) almost in each cellular compartment in cytosol (Cha et al. 2014). Reports are available indicating an enzymatic antioxidant CAT to dismutate H_2O_2, which is necessary to cause detoxification due to ROS throughout stress (Sharma et al. 2012). The upregulation of SOD is concerned with opposing oxidative stress, hence playing a crucial role in plant survival. Reports are available indicating the fact that SOD scavenges cytotoxic H_2O_2, therefore aiding plants survival during stress conditions. GPX, the multiple isozymes, diminish the cytotoxic hydroperoxides and H_2O_2 to alcohols (Boguszewska and Zagdańska 2012). GPX as well retrieves lipid peroxidation that is an outcome of ROS production (Chen et al. 2012). Likewise, APX is found to scavenge H_2O_2 in ascorbate–glutathione cycles using AsA as the electron donor (Sharma et al. 2012).

Nonenzymatic antioxidants, like carotenoid pigments (β-carotene), react with hydroxyl, superoxide, etc., giving prooxidant outcomes in consequence, when O_2 contents are high (Carocho and Ferreira 2013). Carotenoids along with retinoic acid likely control the transcription factors (Sharoni et al. 2012). It not only hampers the commencement of synthesis of tumor necrosis factor-α, oxidation triggered NF-κB, and interleukin (IL)-6 (Ferretti et al. 2012) but also interrupts apoptosis. Reports are available exposing the antiproliferative harm of retinoic acid in plants. This harm is done by triggering of apoptosis mediated by acid receptors (Alizadeh et al. 2014). GSH is the key role player in the antioxidative defense system through exciting ascorbic acid in the course of the ascorbate–glutathione cycle (Wang et al. 2012a, b). GSH takes part in a number of physiological procedures, viz., metabolite's conjugation, signal transduction, stress-responsive gene expression, sulfate transport regulation, and xenobiotic's detoxification (Zagorchev et al. 2013). Glutathione reduces dehydroascorbate (DHA) both enzymatically and nonenzymatically and gets itself oxidized to glutathione disulfide (GSSG). The regeneration reaction to attaining GSH back from GSSG is carried out by glutathione reductase using NADPH as reducing power (Deponte 2013). The high reductive potential of GSH is on account of a nucleophilic cysteine residue. It scavenges cytotoxic H_2O_2 by reacting enzymatically with ROS (Forman et al. 2014). Every stress has its own characteristics, and so each environmental stress results in the production of ROS or nitrogen species (RNS), therefore modifying the cellular redox status, which is a necessary buffering instrument to prevent disproportionate redox reactions (Foyer and Noctor 2003). Along with many others, AsA and GSH are low molecular compounds, while APX, MDHAR, DHAR, and GR are enzymes that are employed in upholding the redox grade of the cell (Mittler 2017). Cyclic handover of electrons during AsA–GSH pathway removes H_2O_2 with no consumption of either AsA or GSH. AsA on oxidation forms MDHA radical, while used as an electron donor by APX to hunt H_2O_2. MDHA can have two fates: it degrades either to AsA and DHA or enzymatically reduced to AsA by NADPH or NADH-dependent MDHAR. GSH acts as a reducing substrate for DHAR in a reaction to reduce DHA to AsA, where sequentially oxidized glutathione (GSSG) is reduced to GSH again, through a NADPH-dependent GR. Thus, these four enzymes, actively participating in this cyclic series of reactions, are highly significant for of plant's resistance/tolerance to oxidative stress and in the maintenance of high ratios of AsA/(AsA + DHA) and GSH/(GSH + GSSG) (Hasanuzzaman et al. 2017). The antioxidant enzymes restrain the damage in cell structure that caused by ROS generation due to salinity. Crop plants develop better salt tolerance due to the presence of an efficient antioxidant system compared with other types of plants. Several reports are available that signifies the differences in impacts of salinity stress on antioxidative activities in *Tanacetum parthenium* L. (Mallahi et al. 2014), *Brassica napus* L. (Ahmadi et al. 2018), *Oryza sativa* L. (Li et al. 2014), and *Glycine max* L. (Farhangi-Abriz and Ghassemi-Golezani 2018). Plants have the presence of some omnipresent natural antioxidants. These include vitamins, carotenoids and so on including endogenous metabolites. The production and rummaging activity of antioxidants constitute the first barrier to the oxidative stress-induced damage in plants found in salinity-affected regions. Antioxidants display prooxidant action based on the circumstances chiefly in respect of quantity and redox status of the cell. In addition, antioxidants might reduce free-radical damage to normal tissues leading to toxicity reduction. It is reported that the cytotoxic machinery of drugs remains unaffected by upregulation of antioxidants. Hence, it is remarkable that antioxidants alleviate the levels of oxidants noticeably that cause oxidative burst. Table 7.1 and Fig. 7.1 summarize the various antioxidant activities, which are responsible for the cellular defense to reduce oxidative stress in all organisms including crops.

Table 7.1 Different types of plants and their combating mechanism under abiotic stress conditions

Type of stress	Plant sp.	Antioxidant mechanism	References
Drought	*Myrothamnus abellifolia*	Reserve of the antioxidant system was enough for eight months. However, AsA, β-carotene, and α-tocopherol contents were totally depleted after eight months of drought	Kranner et al. (2002)
Cadmium	*Triticium aestivum*	Enhancement in GR activity	Khan et al. (2007)
Radiation (UV-B)	*Cassia auriculata*	Enhanced SOD and CAT activity	Agarwal (2007)
Lead chloride/ Lead nitrate	*Vigna radiata*	Enhancement in SOD, APX, GPX, and GR activity	Siddiqui (2013)
Copper	*Oryza sativa*	Upregulation of POX, APX, and DHAR expression	Song et al. (2013)
Cold	*Triticum aestivum*	Increased activity of SOD, POX, GR, and APX	Turk et al. (2014)
Osmotic stress	*Triticum aestivum*	Enhancement in SOD, GR, and APX activity	Naderi et al. (2014)
Lead (Pb^{2+})	*Eichhornia crassipes*	Increased activity of SOD, APX, POX, and MDA content increased with increasing concentration of Pb^{2+}	Malar et al. (2014)
Drought	*Zea mays*	SOD, CAT, and POX activity decreased with severity of drought	Anjum et al. (2017)
Combination of H_2O_2 + salt+ drought stresses	*Nicotiana tabacum*	Overexpression of DHAR	Chang et al. (2017)
Cold	*Solanum lycopersicum*	Enhanced activities of SOD, APX, MDHAR, and DHAR	Liu et al. (2018)

7.4 Conclusion

The balance of threshold cellular ROS content is shifted toward its enhanced production by various environmental tensions (like nutrient scarcity, salt stress, presence of toxic metals, and so on) detrimental to the cellular homeostasis. In plants, the ROS act as mediator for many stress-induced cellular responses through signaling cascades under low concentrations and their detrimental effect to cellular constituents at higher concentrations. Imbalancing of free radical and non-free radical oxygen intermediate components of ROS form the basis of oxidative injury to the cellular machinery. To inhibit these injuries, plants employ enzymatic and nonenzymatic protection mechanisms. Antioxidative defense mechanisms against ROS are induced by nutrients and protective elements. Evidence gained over the last 20 years or more had clearly established ROS as key mediators in the plant signaling responses toward various stresses and their beneficial roles under controlled

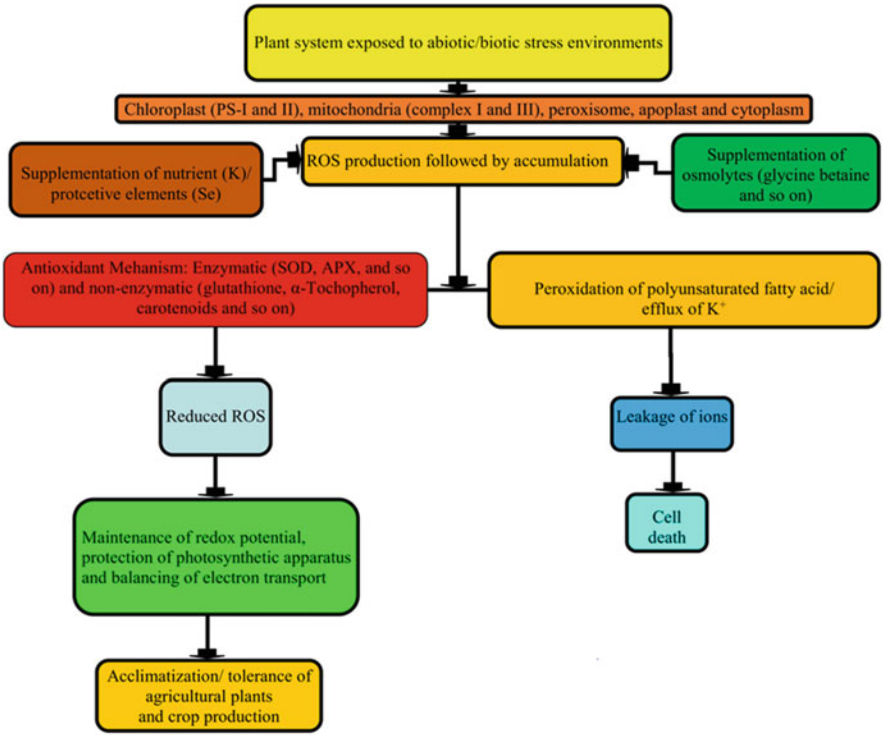

Fig. 7.1 Antioxidant mechanism for combating ROS production in crops under abiotic/biotic stresses

production in normal cellular development. Coordination between ROS response signaling networks can be inferred from the current knowledge, but their exact functioning is still not very clearly understood. Furthermore, there are various stress factors like noise/air pollution, electromagnetic radiations, lights reflected by vehicles, and so on, which have been not explored significantly so far and can have important implications on ROS mechanisms. Studies involving these queries may deliver newer visions on the regulation of coordinated plant gene expression concerning acclimation to changed environments.

References

Agarwal S (2007) Increased antioxidant activity in *Cassia* seedlings under UV-B radiation. Biol Plant 51:157–160

Ahanger MA, Agarwal RM (2017) Potassium improves antioxidant metabolism and alleviates growth inhibition under water and osmotic stress in wheat (*Triticum aestivum* L). Protoplasma 254:1471–1486

Ahanger MA, Tittal M, Mir RA, Agarwal RM (2017) Alleviation of water and osmotic stress-induced changes in nitrogen metabolizing enzymes in *Triticum aestivum* L. cultivars by potassium. Protoplasma 254(5):1953–1963

Ahmad S, Khan H, Shahab U, Rehman S, Rafi Z, Khan MY, Ansari A, Siddiqui Z, Ashraf JM, Abdullah SM, Habib S (2017) Protein oxidation: an overview of metabolism of sulphur containing amino acid, cysteine. Front Biosci 9:71–87

Ahmadi FI, Karimi K, Struik PC (2018) Effect of exogenous application of methyl jasmonate on physiological and biochemical characteristics of *Brassica napus* L. cv. Talaye under salinity stress. S Afr J Bot 115:5–11

Alizadeh F, Bolhassani A, Khavari A, Bathaie SZ, Naji T, Bidgoli SA (2014) Retinoids and their biological effects against cancer. Int Immunopharmacol 18:43–49

Al-Khayri JM, Ansari MI, Singh AK (2021) Nanobiotechnology: mitigation of abiotic stress in plants, 1st edn. Springer, Cham, pp 1–593

Anjum SA, Ashraf U, Tanveer M, Khan I, Hussain S, Shahzad B, Zohaib A, Abbas F, Saleem MF, Ali I, Wang LC (2017) Drought induced changes in growth, osmolyte accumulation and antioxidant metabolism of three maize hybrids. Front Plant Sci 8:69

Birben E, Sahiner UM, Sackesen C, Erzurum S, Kalayci O (2012) Oxidative stress and antioxidant defense. World Allergy Organ J 5:9–19

Birnie-Gauvin K, Costantini D, Cooke SJ, Willmore WG (2017) A comparative and evolutionary approach to oxidative stress in fish: a review. Fish Fish 18:928–994

Boguszewska D, Zagdańska B (2012) ROS as signalling molecules and enzymes of plant response to unfavorable environmental conditions. In: Lushchak V, Semchyshyn HM (eds) Oxidative stress-molecular mechanisms and biological effects. IntechOpen, Rijeka, pp 342–357

Carocho M, Ferreira IC (2013) A review on antioxidants, prooxidants and related controversy: natural and synthetic compounds, screening and analysis methodologies and future perspectives. Food Chem Toxicol 51:15–25

Cha JY, Kim JY, Jung IJ, Kim MR, Melencion A, Alam SS, Yun DJ, Lee SY, Kim MG, Kim WY (2014) NADPH-dependent thioredoxin reductase a (NTRA) confers elevated tolerance to oxidative stress and drought. Plant Physiol Biochem 80:184–191

Chan KX, Phua SY, Crisp P, McQuinn R, Pogson BJ (2016) Learning the languages of the chloroplast: retrograde signaling and beyond. Annu Rev Plant Biol 67:25–53

Chang L, Sun H, Yang H, Wang X, Su Z, Chen F, Wei W (2017) Over-expression of dehydroascorbate reductase enhances oxidative stress tolerance in tobacco. Electron J Biotechnol 25:1–8

Chen L, Hu JY, Wang SQ (2012) The role of antioxidants in photoprotection: a critical review. J Am Acad Dermatol 67:1013–1024

Choudhury FK, Rivero RM, Blumwald E, Mittler R (2017) Reactive oxygen species, abiotic stress and stress combination. Plant J 90:856–867

Deponte M (2013) Glutathione catalysis and the reaction mechanisms of glutathione dependent enzymes. Biochim Biophys Acta 1830:3217–3266

Diaz-Vivancos P, de Simone A, Kiddle G, Foyer CH (2015) Glutathione–linking cell proliferation to oxidative stress. Free Radic Biol Med 89:1154–1164

Embiale A, Hussein M, Husen A, Sahile S, Mohammed K (2016) Differential sensitivity of *Pisum sativum* L. cultivars to water-deficit stress: changes in growth, water status, chlorophyll fluorescence and gas exchange attributes. J Agrobiol 15:45–57

Farhangi-Abriz S, Ghassemi-Golezani K (2018) How can salicylic acid and jasmonic acid mitigate salt toxicity in soybean plants? Ecotoxicol Environ Saf 154:1010–1016

Ferretti G, Bacchetti T, Masciangelo S, Saturni L (2012) Celiac disease, inflammation and oxidative damage: a nutrigenetic approach. Nutrients 4:243–257

Forman HJ, Ursini F, Maiorino M (2014) An overview of mechanisms of redox signalling. J Mol Cell Cardiol 73:2–9

Forrester SJ, Kikuchi DS, Hernandes MS, Xu Q, Griendling KK (2018) Reactive oxygen species in metabolic and inflammatory signalling. Circ Res 122:877–902

Foyer CH (2017) Ascorbic acid. In: Foyer CH (ed) Antioxidants in higher plants. CRC Press, New York, pp 31–58

Foyer CH, Noctor G (2003) Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. Physiol Plant 119:355–364

Furukawa S, Fujita T, Shimabukuro M, Iwaki M, Yamada Y, Nakajima Y, Nakayama O, Makishima M, Matsuda M, Shimomura I (2017) Increased oxidative stress in obesity and its impact on metabolic syndrome. J Clin Invest 114:1752–1761

Gengmao Z, Shihui L, Xing S, Yizhou W, Zipan C (2015) The role of silicon in physiology of the medicinal plant (*Lonicera japonica* L.) under salt stress. Sci Rep 5:12696

Getnet Z, Husen A, Fetene M, Yemata G (2015) Growth, water status, physiological, biochemical and yield response of stay green sorghum {*Sorghum bicolor* (L.) Moench} varieties-a field trial under drought-prone area in Amhara regional state, Ethiopia. J Agron 14:188–202

Gupta KJ, Stoimenova M, Kaiser WM (2005) In higher plants, only root mitochondria, but not leaf mitochondria reduce nitrite to NO, in vitro and in situ. J Exp Bot 56:2601–2609

Halliwell B, Gutteridge JM (2015) Free radicals in biology and medicine, 5th edn. Oxford University Press, Oxford

Hasanuzzaman M, Nahar K, Hossain MS, Mahmud JA, Rahman A, Inafuku M, Oku H, Fujita M (2017) Coordinated actions of glyoxalase and antioxidant defense systems in conferring abiotic stress tolerance in plants. Int J Mol Sci 18(1):200

Husen A, Iqbal M, Aref IM (2017) Plant growth and foliar characteristics of faba bean (*Vicia faba* L.) as affected by indole-acetic acid under water-sufficient and water-deficient conditions. J Environ Biol 38:179–186

Husen A, Iqbal M, Aref MI (2014) Growth, water status and leaf characteristics of *Brassica carinata* under drought stress and rehydration conditions. Brazilian J Bot 37:217–227

Jacobson MD, Weil M, Raff MC (1996) Role of Ced-3/I family proteases in stuarosporine-induced programmed cell death. J Cell Biol 133:1041–1051

Jain P, Pandey B, Singh P, Singh R, Singh SP, Sonkar S, Gupta R, Rathore SS, Singh AK (2021) Plant performance and defensive role of glycine betaine under environmental stress. In: Husen A (ed) Plant performance under environmental stress. Springer, pp 225–248

Jiang C, Zheng Q, Liu Z, Xu W, Liu L, Zhao G, Long X (2012) Overexpression of *Arabidopsis thaliana* Na^+/H^+ antiporter gene enhanced salt resistance in transgenic poplar (*Populus euramericana* “Neva”). Trees 26:685–694

Khan MLR, Khan NA (eds) (2017) Reactive oxygen species and antioxidant systems in plants: role and regulation under abiotic stress. Springer, New York

Khan NA, Samiullah SS, Nazar R (2007) Activities of antioxidative enzymes, sulphur assimilation, photosynthetic activity and growth of wheat (*Triticum aestivum*) cultivars differing in yield potential under cadmium stress. J Agro Crop Sci 193:435–444

Kranner I, Beckett RP, Wornik S, Zorn M, Pfeifhofer HW (2002) Revival of a resurrection plant correlates with its antioxidant status. Plant J 31(1):13–24

Li M, Guo S, Xu Y, Meng Q, Li G, Yang X (2014) Glycine betaine-mediated potentiation of HSP gene expression involves calcium signaling pathways in tobacco exposed to NaCl stress. Physiol Plant 150:63–75

Liu T, Hu X, Zhang J, Zhang J, Du Q, Li J (2018) H_2O_2 mediates ALA-induced glutathione and ascorbate accumulation in the perception and resistance to oxidative stress in *Solanum lycopersicum* at low temperatures. BMC Plant Biol 18:34

Lushchak VI (2014) Free radicals, reactive oxygen species, oxidative stress and its classification. Chem Biol Interact 224:164–175

Malar S, Vikram SS, Favas PJC, Perumal V (2014) Lead heavy metal toxicity induced changes ongrowth and antioxidative enzymes level in water hyacinths *Eichhornia crassipes* (Mart). Bot Stud 55:54–65

Mallahi T, Saharkhiz MJ, Javanmardi J (2014) Salicylic acid changes morpho-physiological attributes of feverfew (*Tanacetum parthenium* L.) under salinity stress. Acta Ecol Sin 38:351–355

Mittal S, Kumari N, Sharma V (2012) Differential response of salt stress on *Brassica juncea*: photosynthetic performance, pigment, proline, D1 and antioxidant enzymes. Plant Physiol Biochem 54:17–26

Mittler R (2017) ROS are good. Trends Plant Sci 22(1):11–19

Mittler R, Vanderauwera S, Suzuki N, Tognetti VB, Vandepoele K, Gollery M, Shulaev V, Van Breusegem F (2011) ROS signaling: the new wave? Trends Plant Sci 16:300–309

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

Naderi R, Valizadeh M, Toorchi M, Shakiba MR (2014) Antioxidant enzyme changes in response to osmotic stress in wheat (*Triticum aestivum* L.) seedling. Acta Biologica Szegediensis 58:95–101

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

Per TS, Khan NA, Reddy PS, Masood A, Hasanuzzaman M, Khan MIR, Anjum NA (2017) Approaches in modulating proline metabolism in plants for salt and drought stress tolerance: phytohormones, mineral nutrients and transgenics. Plant Physiol Biochem 115:126–140

Porwal P, Sonkar S, Singh AK (2021) Plant stress enzymes nanobiotechnology. In: Al-Khayri JM, Ansari MI, Singh AK (eds) Nanobiotechnology: mitigation of abiotic stress in plants. Springer, pp 327–348

Quintero JM, Fournier JM, Benlloch M (2007) Na^+ accumulation in shoot is related to water transport in K^+-starved sunflower plants but not in plants with a normal K+ status. J Plant Physiol 164:60–67

Rogers H, Munne-Bosch S (2016) Production and scavenging of reactive oxygen species and redox signalling during leaf and flower senescence: similar but different. Plant Physiol 171:1560–1568

Schneider JR, Caverzan A, Chavarria G (2019) Water deficit stress, ROS involvement, and plant performance. Arch Agron Soil Sci 65(8):1160–1181

Shah K, Kumar RG, Verma S, Dubey RS (2001) Effect of cadmium on lipid peroxidation, superoxide anion generation and activities of antioxidant enzymes in growing rice seedlings. Plant Sci 161:1135–1144

Sharma P, Jha AB, Dubey RS (2016) Oxidative stress and antioxidative defense systems in plants growing under abiotic stresses. In: Pessarakli M (ed) Handbook of plant and crop stress. CRC Press, New York, pp 109–158

Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot 2012:217037

Sharoni Y, Linnewiel-Hermoni K, Khanin M, Salman H, Veprik A, Danilenko M, Levy J (2012) Carotenoids and apocarotenoids in cellular signalling related to cancer: a review. Mol Nutr Food Res 56:259–269

Siddiqui ZS (2013) Effects of double stress on antioxidant enzyme activity in *Vigna radiata* (L.) Wilczek. Acta Bot Croat 72:145–156

Song Y, Cui J, Zhang H, Wang G, Zhao FJ, Shen Z (2013) Proteomics analysis of copper stress responses in the roots of two rice (*Oryza sativa* L.) varieties. Plant and Soil 366:647–358

Sonkar S, Pandey B, Rathore SS, Sharm L, Singh AK (2021a) Applications of nanobiotechnology in overcoming temperature stress. In: Al-Khayri JM, Ansari MI, Singh AK (eds) Nanobiotechnology: mitigation of abiotic stress in plants. Springer, pp 417–435

Sonkar S, Sharma L, Singh RK, Pandey B, Rathore SS, Singh AK, Porwal P, Singh SP (2021b) Plant stress hormones nanobiotechnology. In: Al-Khayri JM, Ansari MI, Singh AK (eds) Nanobiotechnology: mitigation of abiotic stress in plants. Springer, pp 349–373

Sonkar S, Singh AK, Husen A (2021c) Functions of hydrogen sulfide in plant regulation and response to abiotic stress. In: Husen A (ed) Plant performance under environmental stress. Springer, pp 329–355

Turk H, Erdal S, Genisel M, Atici O, Demir Y, Yanmis D (2014) The regulatory effect of melatonin on physiological, biochemical and molecular parameters in cold-stressed wheat seedlings. Plant Growth Regul 74:139–152

Wang P, Yin L, Liang D, Li C, Ma F, Yue Z (2012a) Delayed senescence of apple leaves by exogenous melatonin treatment: toward regulating the ascorbate–glutathione cycle. J Pineal Res 53:11–20

Wang Y, Yang J, Yi J (2012b) Redox sensing by proteins: oxidative modifications on cysteines and the consequent events. Antioxid Redox Signal 16:649–657

Zagorchev L, Seal CE, Kranner I, Odjakova M (2013) A central role for thiols in plant tolerance to abiotic stress. Int J Mol Sci 14:7405–7432

Environment Stress Tolerance in Plant-Physiological Aspects

8

Sihem Tellah

Abstract

Plants are often exposed to various environmental stresses (ES) such as drought (deficit in precipitation), salinity, high and low temperatures, and high light intensity under both natural and agricultural conditions. These ES significantly affect the growth of the plants, metabolism, and productivity worldwide. Many plants have improved their resistance mechanisms by involving numerous physiological reactions to tolerate ES, but these mechanisms are varied and depend on plant species. Plant responses to environmental constraints depend on the length and severity of the ES and the plant species, age, and developmental stage. Plants possess a number of adaptive, avoidance, or acclimation mechanisms to cope with these ES situations. In addition, major tolerance mechanisms that employ osmoprotectants, proteins, antioxidants, ion transporters, and other factors involved in signaling cascades and transcriptional control are activated to offset stress-induced and physiological and biochemical alterations. Plant survival under environmental stresses depends on the ability to perceive the ES stimulus, generate and transmit the signal, and initiate appropriate physiological and biochemical changes. All ES-induced gene expression and metabolite synthesis also substantially improve tolerance. The physiological and biochemical responses to all kinds of environmental stresses are active research areas. This chapter reviews the recent findings on responses, adaptation, and tolerance to environmental stresses at the cellular, organelles, and whole plant levels and describes various approaches being taken to enhance environment stress tolerance in plants.

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Keywords

Environmental stresses · Effects · Tolerance · Management · Adaptation · Physiological aspects

8.1 Introduction

Plants are subjected to multitude of stresses throughout their life cycle. The responses of plants to environmental stresses (ES) have been important to students of agronomy, ecology, and physiology since the disciplines were first defined. Development of new crop cultivars tolerant to these ES is a major challenge for plant scientists because adverse conditions, in turn, restrict crop plants to reach their full genetic potential of producing high yield (Anjum et al. 2014). Also, agriculture is under pressure to accelerate crop yield to feed rapidly increasing world population that is projected to stabilize at around 9.2 billion toward the year 2050 (Singh 2012). Thus, a clear understanding of the strategies for sustainably improving crop health, development, and productivity under adverse conditions is timely and imperative.

In this book chapter, we will discuss these mechanisms using references selected as representative of recent work and as suitable entrance points to the relevant literature.

Plants, in particular, as sessile organisms, cannot move to more favorable environments; consequently, plant growth and developmental processes are substantially affected, often lethally, by environmental stresses (ES). During their vegetative cycle, plants are subject to the conditions of the ambient environment in which they live. They react by adapting to changes in these conditions when they become unfavorable. The variation in growth conditions is caused by stresses, which are biotic or abiotic in nature. In arid and semiarid environments, environmental stresses impose limits on the development of the plant. Resistance to these stresses is dependent on the genotype, which develops morphological, physiological, and/or biochemical mechanisms to escape (dodge), avoid, or tolerate the constraint (Levitt 1982).

Within the framework of sustainable agriculture, the development of tolerant and efficient cultivars is one of the most possible approaches to reduce the deleterious effects of various biotic and abiotic constraints. Adaptation to different environmental constraints is a complex phenomenon that integrates both agromorphological modifications and physiological, biochemical, and molecular adjustments (Pfeiffer et al. 2000).

There are several options in environmental stresses in plants, including developmental, physiological, morphological, ecological, biochemical, and molecular mechanisms. Typically, the mechanisms involved in plant tolerance to environmental stresses follow a general plan: maintaining cell water homeostasis under these binding conditions.

8.2 Concept of Stress

According to the definitions, stress in plants appears with different meanings in biology, which converge mainly on any environmental factor unfavorable for a plant (Levitt 1982). According to Jones et al. (1989), a stress designates both the action of an aggressive agent and the reactions it causes in the attacked organism, a force which tends to inhibit normal systems. On the other hand, environmental stresses resulting from the fluctuation of abiotic factors (drought, salinity, and temperature) affect the conditions of growth, development, and yield of plants (Madhava Rao et al. 2006). Il existe différents types de stress environnementaux (Fig. 8.1).

8.3 Effect of Environmental Stresses in Plants

8.3.1 Physiological Effect of Drought Stress on Plants

Drought is one of the most important environmental stresses that in many parts of the world, especially in warm and dry areas of crop yield, are limited (Porudad and Beg 2003).

Drought is a multidimensional stress factor; therefore, its effects on plants are complex and can affect different aspects of plant growth, development, and metabolism (Salehi-Lisar and Bakhshayeshan-Agdam 2020). It is the most important factor limiting plant yields throughout the world.

In terms of plant physiology, dryness causes of stress in plant growth yield 50%–30% reduction in drought stress due to low humidity in plant growth that occurs as a result of the high evapotranspiration, temperature, high intensity of sunlight (Ghodsi et al. 1998), and high temperature caused by the drought stress of increased respiration, photosynthesis, and enzyme activity in the plant. Drought in the sunlight reaction of the photosynthesis, and continued production of free radicals of oxygen

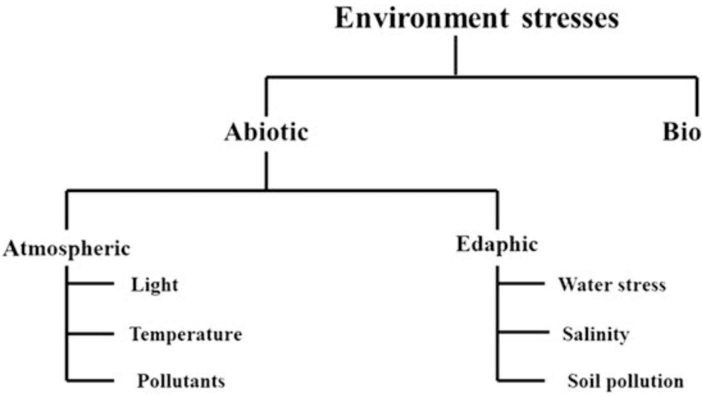

Fig. 8.1 Principal environmental stresses

leading to plant death is light and oxidation. Nutrients absorbed from the upper soil horizon, which is found in most foods, the drought reduced (Bagheri 2009). The increase in drought conditions and accumulation of salts and ions in the upper layers of the soil around the roots cause osmotic stress and ion toxicity.

It is therefore important to gain a better understanding regarding the effect of frequent drought stress on biochemical and physiological processes in plants (Da Silva et al. 2013).

In the study of physiological phenomena of drought stress in plants, it was reported that the plant water status, often by measuring the water potential of tissues, specified by decreasing water potential, decreases cell growth and protein synthesis. The flow of carbon dioxide and leaf transpiration decreases, but the accumulation of proline and abscisic acid stress increases (Heidaiy and Moaveni 2009). In condition of drought stress, photosynthesis by stomatal closure and transfer of carbon dioxide in chloroplasts and cell water potentially decreased and are affected. Under drought stress, root and shoot growth is affected and may reduce the level of plants. In condition of drought stress, crop yield reduces largely the following methods: (1) the reduction of photosynthesis active radiation absorbed by vegetation, (2) the reduction the efficiency of radiation, and (3) the reduction in harvest index. In corn dry matter, the reduction in water consumption will decline (Sajedi and Sajedi 2008).

Drought impairs normal growth (Fig. 8.2), disturbs water relations, and reduces water use efficiency in plants. Plants, however, have a variety of physiological and biochemical responses at cellular and whole organism levels, making it a more complex phenomenon. The rate of photosynthesis is reduced mainly by stomatal closure, membrane damage, and disturbed activity of various enzymes, especially those involved in ATP synthesis (Farooq et al. 2012).

Effect of drought stress on the vegetative growth of peanut (*Arachis hypogaea* L.) cv Berrihane. *Plant growth and imposition of water stress*: Plants were grown in pots under controlled conditions. During their growth, plants were supplied with water to replenish the field capacity of their soil substrate, which was calculated by the method of weighing. Two hundred mL of a 50% mixture of deionized + tap water were provided to each pot every 4 days. Water stress was imposed to six-week-old seedlings of peanut by withholding irrigation. The measurements on plant material were carried out after 10, 15, and 25 days of water deprivation (water-stressed plants, denoted as S-10, S-15, and S-25 in the Fig. 8.1), assumed to impose conditions of mild, moderate, or severe water stress, respectively. For each of the above stress durations, coeval, well watered plants were set as controls (denoted as W-10, W-15 and W-25 plants). In general, it can be said that the stress conditions in the organs of plants are growing faster than other organs that are damaged.

8.3.2 Physiological Effect of Heat Stress on Plants

Heat stress affects all aspects of plant processes like germination, growth, development, reproduction, and yield (Hasanuzzaman et al. 2013a, b; Mittler et al. 2004) (Fig. 8.3). Heat stress differentially affects the stability of various proteins,

Fig. 8.2 Effect of drought stress on the vegetative growth of peanut (*Arachis hypogaea*) cv Berrihane. Water-stressed plants, denoted as S-10, S-15 and S-25; well watered plants were set as control (Tellah 2016)

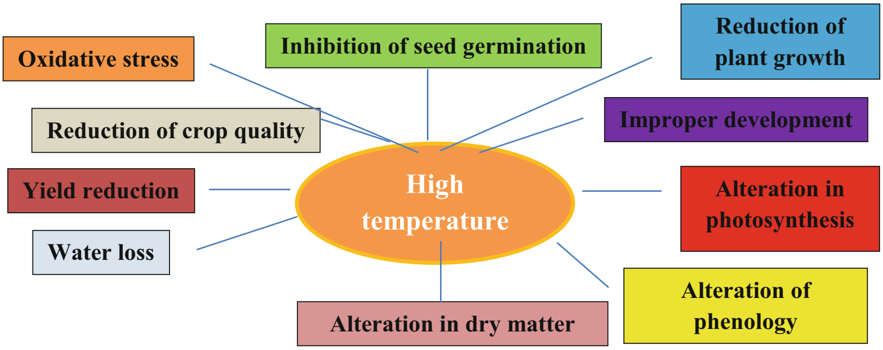

Fig. 8.3 Principal effects of high temperature on plants

membranes, RNA species, and cytoskeleton structures and alters the efficiency of enzymatic reactions in the cell for which the major physiological processes obstacle and creates metabolic imbalance (Ruelland and Zachowski 2010; Pagamas and Nawata 2008).

Cao et al. (2008) demonstrated in their study on rice that physiological parameters that are associated with heat stress, the oxidation activity in roots, and the RNA content in young panicles reduced significantly and the malondialdehyde (MDA) content in leaves and the ethylene evolution rate in young panicles increased significantly. These physiological characteristics were more sensitive to heat stress in Shuanggui 1 than in Huanghuazhan.

8.3.3 Physiological Effect of Salt Stress on Plants

All plants are subjected to multitude of stresses throughout their life cycle. The major environmental factor that currently reduces plant productivity is salinity (Majeed et al. 2010).

The productivity of crops is adversely affected by high salt content in most of the soils (Munns and Termaat 1986).

Soil salinity affects various physiological and biochemical processes, which result in reduced biomass production. This salt stress affects plant physiology and appears on whole plant level at almost all growth stages including germination, seedling, vegetative, and maturity stages, as well as cellular levels through osmotic and ionic adjustments that result in reduced biomass production. Despite causing osmotic and ionic stress, salinity causes ionic imbalances that may impair the selectivity of root membranes and induce potassium deficiency (Nawaz et al. 2010).

The detrimental effects of salinity stress are observed at cellular, organ, and whole plant level at osmotic phase (early/short-term response) and ionic phase (late/long-term response). High salinity exerts its negative impact on major plant processes such as disrupting the osmotic and ionic equilibrium, protein synthesis, photosynthesis, energy, and lipid metabolism (Muchate et al. 2016).

The accumulation of high amounts of toxic salts in the leaf apoplast leads to dehydration and turgor loss and eventually death of leaf cells and tissues (Marschner 1995). As a result of these changes, the activities of various enzymes and plant metabolism are affected (Lacerda et al. 2003).

Salt stress causes various effects on plant physiology such as increased respiration rate, ion toxicity, changes in plant growth, mineral distribution, and membrane instability resulting from calcium displacement by sodium (Marschner 1986), membrane permeability (Gupta et al. 2002), and decreased photosynthetic rate (Hasegawa et al. 2000; Munns 2002; Ashraf and Shahbaz 2003; Kao et al. 2003; Sayed 2003).

Salt stress enhances the accumulation of NaCl in chloroplasts of higher plants, affects growth rate, and is often associated with decrease in photosynthetic electron transport activities (Kirst 1989). In higher plants, salt stress inhibits photosystem (PS)-II activity (Kao et al. 2003; Parida et al. 2003).

The responses to increasing levels of salt stress were evaluated by germination screening, aimed at identifying the most salt tolerant among the cowpea landraces according to their region of provenance. Cowpea (*Vigna unguiculata* subsp. *unguiculata* (L.) *Walp*.) landraces collected in different regions of the Algerian Maghreb and the Sahel (Tellah et al. 2020) were used: P1 and P2 from El Kala; P3, P4, and P18 from Adrar (Sahara); P6 from Tizi Ouzou (Kabylia, see above); P19 from El Golea (Al-Manīʿa, Sahara); P31, and P32 from In Salah (Sahara); P33 from Bechar (Sahara); and NG1 from Niger.

Four levels of NaCl, namely, 0 (control,T0), 5 (T1), 10 (T2), or 15 (T3) g L − 1, assumed to represent mild, moderate, or severe salt stress, respectively, were compared for their effects on seed germination and kinetics during conventional seed germination experiments conducted in Petri dishes.

The results obtained indicated that among the 11 populations tested, the following four showed negligible levels of germination, probably due to inactivation following seeds conservation: P3 and P4 (0% germination at all treatments), P6 (10% at T0 and T1, 3.33% at T2 and 0% at T3), and P31 (10% at T0, 3.33% at T1 and T3, 0% at T2). Further, the experiments pointed out that the effect of NaCl was more pronounced in the case of severe salt stress (T3), which decreased the maximum germination rate and delayed germination kinetics (data not shown). The NG1, P32, and P33 cowpea seeds showed the greatest tolerance to salt, whose negative effects, in the first two landraces, became evident only under severe stress. The P33 landrace was slightly affected in the presence of moderate salt stress, i.e., T2, showing a maximum germination rate that was as high as 96.66% compared with a 100% value in its unstressed control. On the other side, the P2 landrace, a provenance of the El Kala region, showed the greatest sensitivity to salt stress, its maximum germination rate reaching 46.66% at T1 and T2, and only 16.66% at T3, as compared with a 60% germination rate in its unstressed control (T0; Fig. 8.4).

8.4 Plant Adaptation to Environmental Stresses: Physiological Aspects

Plants are subjected to a wide range of abiotic stresses, such as drought, salinity, extreme temperatures, pollution, UV radiation, etc. Abiotic stress adversely affects crop production worldwide, causing yield reductions for most major crops.

Crops are able to tolerate certain environmental stresses through their innate defense mechanism. However, the degree of tolerance and adaptability to abiotic stresses may differ from species and varieties. Crop in their early stages does not show any visible symptoms, but their physiology can undergo significant changes (Cramer et al. 2011).

Drought tolerance is a complex phenomenon associated with cuticle thickness, stomatal regulation, root system, hormonal balances, antioxidant defense system, osmotic adjustment, and maintenance of tissue water contents (Farooq et al. 2012).

An overview of drought, heat, and salt physiological resistance mechanisms at various levels in crop plants is briefly described.

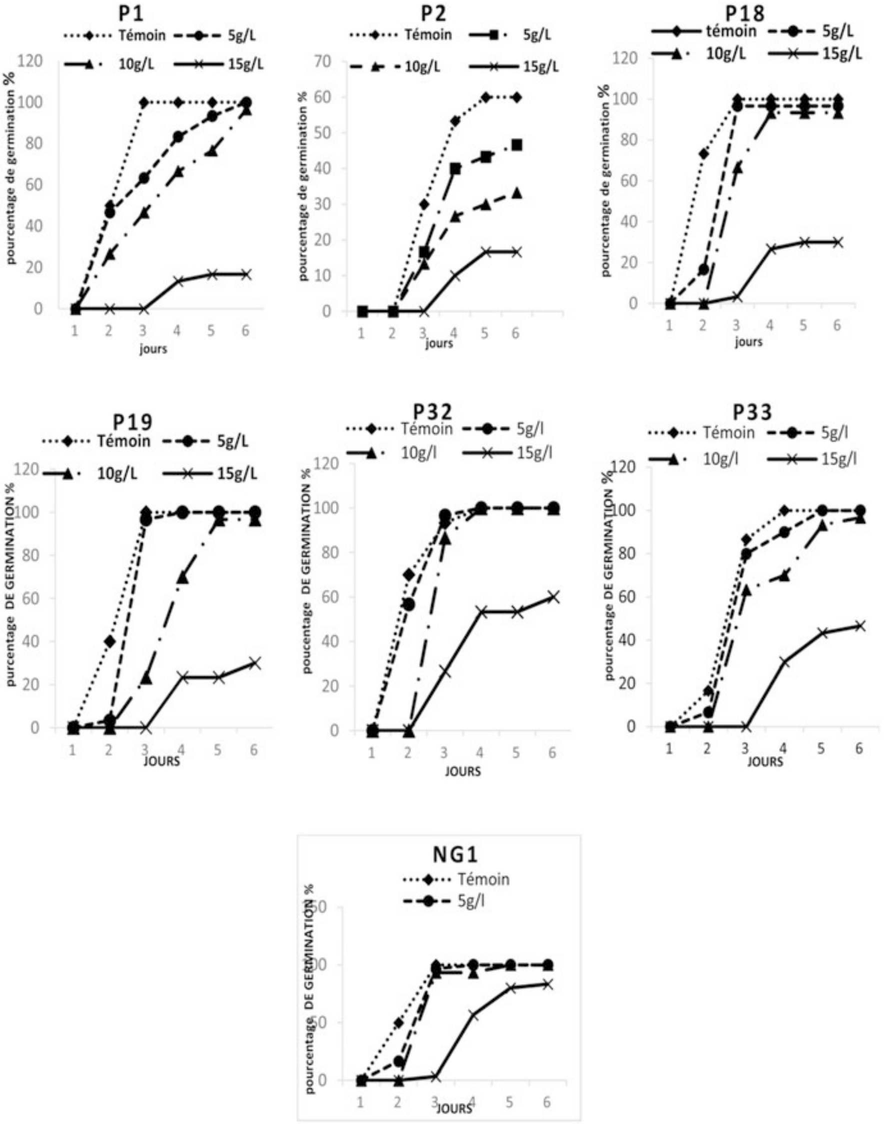

Fig. 8.4 Effects of different concentrations of NaCl on seed germination kinetics of seven populations of cowpea landraces studied for 6 days. Each point represents the average of three replicates (Tellah et al. 2020)

8.4.1 Drought Resistance Mechanisms: Physiological Adaptations

Dehydration-tolerant plants maintain metabolic activities at low tissue water potential. Osmotic adjustment, antioxidant defense system, and changed dynamics of

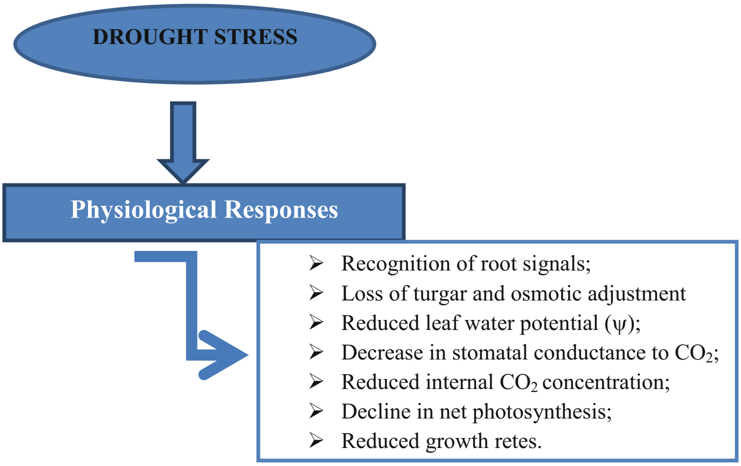

Fig. 8.5 Physiological responses of drought stress tolerance in plants

phytohormones are among the major physiological adaptations of plants under drought (Farooq et al. 2012).

Plant responses to a water deficit depend on the length and severity of the water deficiency and the plant species, age, and developmental stage (Farooq et al. 2009). Many plants have developed resistance mechanisms to tolerate drought stress, but these mechanisms are varied and depend on the plant species. There are several options in drought tolerance in plants, including developmental, physiological, morphological, ecological, biochemical, and molecular mechanisms. Typically, the mechanisms involved in plant tolerance to drought follow a general plan: maintaining cell water homeostasis under drought conditions (Salehi-Lisar and Bakhshayeshan-Agdam 2020) (Fig. 8.5).

Osmotic adjustment, antioxidant activities, and altered growth regulators are among the major physiological adaptations of plants under drought stress. Increased accumulation of osmoprotectants such as proline, GB, amino acid, and sugars are involved in osmoregulation. Scavenging of ROS by enzymatic and nonenzymatic systems, cell membrane stability, expression of aquaporin, and stress proteins such as LEA are also vital mechanisms of dehydration tolerance (Farooq et al. 2012).

8.4.2 Physiological, Biochemical, and Molecular Mechanisms of Heat Stress Tolerance in Plants

Among the ever-changing components of the environment, the constantly rising ambient temperature is considered one of the most detrimental stresses (Hasanuzzaman et al. 2013a, b).

A gradual rise in atmospheric temperature is going to be a major challenge for crop research in near future. To this end, exhaustive molecular genetic studies were recommended for both understanding and getting more insights into thermo-sensing mechanisms in thermal-stressed crops (Anjum 2015).

Heat stress causes multifarious and often adverse alterations in plant growth, development, and physiological processes and yield. One of the major consequences of HT stress is the excess generation of reactive oxygen species (ROS), which leads to oxidative stress (Hasanuzzaman et al. 2012, 2013a, b).

A plant is able, to some extent, to tolerate heat stress by physical changes within the plant body and frequently by creating signals for changing metabolism. Plants alter their metabolism in various ways in response to HT, particularly by producing compatible solutes that are able to organize proteins and cellular structures, maintain cell turgor by osmotic adjustment, and modify the antioxidant system to reestablish the cellular redox balance and homeostasis (Valliyodan and Nguyen 2006; Janska et al. 2010).

In conditions such as HT, modification of physiological and biochemical processes by gene expression changes gradually leads to the development of heat tolerance in the form of acclimation, or in the ideal case, to adaptation (Moreno and Orellana 2011; Hasanuzzaman et al. 2010a, b).

In recent times, exogenous applications of protectants in the form of osmoprotectants (proline, Pro; glycine betaine, GB; trehalose, Tre; etc.), phytohormones (abscisic acid, ABA; gibberellic acids, GA; jasmonic acids, JA; brassinosterioids, BR; salicylic acid, SA; etc.), signaling molecules (e.g., nitric oxide, NO), polyamines (putrescine, Put; spermidine, Spd and spermine, Spm), trace elements (selenium, Se; silicon, Si; etc.), and nutrients (nitrogen, N; phosphorus, P; potassium, K, calcium, Ca; etc.) have been found effective in mitigating HT stress-induced damage in plants (Hasanuzzaman et al. 2010a, b; Barnabás et al. 2008).

In addition, the results of study conducted by CAO et al. (2008) indicate that the heat tolerant in rice is subject to high activity of roots, strong antioxidative defense system, high RNA content, little ethylene synthesis, and low MDA content in plants during meiosis.

Plant scientists involved in research on HT stress are endeavoring to discover the plant responses that lead to heat tolerance, and they are also trying to investigate how plants can be managed in HT environments. Recent widely studied molecular approaches have included omics techniques and the development of transgenic plants through manipulation of target genes (Kosová et al. 2011; Schöffl et al. 1999). Investigation of these underlying molecular processes may provide ways to develop stress tolerant varieties and to grow agriculturally important crop plants under HT.

8.4.3 Adaptive Responses, Tolerance Mechanism for Salt Tolerance

Salinity is an important abiotic environmental stress factor threatening agricultural productivity throughout the world (Muchate et al. 2016). Mechanisms for tolerance of the salt-specific effects of salinity are of two main types: those minimizing the entry of salt into the plant and those minimizing the concentration of salt in the cytoplasm (Nawaz et al. 2010).

To adapt and tolerate salt stress, plants have evolved physiological and biochemical mechanisms orchestrated by multiple biochemical pathways of ion homeostasis, osmolytes synthesis, ROS scavenging, and hormonal balance (Muchate et al. 2016).

Different scientists have reported that variation in salt tolerance in a number of crop species depends on the extent of Na^+ exclusion at root level or ability to compartmentalize salts in the vacuole (Munns 2002, 2005; Ashraf 2004).

Carden et al. (2003) found that the salt-tolerant variety maintained a tenfold lower cytosolic Na^+ in the root cortical cells than the more sensitive variety. It is well established that high accumulation of Na^+ in shoots inhibits enzyme activity and other metabolic processes such as protein synthesis and photosynthesis (Ashraf 2004; Munns 2005), thereby reducing leaf growth or causing leaf death. In another study, Wyn Jones et al. (1984) found that the higher salt tolerance of *Agropyron junceum* to that of *Agropyron intermedium* was related to its efficient exclusion of both Na^+ and Cl^-.

A number of studies have shown that photosynthetic capacity of different species is reduced due to salinity (Ashraf 2004; Dubey 2005). It is evident that higher photosynthetic capacity causes increased plant growth under normal or stress conditions as has earlier been observed in a number of plant spp., e.g., in *Zea mays* (Crosbie and Pearce 1982), cotton (Pettigrew and Meredith 1994), *Brassica* spp. (Nazir et al. 2001), and wheat (Raza et al. 2007). Furthermore, photosynthesis is also one of the main contributing factors in salt-induced reduction in plant growth and yield. Tolerance of photosynthetic system to salinity depends on how effectively plant excludes or compartmentalizes the toxic ions. However, the extent of the adverse effects of salt stress on photosynthesizing tissue or on growth varies with the type of species, level of stress, and duration of stress (Nawaz 2010).

8.5 Genetically Engineering Stress-Responsive Genes

Abiotic stresses affect crop plants and cause decreases in plant quality and productivity. Plants can overcome environmental stresses by activating molecular networks, including signal transduction, stress perception, metabolite production, and expressions of specific stress-related genes. Recent research suggests that chemical priming is a promising field in crop stress management because plants can be primed by chemical agents to increase their tolerance to various environmental stresses (Nguyen et al. 2018).

Recent studies have shown that ROS play a key role in plants as signal transduction molecules involved in mediating responses to pathogen infection, environmental stresses, programmed cell death, and developmental stimuli (Mittler et al. 2004; Torres and Dangl 2005). At the molecular level, such adaptation involves activation of cascade(s) of gene modulations and synthesis of defense metabolites. In recent years, several candidate genes have been identified and employed to facilitate genetic engineering efforts to improve environmental stresses tolerance in crop plants. However, there is a further need of improvement for successful release of tolerant cultivars at the field level.

Development of several functional tools like molecular maps, express sequence tags (ESTs), and understanding the mechanism of transgenes expression in chloroplasts particularly in important bioenergy crops can help in the minimization of the rapidly increasing marginal lands and the contributions. Transcription factors (TFs) represent master switches controlling several target stress-responsive genes and are considered most important for regulation of gene expression. Stress tolerance in plants can be engineered through getting insights into homeobox-TFs and APETALA2/ethylene response element-binding protein (AP2/EREBP) in abiotic/biotic stress responses and their potential use as target genes. The strategy of employing DREB-like proteins, homeobox genes, APETALA2 gene-family, and G-proteins for overcoming environmental-stresses and increasing crop-yield under adverse conditions. Notably, exhaustive studies on the potential role of the dehydration-responsive element-binding proteins (DREB2)-like proteins and their interaction with abscisic acid particularly during seed-germination/seedling-growth may give us an insight in plant developmental processes and stress adaptation/tolerance mechanisms. Regulation of stress related pathways, including reactive oxygen species production, stomatal regulation, and processes related to plant water relations can be modulated by G-proteins and related machinery. G-proteins were suggested herein as the key proteins for overcoming environmental stresses and increasing crop yield (Anjum 2015).

Upon stress, plants perceive the external and internal signals through different independent or interlinked pathways, which are used to regulate various responses for its tolerance development (Kaur and Gupta 2005; Fig. 8.6).

8.6 Sustainable Agriculture Practices

Abiotic stresses are currently responsible for significant losses in quantity and reduction in quality of global crop productions. In consequence, resilience against such stresses is one of the key aims of farmers and is attained by adopting both suitable genotypes and management practices. This latter aspect was reviewed from an agronomic point of view, taking into account stresses due to drought, water excess, salinity, and lodging. For example, drought tolerance may be enhanced by using lower plant density, anticipating the sowing or transplant as much as possible, using grafting with tolerant rootstocks, and optimizing the control of weeds. Water excess or hypoxic conditions during winter and spring can be treated with nitrate fertilizers, which increase survival rate. Salinity stress of sensitive crops may be alleviated by maintaining water content close to the field capacity by frequent and

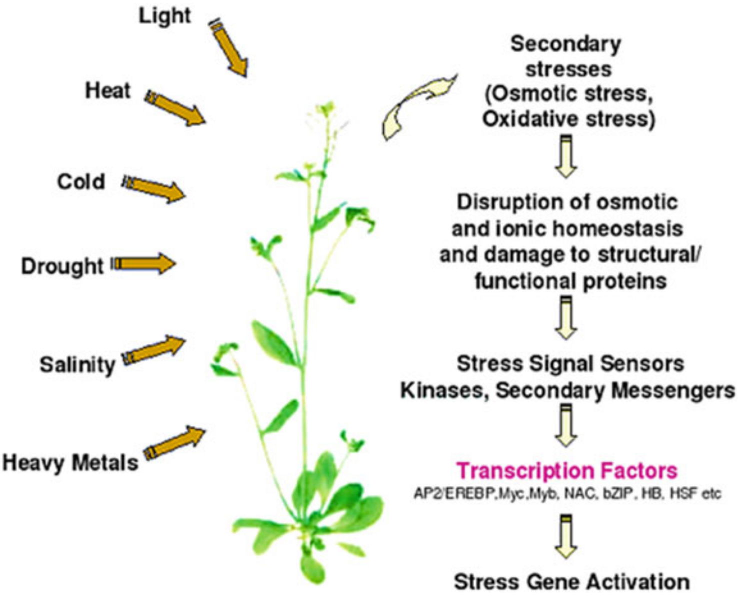

Fig. 8.6 Schematic illustration of heat-induced signal transduction mechanism and development of heat tolerance in plants

low-volume irrigation. Lodging can be prevented by installing shelterbelts against dominant winds, adopting equilibrated nitrogen fertilization, choosing a suitable plant density, and optimizing the management of pests and biotic diseases harmful to the stability and mechanic resistance of stems and roots (Mariani and Ferrante 2017).

Often, abiotic stress management is sought at genetic level by use of biotechnological tools and identification of tolerant genotypes, which is a good approach, but with the use of agronomical tools and techniques, it can offer an adequate and rapid solution for reducing crop yield losses in a sustainable manner. With the advent of global climate change and food security, the interaction with genetics and management has become crucial with the need to increase global agricultural production while maintaining the quality requirement of the market. So better crop management practices such as conservation tillage, zero tillage, and increasing water use efficiency along with the application of micronutrient and phytohormones have to be continuously revised and creating innovations in crop tolerance and genetic improvement.

8.7 Conclusion and Future Perspective

Environmental stresses (ES) are considered as major constraints to crop production due to the rapid changes in the global climate and threat to the food security along with environmental sustainability. Abiotic stresses such as drought, salinity, and high or low temperatures are among the major cause of reduced crop yield. Crop responses to this stresses are an important aspect to consider for management options. Hence, there is an urgent need to improve our understanding of the complex mechanisms associated with environmental stress tolerance and to develop elite crop varieties that are more resilient to conditions of these stresses without affecting other agronomic and quality parameters.

Therefore, plant responses and adaptation to different environmental stresses and the mechanisms underlying the development of environment stress tolerance in plants need to be better understood for important agricultural crops. Under environmental stress conditions, plants accumulate different metabolites (such as antioxidants, osmoprotectants, heat shock proteins [HSPs], etc.), and different metabolic pathways and processes are activated. These changes emphasize the importance of physiological and molecular studies to reveal the mechanisms underlying stress responses. In addition, understanding the nature of the signaling cascades and the specific genes expressed in response to environmental stresses will be valuable for developing stress tolerant plants. Molecular approaches that uncover the response and tolerance mechanisms will pave the way to engineering plants capable of tolerating environmental stresses and could be the basis for development of crop varieties capable of producing economic yields under different environmental stresses.

References

Anjum NA (2015) Plant acclimation to environmental stress: a critical appraisal. Front Plant Sci 6: 445. https://doi.org/10.3389/fpls.2015.00445

Anjum NA, Gill SS, Gill R (2014) Plant adaptation to environmental change: significance of amino acids and their derivatives, 1st edn. CABI, Wallingford. https://doi.org/10.1079/9781780642734.0317

Ashraf M (2004) Some important physiological selection criteria for salt tolerance in plants. Flora 199:361–376

Ashraf M, Shahbaz M (2003) Assessment of genotypic variation in salt tolerance of early CIMMYT hexaploid wheat germplasm using photosynthetic capacity and water relations as selection criteria. Photosynthetica 41:273–280

Bagheri A (2009) Effects of drought stress on chlorophyll, proline and rates of photosynthesis and respiration and activity of superoxide dismutase and peroxidase in millet (*Panicum milenaceum* L.). In: National conference on water scarcity and drought management in agriculture. Islamic Azad University, Arsanjan, p. 16

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

Cao Y-Y, Duan H, Yang L-N, Wang Z-Q, Zhou S-C, Yang J-C (2008) Effect of heat stress during meiosis on grain yield of rice cultivars differing in heat tolerance and its physiological mechanism. Acta Agronomica Sinica 34:2134–2142

Carden DE, Walker DJ, Flowers TJ, Miller AJ (2003) Single-cell measurements of the contributions of cytosolic Na+ and K+ to salt tolerance. Plant Physiol 131:676–683

Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K (2011) Effects of abiotic stress on plants: a systems biology perspective. BMC Plant Biol 11:163

Crosbie TM, Pearce RB (1982) Effects of recurrent phenotypic selection for high and low photosynthesis on agronomic traits in two maize populations. Crop Sci 22:809–813 da Silva EC, de Albuquerque MB, de Azevedo Neto AD, da Silva CD Jr (2013) Drought and its consequences to plants—from individual to ecosystem. InTech, Rijeka. https://doi.org/10.5772/53833

Dubey RS (2005) Photosynthesis in plants under stressful conditions. In: Pessarakli M (ed) Handbook of photosynthesis, 2nd edn. CRC Press, Florida, pp 479–497

Farooq M, Hussain M, Wahid A, Siddique KHM (2012) Drought stress in plants: an overview. In: Aroca R (ed) Plant responses to drought stress. Springer, Berlin. https://doi.org/10.1007/978-3-642-32653-0_1

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

Ghodsi M, Nuzeri M, Zarea-Fizabady A (1998) The reaction of new cultivars and Alite lines on spring wheat into drought stress, collection of abstract articles of 5th Iranian agronomy and plant breeding conference, Karaj, p 252

Gupta NK, Meena SK, Gupta S, Khandelwal SK (2002) Gas exchange, membrane permeability, and ion uptake in two species of Indian jujube differing in salt tolerance. Photosynthetica 40: 535–539

Hasanuzzaman M, Hossain MA, da Silva JAT, Fujita M (2012) In: Bandi V, Shanker AK, Shanker C, Mandapaka M (eds) Plant responses and tolerance to abiotic oxidative stress: antioxidant defenses is a key factor. In crop stress and its management: perspectives and strategies. Springer, Berlin, pp 261–316

Hasanuzzaman M, Hossain MA, Fujita M (2010a) Physiological and biochemical mechanisms of nitric oxide induced abiotic stress tolerance in plants. Am J Plant Physiol 5:295–324

Hasanuzzaman M, Hossain MA, Fujita M (2010b) Selenium in higher plants: physiological role, antioxidant metabolism and abiotic stress tolerance. J Plant Sci 5:354–375

Hasanuzzaman M, Nahar K, Fujita M (2013a) Extreme temperatures, oxidative stress and antioxidant defense in plants. In: Vahdati K, Leslie C (eds) Abiotic stress—plant responses and applications in agriculture, vol 2013. InTech, Rijeka, pp 169–205

Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M (2013b) Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci 14(5):9643–9684. https://doi.org/10.3390/ijms14059643

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular response to high salinity. Annu Rev Plant Physiol Plant Mol Biol 51:463–499

Heidaiy Y, Moaveni P (2009) Study of drought stress on accumulation and proline among aba in different genotypes forage corn. Res J Biol Sci 4:1121–1124

Janska A, Marsik P, Zelenkova S, Ovesna J (2010) Cold stress and acclimation: what is important for metabolic adjustment? Plant Biol 2010(12):395–405

Jones HG, Flowers TJ, Jones MB (1989) Plants under stress. Cambridge University Press, Cambridge

Kao WY, Tsai TT, Shih CN (2003) Photosynthetic gas exchange and chlorophyll a fluorescence of three wild soybean species in response to NaCl treatments. Photosynthetica 41:415–419

Kaur N, Gupta AK (2005) Signal transduction pathways under abiotic stresses in plants. Curr Sci 2005(88):1771–1780

Kirst GO (1989) Salinity tolerance of eukaryotic marine algae. Annu Rev Plant Physiol Plant Mol Biol 40:21–53

Kosová K, Vítámvás P, Prášil IT, Renaut J (2011) Plant proteome changes under abiotic stress-contribution of proteomics studies to understanding plant stress response. J Proteomics 2011(74):1301–1322

Lacerda CF, Cambraia J, Cano MAO, Ruiz HA, Prisco JT (2003) Solute accumulation and distribution during shoot and leaf development in two sorghum genotypes under salt stress. Environ Exp Bot 49:107–120

Levitt J (1982) Responses of plants to environmental stresses. Volume II. Water, radiation, salt, and other stresses. Academic Press, New York, p 607

Madhava Rao KV, Raghavendra AS, Janardhan RK (2006) Physiology and molecular biology of stress tolerance in plants. Springer, Dordrecht, pp 1–14

Majeed A, Nisar MF, Hussain K (2010) Effect of saline culture on the concentration of Na^+, K^+ and cl^- in *Agrostis tolonifera*. Curr Res J Biol Sci 2(1):76–82

Mariani L, Ferrante A (2017) Agronomic management for enhancing plant tolerance to abiotic stresses—drought, salinity, hypoxia, and lodging. Horticulturae 3:5. https://doi.org/10.3390/horticulturae3040052www.mdpi.com/journal/horticultura

Marschner H (1986) Mineral nutrition in higher plants. Academic Press, London, pp 477–542

Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic Press, San Diego, p 889

Mittler R, Vanderauwera S, Gollery M, Breusegem FV (2004) Reactive oxygen gene network of plants. Trends Plant Sci 9:490–498

Moreno AA, Orellana A (2011) The physiological role of the unfolded protein response in plants. Biol Res 2011(44):75–80

Muchate NS, Nikalje GC, Rajurkar NS et al (2016) Plant salt stress: adaptive responses, tolerance mechanism and bioengineering for salt tolerance. Bot Rev 82:371–406. https://doi.org/10.1007/s12229-016-9173-y

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

Munns R (2005) Genes and salt tolerance: bringing them together. New Phytol 167:645–663

Munns R, Termaat A (1986) Whole plant responses to salinity. Aust J Plant Physiol 13:143–160

Nawaz K, Hussain K, Majeed A, Khan F, Afghan S, Ali K (2010) Fatality of salt stress to plants: morphological, physiological and biochemical aspects. Afr J Biotechnol 9(34):5475–5480

Nazir N, Ashraf M, Rasul E (2001) Genomic relationships in oilseed *Brassica* with respect to salt tolerance-photosynthetic capacity and ion relations. Pak J Bot 33:483–501

Nguyen H, Lin K-H, Ho S-L, Chiang C-M, Yang C-M (2018) Enhancing the abiotic stress tolerance of plants: from chemical treatment to biotechnological approaches. Physiol Plant 164(4): 452–466. https://doi.org/10.1111/ppl.12812

Pagamas P, Nawata E (2008) Sensitive stages of fruit and seed development of chili pepper (*Capsicum annuum* L. var. Shishito) exposed to high-temperature stress. Sci Hortic 117:21–25

Parida AK, Das AB, Mittra B (2003) Effects of NaCl stress on the structure, pigment complex composition, and photosynthetic activity of mangrove *Bruguiera parviflora* chloroplasts. Photosynthetica 41:191–200

Pettigrew WT, Meredith WR (1994) Leaf gas exchange parameters vary among cotton genotypes. Crop Sci 34:700–705

Pfeiffer WH, Sayre KD, Reynolds MP (2000) Enhancing genetic grain yield potential and yield stability in durum wheat. Options Méditerranéennes 40:83–93

Porudad SS, Beg A (2003) Safflower dryland areas of Iran. In: Proceeding of 7th international conference on development drylands. 14–17 Sep, Tehran, Iran

Raza SH, Athar HR, Ashraf M, Hameed A (2007) Glycine betaine-induced modulation of antioxidant enzymes activities and ion accumulation in two wheat cultivars differing in salt tolerance. Environ Exp Bot. https://doi.org/10.1016/j.envexpbot.2006.12.009

Ruelland E, Zachowski A (2010) How plants sense temperature. Environ Exp Bot 2010(69): 225–232

Sajedi N, Sajedi AS (2008) Effect of drought stress on physiological characteristics of maize mycorrhiza and zinc. J Crop Sci 11(3):202–222

Salehi-Lisar SY, Bakhshayeshan-Agdam H (2020) Agronomic crop responses and tolerance to drought stress. In: Agronomic crops. Springer, Singapore, pp 63–91

Sayed OH (2003) Chlorophyll fluorescence as a tool in cereal crop research. Photosynthetica 41: 321–330

Schöffl F, Prandl R, Reindl A (1999) In: Shinozaki K, Yamaguchi-Shinozaki K (eds) Molecular responses to heat stress. In: Molecular responses to cold, drought, heat and salt stress in higher plants. R.G. Landes, Austin, pp 81–98

Singh RB (2012) Climate change and food security. In: Tuteja N, Gill SS, Tuteja R (eds) Improving crop productivity in sustainable agriculture. Wiley, Weinheim, pp 1–22. https://doi.org/10.1002/9783527665334.ch1

Tellah S (2016) Etude des mécanismes agrophysiologiques, morphologiques et moléculaires impliqués dans la tolérance au stress hydrique chez quelques populations locales d'arachide (*Arachis hypogaea* L.). PhD dissertation, Ecole Nationale Supérieure Agronomique. El Harrach, Alger

Tellah S, Amri-Tiliouine W, Nabi F, Sorgona A, Badiani M (2020) Ecosystem services of the crop wild relatives, in particular, food legume landraces-rhizobia association in Northern Africa and the adaptation of their genetic material to agronomic and environmental objectives. In: Amaresan N, Murugesan S, Kumar K, Sankaranarayanan A (eds) Microbial mitigation of stress responses of food legumes. CRC Press, Boca Raton, pp 25–38

Torres MA, Dangl JL (2005) Functions of the respiratory burst oxidase in biotic interactions, abiotic stress and development. Curr Opin Plant Biol 8:397–403

Valliyodan B, Nguyen HT (2006) Understanding regulatory networks and engineering for enhanced drought tolerance in plants. Curr Opin Plant Biol 2006(9):189–195

Wyn Jones RG, Gorham J, McDonnell E (1984) Organic and inorganic solute contents as selection criteria for salt tolerance in the Triticeae. In: Staples R, Toennissen GH (eds) Salinity tolerance in plants: strategies for crop improvement. Wiley, New York, pp 189–203

Role of Hormones in Crop Plants Root System Architecture Under Changing Environmental Conditions

9

Paras Porwal, Rachana Singh, and Azamal Husen

Abstract

Globally, the continuous changing environment mainly due to the natural or anthropogenic activities has limited the agricultural crop plants productivity. Like aerial plant part, the underground root architecture is also influenced under adverse situations. Root system plays an important role in terms of water, nutrient absorption, and soil anchoring, thus overall affecting the growth and yield. It has been noticed that the plant hormones for instance abscisic acid, auxins, cytokinins, ethylene, and strigolactones played an important role in regulation of root morphology. Therefore, it is believed that the root system engineering offers a new opening for sustainable crop pants production under changing environmental conditions. This chapter focuses on our current understanding of hormones involved in determining the root system architecture under changing environmental conditions.

Keywords

Crop production · Root growth · Phytohormones · Abiotic stress

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9.1 Introduction

Globally, a major part of economy is governed by the agriculture sector. Agricultural crop plant productivity is affected by abiotic (cold, heat, drought, salinity, etc.) and biotic (diseases or pests) stresses. Under these situations, crop plants are forced to make adaptation to combat with the environmental changes, which lead to changes in their physiological, metabolic, and molecular functions (Husen et al. 2014; Iqbal et al. 2015; Getnet et al. 2015; Embiale et al. 2016; Hussein et al. 2017; Yurchenko et al. 2018; Chi et al. 2019; Wang et al. 2020; Ansari et al. 2021). Hormones are known to protect and accelerates the growth and development of crop plants under water scarcity, soil salinity, temperature variation, and metal toxicity (Wang et al. 2014, 2019; Husen et al. 2016, 2017, 2018, 2019; Siddiqi and Husen 2017, 2019, 2021; Podlešáková et al. 2019, Prerostova et al. 2020; Chi et al. 2020; Heidari et al. 2020; Nolan et al. 2017, 2020).

In present scenario, it becomes a challenging task to meet growing food demand of exponentially increased population. To meet the short-term demand of food various pesticides, chemical fertilizers and many other inputs have been explored, but on long-term use, they proved to be harmful for humans and ecosystem. Though people have started working on crop improvement, but all the efforts have been channelized on aboveground traits of crop, whereas roots (hidden-half) still remains the underutilized for crop improvement (Wachsman et al. 2015). Generally, roots are not involved in carbon fixation, but they contribute significantly in overall growth and fitness of the plant. A major amount of generated photosynthetic energy is being utilized for root growth and securing soil resources. In addition to provide strength, roots are also involved in several essential processes like nutrient absorption, plant adaptation, productivity, and soil anchoring (Atkinson et al. 2014; Koevoets et al. 2016; Li et al. 2016; Gray and Brady 2016). Moreover, some root traits enable crop plants to sustain under abiotic stress conditions that have been labeled as traits of *second green revolution* (Den Herder et al. 2010). Root system plays a very decisive role in bridging the yield gap, which is composite effect of soil management practices, climate change, and genetics. Soil provides water, nutrients, and stability to the plants and is affected by several extrinsic factors. Water and nutrients are not uniformly dispersed in soil. So to utilize optimum available resources from the soil, the components of root system must be spatially arranged, which is labeled as root system architecture. Root system architecture must be able to optimize root system and can assess soil conditions to secure and forage nutrient resources while excluding toxic substances for the plant especially under abiotic stress conditions (Mickelbart et al. 2015). Therefore, identifying the root architecture development and its adaptation possesses a great potential for maintaining the productivity gap under adverse conditions of the root environment (Zhu et al. 2011). Taken together, the present chapter summarizes the role of various plant hormones in regulating the root system architecture under changing environmental conditions (Fig. 9.1).

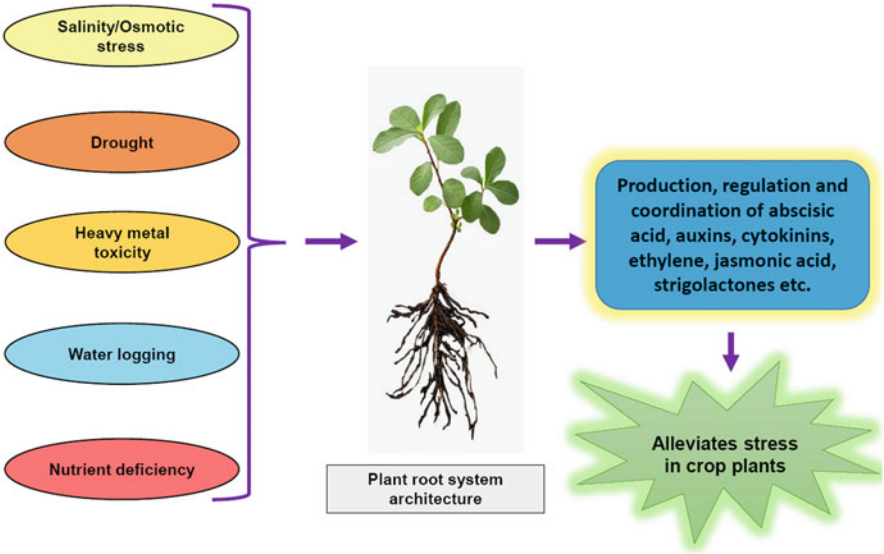

Fig. 9.1 Plant hormones in abiotic stress alleviation

9.2 Origin, Architecture, and Function of Roots

In majority of plants, the root system is divided into two parts: the primary roots and adventitious roots. Primary roots are formed embryonically (Scheres et al. 1994), and adventitious roots or secondary roots are formed post embryonically (Bellini et al. 2014). The root system of dicotyledonous plant and monocotyledonous plant are different in their arrangements. Dicots consist of tap root system in which there is well-developed main root followed by lateral roots (LR), while monocots have fibrous root system (Coudert et al. 2013). With the basic function of root to provide nutrition to the plants, they play variety of roles such as keeping the crop plants attached to the ground (Koevoets et al. 2016). They are capable to develop strategy to deal with underground pathogens (Ray et al. 2018; Elhady et al. 2018), to improve the soil nutrition, roots form symbiotic relationship with beneficial microorganisms presents in rhizosphere (Santander et al. 2017). Roots also help to search water and nutrients when they are not present in abundance (Li et al. 2016). The factors, which determine the development of plant, are habitat in which it is growing and availability of nutrients and water.

9.3 Hormones in Crop Plants Root System Architecture Under Changing Environmental Conditions

To deal with the diversity of soil, the normal root like organs of the plant evolved as complex root system. Plants show a varied variety of root system architecture depending on the species. Several changes occur in soil due to climate change like high salinity of soil, deficiencies of nutrients, and variation in water content (drought and excessive water). To deal with all kind of environmental challenges, plants develop diverse mechanisms by changing and giving flexibility in its growth and development. All these changes do not happen only phenotypically, but the complete molecular mechanism regulates the process and delegate the network of gene regulation, signal transduction, signal responses, signal sensing, and phenotype (Shao et al. 2008). Like aerial plant part, the roots also deal with all these abiotic stresses. Different abiotic stresses affect the root system architecture in several ways. They are responsible to sense various signals and respond against unfavorable conditions by synchronizing the processes inside the root tissue that activate shoot tissue, which in turn help the whole plant to adapt and deal with stresses. Along with the improvement in root, the elongated aerial parts of the plant can also be seen under abiotic stress. It is an adaptation response of crop plant to translate the stress and convert it into high yield. Overall, the development of root architecture is the core to deal with abiotic stress and adaptation of plants. There are some very critical regulators that help and control this whole process of adaptation, and they are known as phytohormones, namely, auxins, cytokinins, gibberellins, ethylene, jasmonic acid, abscisic acid, brassinosteroids, etc. Further explanation is given in the following subheadings.

Auxin

Auxins are indolic compounds and best studied phytohormone involved to deal with different stress conditions and enhance plant growth (Singh et al. 2017). Many scientists have studied on *Brassica* as a model system to understand the process of adaptation under environmental stress and by adjusting the root architecture. The phytohormone, auxin mediates this adaptation process by increasing its level (Sirrenberg et al. 2007; Schäfer et al. 2009; Hilbert et al. 2012, 2013; Lee et al. 2011; Dong et al. 2013). Similar finding was reported on the *Brassica* crops (Lee et al. 2011; Dong et al. 2013). The maintenance of auxin levels is very critical for the development of plants specifically, for the propagation of the plant root system. This control can be achieved by regulating the biochemical processes, which can modify cellular auxin levels. The genes responsible for conjugation of indole-3-acetic acid (IAA) and auxin biosynthesis, expressed in roots, play vital role in the root development process and found to be affected by various stress conditions.

Cytokinin

Cytokinin (CK) regulates organ size, tissue pattern, meristem activity, and stomatal opening and acts as a key dynamics for cell division in plants. Its function has been detected as a systemic response of numerous abiotic and biotic stress (Cortleven et al. 2019). CK triggers antioxidant defense mechanism as a response of heat and light stress. The synthesis of CK in roots decreases during stress conditions. It modulates the expression of gene in stem, thereby minimizing the adverse effect on plants (Prerostova et al. 2020).

Gibberellins

It is also a plant hormone responsible for regulating numerous activities in plant such as seed germination (breaking dormancy), flowering time, senescence, stem elongation, and seedless fruits. The decreased level of gibberellins (GA) has been reported to promote plant growth in stress conditions like cold and saline stress (osmotic stress), whereas increased level promotes plant growth under submergence and shading by interfering various signaling molecules and pathways (Colebrook et al. 2014).

Ethylene

Ethylene is a gaseous phytohormone. It is known for senescence and fruit ripening in plants. Ethylene was found to block root elongation, decrease root development by reducing cell proliferation at root apical meristem and contributed as a plant adaptation response under various stresses such as alkali stress, drought, salinity, and phosphate starvation (Arraes et al. 2015; Street et al. 2015; Li et al. 2015).

Jasmonic Acid

Jasmonic acid (JA) is needed for normal growth and stress response (molecular and physiological) of the plant. This phytohormone regulates the stomatal opening, aquaporin (water channel) expression, and root expansion and minimizes oxidative damage in plants. It has been reported to minimize the adverse effects of salinity and drought by interfering hormone signaling pathways (Riemann et al. 2015).

Abscisic Acid

Abscisic acid (ABA) is the most studied phytohormone for stress. It facilitates seed germination, regulates uptake and movement of water in plants, controls stomatal closure and opening (responsible for photosynthetic activity of plant), decreases oxidative damage under stress conditions, and ultimately amends the RSA (Harris 2015). In several research studies, it was confirmed that under drought conditions, ABA synthesis increases, which maintains the root development (Spollen et al. 2000; Sharp et al. 1994). The internal concentration of ABA is responsible for root morphology under drought conditions (Rosales et al. 2019). ABA regulates the development of lateral and primary roots and respond different under changed stress conditions like under saline conditions; it changes RSA and carry out dormancy period while after overcoming the short period of saline stress ABA again promotes the root growth (Chen et al. 2017).

Brassinosteroids (BRs)

Studies suggests that this phytohormone shows its response against several stress conditions like drought (Kagale et al. 2007; Sahni et al. 2016), is responsible for growth of plants and their development (Chen et al. 2017), and enhances waving frequency and rotation in roots of *Arabidopsis* (Lanza et al. 2012).

Strigolactones (SLs)

Strigolactones (carotenoid derivatives) are class of plant hormones that are synthesized in roots exudates and ravish to shoot by SL transporter (Kretzschmar et al. 2012). They act as an indicator molecule (endogenous and exogenous) to nutrient stress for root and shoot both in plants. SLs endogenously act as phytohormones and exogenously as in rhizosphere. In nutrient-deprived situations, SLs acts as a signaling molecule for enhancing the interaction among root system and arbuscular mycorrhizal fungi (Bouwmeester et al. 2003). Additionally, SLs regulate availability of nitrogen, phosphorus, light intensity, salinity, and drought.

Salicylic Acid (SA)

Salicylic acid (2-hydroxy benzoic acid) is well established in regulating numerous physiological and biochemical processes in plant such as photosynthesis, membrane permeability, enzymes performance, seed germination, stomatal closure, respiration, cell growth, nutrient transfer, ion absorption, fruit yield, etc. It is synthesized either by phenylalanine (occurs in cytosol) or isochorismate (occurs in chloroplast) biosynthetic pathways (Lefevere et al. 2020). SA enhances plant disease resistance and acts as a transmitter to sustain plant growth under several strains like drought, cold, heat, heavy metal, saline, and ammonia tension (Saleh and Abduljabbar 2019).

9.3.1 Hormones and Response of Root Under Salinity Stress

The plants, which can survive under saline stress, are classified as *Halophytes*, which can withstand at very high concentration of saline i.e. 200 mM NaCl (Rozema and Flowers 2008), and others, which cannot tolerate salinity and die, are classified as *Glycophytes*. However, most of the crop plants belong to glycophytes category. Therefore, salinity and alkalization of soil are reported to be most dangerous abiotic stress that limits the crop plant productivity worldwide especially when alkalization is a result of excessive sodium bicarbonate or sodium carbonate (Chen et al. 2009). Salinity of soil is a major factor for soil degradation; it occurs naturally and by human interventions such as unwarranted use of chemical fertilizers. The plants mainly deal with ionic and osmotic changes under salinity stress (Yeo et al. 1999). In saline soil, root surface is not able to uptake nutrition of potassium due to excessive sodium and chloride ion concentration. Under continuous stress of salinity, plants develop numerous changes, physiologically and biochemically. These changes depend on the duration and brutality of stress for plants. Primary root development is inhibited significantly under alkaline conditions (Li et al. 2015). Alkaline soils are depicted by inconsiderable amount of water content, low fertility, high-pitched exchangeable sodium, and pH (Lv et al. 2012).

9.3.2 Hormones and Response of Root Under Drought

Water deficiency in soil is considered as drought, and it causes imbalance of ion in cell by inhibiting the uptake of potassium ion and increase in sodium ion. The study was conducted by Farooq et al. (2015) on the crops, viz., wheat, maize, and barely. In another study, the decrease in soluble protein content was observed when sorghum and tomato plants were grown under drought condition (Chandra et al. 2007). Phytohormones play a very crucial role in modulating the growth and development of the crop plants under various stress conditions. The crop plants grown under drought conditions reported for enhanced synthesis of salicylic acid (SA) (Munne-Bosch and Penuelas 2003), due to inducible genes PR1 and PR2 under drought stress (Kang et al. 2013). The level of SA was found to increase by fivefold in *Phillyrea angustifolia* and twofold in barley roots (Bandurska and Stroiński 2005). Depending on its severity, timing, and growth stage, drought stress can affect the plants physiology, morphology, and at molecular level also. As drought stress affects the plant growth and its morphology, we can easily notice the change in leaf area, leaf number, and thickness of leaf and shortening of shoots. Roots play a key role for the crop plant to survive under drought condition that can be determined by the root growth, size, proliferation, and density (Ball et al. 1994).

9.3.3 Hormones and Response of Root Under Heavy Metal Stress

The sudden increase of the heavy metal pollution due to various anthropogenic activities in our surrounding environment such as waste processing and sewage mining is a matter of concern and a big threat to food security and natural ecosystem worldwide (Ayangbenro and Babalola 2017; Harguinteguy et al. 2016). Heavy metal is of two types, i.e., essential and nonessential metals. The essential metals such as iron (Fe), zinc (Zn), nickel (Ni), selenium (Se), copper (Cu), manganese (Mn), and molybdenum (Mo) have their substantial role in many cellular, redox reactions, and pigment synthesis (Chaffai and Koyama 2011), while nonessential metals such as arsenic (As), cadmium (Cd), silver (Ag), chromium (Cr), mercury (Hg), and lead (Pb) have no contribution in any of the biological processes but are known to impose their toxic effects even at very low concentration such as deterioration of soil quality and reduced plant growth, thereby affecting health and productivity of the plants (Seth 2012). These nonessential heavy metals interfere numerous physicochemical reactions by altering biomolecules and regulatory proteins and causes toxicity by increasing oxidative stress that induces overproduction of reactive oxygen species (ROS), which leads to apoptosis and results in membrane peroxidation, DNA, RNA damage, enzyme inhibition, and protein oxidation in the plants (Choppala et al. 2014; Shahid et al. 2014). The negative aspects of heavy metal toxicity on the plants are reduction in photosynthetic rate, chlorophyll content, stomatal conductance, transpiration rate, water absorption by roots, necrosis, chlorosis, cellular membranes breakage, and many more. The uptake of these heavy metals in the plants are performed by the cortical cells of the root, while its movement to the root surface depends upon diffusion mechanism, root interception, mass flow (Anjum et al. 2012), and movement from root to shoot occurs through xylem. Generally, plants utilize two types of strategy to avoid heavy metal stress, i.e., avoidance and tolerance (intra/extra cellular detoxification). Avoidance strategy restrict the metal uptake into the plant through the root tissues (first line of extracellular defense) through the strategies such as secreting organic acids that can bind metals, rhizosphere pH alteration, developing redox barrier, mycorrhiza immobilization, complexation via root exudates, etc. Moreover, plant roots also produce carbohydrates, amino acids (organic acids), inorganic ions, water, CO_2, mucilaginous substances, allelopathic compounds, siderophores etc. that are commonly known as root exudates. These root exudates form the stable ligand in the polluted soil and convert the metal into least toxic (external detoxification) (Dalvi and Bhalerao 2013). In case of internal detoxification, the chelation occurs in the cytosol through organic acid that transform metal ion into less toxic (Sunitha et al. 2013). As a result of adaptation to metal toxicity and involvement in defense signaling pathways, increased synthesis rate of various hormones like salicylic acid, gibberellic acid, ethylene, and jasmonic acid has been observed (Peleg and Blumwald 2011).

9.3.4 Hormones and Response of Root Under Nutrient Stress

Generally, plant utilizes macromolecules such as nitrogen (N) and phosphorus (P) for their protein and nucleic acid formation, while other nutrients facilitate membrane transport and cofactors for various enzymes. The inability of crop plant to uptake nutrient from the soil leads to nutrient stress, like the phosphate availability to crop plant decreases under increased salinity (Hu and Schmidhalter 2005). Nutrient insufficiency in soil and crop plant might be due to various reasons such as soil pH, composition, and disproportion of nutrients due to leaching (due to vertical water flow) and plant cycling. Leaching causes the mobile nutrient such as nitrate and chloride to pile up in deeper soil strata over time while plant cycling drain low mobile nutrients such as phosphate and potassium from root zone and bring together in topsoil (Koevoets et al. 2016). Plants can adapt in their root architecture to scrounge soil parts in which nutrient availability is eminent. Each nutrient deficiency have its separate response that leads to adaptation and changes in the root system architecture such as *Arbidopsis* developing on agar plates (Gruber et al. 2013)

Nitrogen Deficiency

Being highly mobile, nitrate is much susceptible for leaching as compared with phosphate. Poor nitrate accessibility limits crop plant growth but does not obstruct lateral and primary root elongation, thereby strengthening the root system to penetrate deep layers of soil causing increase in root to shoot ratio (Gruber et al. 2013). In maize (*Zea mays* L.) root system consists of primary, seminal, and crown roots. The deep root system proved to enhance nitrogen acquisition in plants like in maize, reduced number of crown roots (shoot-borne roots), and penetrate 45% more in deep soil (Saengwilai et al. 2014). In general, the density of lateral roots (LR) is not affected in fixed nitrate limitation. However, strong increase in density of LR was observed in maize and *Arabidopsis* under heterogeneous environment (Dinaint Zandt et al. 2015). Drew (1975) also reported strong proliferation of LR when barley was grown under high concentration of nitrate, potassium, phosphate, and ammonium and limited growth in other zones. It is proved from numerous research studies that crop plants are efficient to locate their root system in nutrient rich soil. NRT1.1 (nitrate transporter) transports auxin; high nitrate concentration prevents auxin out of lateral root tips leading it to accumulate and stimulate lateral roots growth (Mounier et al. 2014). On the other hand, nitrate deficiency can induce high-affinity nitrate transporter gene (NRT2.1) and galvanize ethylene production (Zheng et al. 2013).

Phosphorus Deficiency

The decaying of organic matter is the chief source of phosphorus in soil. It constitutes the elementary structure in plants such as nucleic acids (DNA and RNA) and phospholipid membranes (Shen et al. 2011). Due to high plant cycling and low mobility, it is found in the upper strata of soil. The plant needs phosphorus in high quantity; any limitation to it directly influences the aquaporin (water channels) activity plant and ultimately uptake of water through roots. Aquaporin are regarded as the plumber system of plants that facilitate transport of water between the cells when they are in phosphorylated state (Wang et al. 2016). In root system architecture, increase in lateral roots, root hairs, and decrease in main root have been observed when plants such as maize, rice, and *Arabidopsis* were grown in phosphate deficit soil leading to develop shallow root system (Kawa et al. 2016). It was reported that roots of apple (*Malus domestica*) can survive in drought and phosphorus deficit soil by modulating the molecular expression of some phosphorus-related transporter genes of Sun et al. (2017). During starvation of either nitrogen or phosphorus synthesis of SL, hormone is increased and an adaptation response development of shoot is stopped, while root system continue engrossing nutrient from the soil (Marzec et al. 2013). In *Arabidopsis*, under optimum availability of phosphate, strigolactones impede elongation of lateral roots and foster elongation of primary roots, whereas reverse is reported under phosphate insufficiency (Matthys et al. 2016). Thus, it can be concluded that nutrients availability such as nitrogen or phosphorus regulates strigolactone function to mold root system architecture.

9.4 Conclusions and Future Outlook

Over the years, a considerable progress has been attained to uncover the root system response and phytohormones role in understanding the physiological, biochemical, and molecular mechanism under numerous stressed conditions, but still more research work is needed to explore the untapped attributes like the importance of root exudates especially the change in their concentration against stressed conditions (drought, salinity, and nutrient deficiency), hormone signaling, various receptors, intervening produce, and their interaction with other signal molecules (crosstalk mechanisms) present in the root structure. In future, stress resistant/tolerant variety of plants can be developed by better understanding the adaptation/tolerance strategies of plant, and communication between roots and shoot of the plant under stressed conditions in terms of hormone regulation, managing transportation and storing water in tissues, morphological variations in root, reducing nutrient requirement, and oxidative damage by free radicals.

References

Anjum NA, Pereira ME, Ahmad I, Duarte AC, Umar S, Khan NA (2012) Phytotechnologies: remediation of environmental contaminants. CRC Press, New York

Ansari MKA, Ahmad A, Umar S, Iqbal M, Zia MH, Husen A, Owens G (2021) Suitability of Indian mustard genotypes for phytoremediation of mercury-contaminated sites. S Afr J Bot 142:12–18. https://doi.org/10.1016/j.sajb.2021.05.011

Arraes FBM, Beneventi MA, Lisei de Sa ME, Paixao JFR, Albuquerque EVS, Marin SRR, Purgatto E, Nepomuceno AL, Grossi-de-Sa MF (2015) Implications of ethylene biosynthesis and signaling in soybean drought stress tolerance. BMC Plant Biol 15:1–20

Atkinson JA, Rasmussen A, Traini R, Voss U, Sturrock C, Mooney SJ, Wells DM, Bennett MJ (2014) Branching out in roots: uncovering form, function, and regulation. Plant Physiol 166: 538–550

Ayangbenro A, Babalola O (2017) A new strategy for heavy metal polluted environments: a review of microbial biosorbents. Int J Environ Res Public Health 14(1):94

Ball RA, Oosterhuis DM, Mauromoustakos A (1994) Growth dynamics of the cotton plant during water-deficit stress. Agron J 86:788–795

Bandurska H, Stroiński A (2005) The effect of salicylic acid on barley response to water deficit. Acta Physiol Plant 27:379–386

Bellini C, Pacurar DI, Perrone I (2014) Adventitious roots and lateral roots: similarities and differences. Annu Rev Plant Biol 65:639–666

Bouwmeester HJ, Matusova R, Zhongkui S, Beale MH (2003) Secondary metabolite signalling in host–parasitic plant interactions. Curr Opin Plant Biol 6(4):358–364. https://doi.org/10.1016/S1369-5266(03)00065-7

Chaffai R, Koyama H (2011) Heavy metal tolerance in *Arabidopsis thaliana*. In: Advances in botanical research. Academic Press, Amsterdam, pp 1–49

Chandra A, Anand A, Dubey A (2007) Effect of salicylic acid on morphological and biochemical attributes in cowpea. J Environ Biol 28:193–196

Chen WC, Cui PJ, Sun HY, Guo WQ, Yang CW, Jin H, Fang B, Shi DC (2009) Comparative effects of salt and alkali stresses on organic acid accumulation and ionic balance of seabuckthorn (*Hippophae rhamnoides* L.). Ind Crop Prod 30:351–358

Chen Y, Feng L, Wei N, Liu ZH, Hu S, Li XB (2017) Overexpression of cotton PYL genes in *Arabidopsis* enhances the transgenic plant tolerance to drought stress. Plant Physiol Biochem 115:229–238

Chi C, Li X, Fang P, Xia X, Shi K, Zhou Y, Zhou J, Yu J (2020) Brassinosteroids act as a positive regulator of NBR1-dependent selective autophagy in response to chilling stress in tomato. J Exp Bot 71(3):1092–1106. https://doi.org/10.1093/jxb/erz466

Chi YH, Koo SS, Oh HT, Lee ES, Park JH, Phan KT, Wi SD, Bae SB, Paeng SK, Chae HB, Kang CH, Kim MG, Kim W-Y, Yun D-J, Lee SY (2019) The physiological functions of universal stress proteins and their molecular mechanism to protect plants from environmental stresses. Front Plant Sci 10:750

Choppala G, Saifullah BN, Bibi S, Iqbal M, Rengel Z, Kunhikrishnan A, Ashwath N, Ok YS (2014) Cellular mechanisms in higher plants governing tolerance to cadmium toxicity. Crit Rev Plant Sci 33(5):374–391. https://doi.org/10.1080/07352689.2014.903747

Colebrook EH, Thomas SG, Phillips AL, Hedden P (2014) The role of gibberellin signalling in plant responses to abiotic stress. J Exp Biol 217(1):67–75. https://doi.org/10.1242/jeb.089938

Cortleven A, Leuendorf JE, Frank M, Pezzetta D, Bolt S, Schmülling T (2019) Cytokinin action in response to abiotic and biotic stresses in plants. Plant Cell Environ 42(3):998–1018. https://doi.org/10.1111/pce.13494

Coudert Y, Le-Thi A, Gantet P (2013) Rice: a model plant to decipher the hidden origin of adventitious roots. In: Plant roots: the hidden half, 4th edn, pp 145–154

Dalvi AA, Bhalerao SA (2013) Response of plants towards heavy metal toxicity: an overview of avoidance, tolerance and uptake mechanism. Ann Plant Sci 2(09):362–368

Den Herder G, Van Isterdael G, Beeckman T, De Smet I (2010) The roots of a new green revolution. Trends Plant Sci 15(11):600–607

Dinaint Zandt D, Marié C, Kirchgessner N, EJW V, Hund A (2015) High-resolution quantification of root dynamics in split-nutrient rhizoslides reveals rapid and strong proliferation of maize roots in response to local high nitrogen. J Exp Bot 66:5507–5517. https://doi.org/10.1093/jxb/erv307

Dong S, Tian Z, Chen PJ, Senthil KR, Shen CH, Cai D, Oelmüller R, Yeh KW (2013) The maturation zone is an important target of *Piriformospora indica* in Chinese cabbage roots. J Exp Bot 64:4529–4540

Drew MC (1975) Comparison of the effects of a localised supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. New Phytol 75:479–490. https://doi.org/10.1111/j.1469-8137.1975.tb01409.x

Elhady A, Adss S, Hallmann J, Heuer H (2018) Rhizosphere microbiomes modulated by pre-crops assisted plants in defense against plant-parasitic nematodes. Front Microbiol 2018:9. https://doi.org/10.3389/fmicb.2018.01133

Embiale A, Hussein M, Husen A, Woldemariam S, Mohammed K (2016) Differential sensitivity of *Pisum sativum* L. cultivars to water-deficit stress: changes in growth, water status, chlorophyll fluorescence and gas exchange attributes. J Agron 15(2):45–57. https://doi.org/10.3923/ja.2016

Farooq M, Hussain M, Wakeel A, Siddique KHM (2015) Salt stress in maize: Effects, resistance mechanisms, and management. A review. Agron Sustain Dev 35:461–481

Getnet Z, Husen A, Fetene M, Yemata G (2015) Growth, water status, physiological, biochemical and yield response of stay green sorghum (*Sorghum bicolor* (L.) Moench) varieties-a field trial under drought-prone area in Amhara regional state, Ethiopia. J Agron 14(4):188–202. https://doi.org/10.3923/ja.2015.188.202

Gray SB, Brady SM (2016) Plant developmental responses to climate change. Dev Biol 419:64–77

Gruber BD, Giehl RFH, Friedel S, von Wirén N (2013) Plasticity of the *Arabidopsis* root system under nutrient deficiencies. Plant Physiol 163:161–179. https://doi.org/10.1104/pp.113.218453

Harguinteguy CA, Cofré MN, Fernández-Cirelli A, Pignata ML (2016) The macrophytes *Potamogeton pusillus* L. and *Myriophyllum aquaticum* (Vell.) Verdc. as potential bioindicators of a river contaminated by heavy metals. Microchem J 124:228–234

Harris JM (2015) Abscisic acid: hidden architect of root system structure. Plan Theory 4:548–572

Heidari P, Mazloomi F, Nussbaumer T, Barcaccia G (2020) Insights into the SAM synthetase gene family and its roles in tomato seedlings under abiotic stresses and hormone treatments. Plants 9(5):586. https://doi.org/10.3390/plants9050586

Hilbert M, Nostadt R, Zuccaro A (2013) Exogenous auxin affects the oxidative burst in barley roots colonized by *Piriformospora indica*. Plant Signal Behav 8:e23572. https://doi.org/10.4161/psb.23572

Hilbert M, Voll LM, Ding Y, Hofmann J, Sharma M, Zuccaro A (2012) Indole derivative production by the root endophyte *Piriformospora indica* is not required for growth promotion but for biotrophic colonization of barley roots. New Phytol 196:520–534

Hu Y, Schmidhalter U (2005) Drought and salinity: a comparison of their effects on mineral nutrition of plants. J Plant Nutr Soil Sci 168:541–549. https://doi.org/10.1002/jpln.200420516

Husen A, Iqbal M, Aref I (2016) IAA-induced alteration in growth and photosynthesis of pea (*Pisum sativum* L.) plants grown under salt stress. J Environ Biol 37(3):421–429

Husen A, Iqbal M, Aref I (2017) Plant growth and foliar characteristics of faba bean (*Vicia faba* L.) as affected by indole-acetic acid under water-sufficient and water-deficient conditions. J Environ Biol 38:179–186. https://doi.org/10.22438/jeb/38/2/MS-247

Husen A, Iqbal M, Aref IM (2014) Growth, water status, and leaf characteristics of *Brassica carinata* under drought and rehydration conditions. Rev Bras Bot 37(3):217–227. https://doi.org/10.1007/s40415-014-0066-1

Husen A, Iqbal M, Khanam N, Aref I, Sohrab S, Masresha G (2019) Modulation of salt-stress tolerance of niger (*Guizotia abyssinica*), an oil seed plant, by application of salicylic acid. J Environ Biol 40:96–104. https://doi.org/10.22438/jeb/40/1/MRN-808

Husen A, Iqbal M, Sohrab SS, Ansari MKA (2018) Salicylic acid alleviates salinity-caused damage to foliar functions, plant growth and antioxidant system in Ethiopian mustard (*Brassica carinata* a. Br.). Agric Food Secur 7:44. https://doi.org/10.1186/s40066-018-0194-0

Hussein M, Embiale A, Husen A, Aref I, Iqbal M (2017) Salinity-induced modulation of plant growth and photosynthetic parameters in faba bean (*Vicia faba*) cultivars. Pak J Bot 49:867–877

Iqbal M, Ahmad A, Ansari MKA, Qureshi MI, Aref IM, Khan PR, Hegazy SS, El-Atta H, Husen A, Hakeem KR (2015) Improving the phytoextraction capacity of plants to scavenge metal(loid)-contaminated sites. Environ Rev 23(1):44–65. https://doi.org/10.1139/er-2014-0043

Kagale S, Divi UK, Krochko JE, Keller WA, Krishna P (2007) Brassinosteroid confers tolerance in *Arabidopsis thaliana* and *Brassica napus* to a range of abiotic stresses. Planta 225:353–364

Kang GZ, Li GZ, Liu GQ, Xu W, Peng XQ, Wang CY (2013) Exogenous salicylic acid enhances wheat drought tolerance by influence on the expression of genes related to ascorbate-glutathione cycle. Biol Plant 57:718–724

Kawa D, Julkowska M, Montero Sommerfeld H, Horst AT, Haring MA, Testerink C (2016) Phosphate-dependent root system architecture responses to salt stress. Plant Physiol 172:690–706

Koevoets IT, Venema JH, Elzenga JTM, Testerink C (2016) Roots withstanding their environment: exploiting root system architecture responses to abiotic stress to improve crop tolerance. Front Plant Sci 2016:7. https://doi.org/10.3389/fpls.2016.01335

Kretzschmar T, Kohlen W, Sasse J, Borghi L, Schlegel M, Bachelier JB, Reinhardt D, Bours R, Bouwmeester HJ, Martinoia E (2012) A petunia ABC protein controls strigolactone-dependent symbiotic signalling and branching. Nature 483(7389):341–344. https://doi.org/10.1038/nature10873

Lanza M, Garcia-Ponce B, Castrillo G, Catarecha P, Sauer M, Rodriguez-Serrano M, Páez-García A, Sánchez-Bermejo E, Tc M, Leo del Puerto Y et al (2012) Role of actin cytoskeleton in brassinosteroid signaling and in its integration with the auxin response in plants. Dev Cell 22:1275–1285

Lee YC, Johnson JM, Chien CT, Sun C, Cai D, Lou B, Oelmüller R, Yeh KW (2011) Growth promotion of Chinese cabbage and *Arabidopsis* by *Piriformospora indica* is not stimulated by mycelium-synthesized auxin. Mol Plant Microbe Interact 24:421–431

Lefevere H, Bauters L, Gheysen G (2020) Salicylic acid biosynthesis in plants. Front Plant Sci 11:338

Li J, Xu HH, Liu WC, Zhang XW, Lu YT (2015) Ethylene inhibits root elongation during alkaline stress through AUXIN1 and associated changes in AUXIN accumulation. Plant Physiol 168:1777–1791

Li X, Zeng R, Liao H (2016) Improving crop nutrient efficiency through root architecture modifications. J Integr Plant Biol 58:193–202

Lv DK, Ge Y, Jia B, Bai X, Bao PH, Cai H, Wei J, Zhu YM (2012) miR167c is induced by high alkaline stress and inhibits two auxin response factors in *Glycine soja*. J Plant Biol 55:373–380

Marzec M, Muszynska A, Gruszka D (2013) The role of strigolactones in nutrient-stress responses in plants. Int J Mol Sci 14:9286–9304

Matthys C, Walton A, Struk S, Stes E, Boyer FD, Gevaert K, Goormachtig S (2016) The whats, the wheres and the hows of strigolactone action in the roots. Planta 243(6):1327–1337. https://doi.org/10.1007/s00425-016-2483-9

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

Mounier E, Pervent M, Ljung K, Gojon A, Nacry P (2014) Auxin-mediated nitrate signalling by NRT1.1 participates in the adaptive response of *Arabidopsis* root architecture to the spatial heterogeneity of nitrate availability. Plant Cell Environ 37:162–174. https://doi.org/10.1111/pce.12143

Munne-Bosch S, Penuelas J (2003) Photo and antioxidative protection, and a role for salicylic acid during drought and recovery in field grown *Phillyrea angustifolia* plants. Planta 217:758–766

Nolan T, Chen J, Yin Y (2017) Cross-talk of Brassinosteroid signaling in controlling growth and stress responses. Biochem J 474(16):2641–2661. https://doi.org/10.1042/BCJ20160633

Nolan TM, Vukašinović N, Liu D, Russinova E, Yin Y (2020) Brassinosteroids: multidimensional regulators of plant growth, development, and stress responses. Plant Cell 32(2):295–318. https://doi.org/10.1105/tpc.19.00335

Peleg Z, Blumwald E (2011) Hormone balance and abiotic stress tolerance in crop plants. Curr Opin Plant Biol 14(3):290–295

Podlešáková K, Ugena L, Spíchal L, Doležal K, De Diego N (2019) Phytohormones and polyamines regulate plant stress responses by altering GABA pathway. N Biotechnol 48:53–65. https://doi.org/10.1016/j.nbt.2018.07.003

Prerostova S, Dobrev PI, Kramna B, Gaudinova A, Knirsch V, Spichal L, Zatloukal M, Vankova R (2020) Heat acclimation and inhibition of cytokinin degradation positively affect heat stress tolerance of *arabidopsis*. Front Plant Sci 11:87

Ray S, Mishra S, Bisen K, Singh S, Sarma BK, Singh HB (2018) Modulation in phenolic root exudate profile of *Abelmoschus esculentus* expressing activation of defense pathway. Microbiol Res 207:100–107

Riemann M, Dhakarey R, Hazman M, Miro B, Kohli A, Nick P (2015) Exploring Jasmonates in the hormonal network of drought and salinity responses. Front Plant Sci 6:1077

Rosales MA, Maurel C, Nacry P (2019) Abscisic acid coordinates dose-dependent developmental and hydraulic responses of roots to water deficit. Plant Physiol 180:2198–2211

Rozema J, Flowers T (2008) Ecology: crops for a salinized world. Science 322(5907):1478–1480

Saengwilai P, Tian X, Lynch JP (2014) Low crown root number enhances nitrogen acquisition from low-nitrogen soils in maize. Plant Physiol 166:581–589. https://doi.org/10.1104/pp.113.232603

Sahni S, Prasad BD, Liu Q, Grbic V, Sharpe A, Singh SP, Krishna P (2016) Overexpression of the brassinosteroid biosynthetic gene DWF4 in *Brassica napus* simultaneously increases seed yield and stress tolerance. Sci Rep 6:1–14

Saleh A, Abduljabbar I (2019) Review on the role of salicylic acid in plants. In: Hasanuzzaman M (ed) Sustainable crop production, 1st edn. IntechOpen, London, pp 1–6

Santander C, Aroca R, Ruiz-Lozano JM, Olave J, Cartes P, Borie F, Cornejo P (2017) Arbuscular mycorrhiza effects on plant performance under osmotic stress. Mycorrhiza 27:639–657

Schäfer P, Pfiffi S, Voll LM, Zajic D, Chandler PM, Waller F, Scholz U, Pons-Kühnemann J, Sonnewald S, Sonnewald U, Kogel KH (2009) Manipulation of plant innate immunity and gibberellin as factor of compatibility in the mutualistic association of barley roots with *Piriformospora indica*. Plant J 59:461–474

Scheres B, Wolkenfelt H, Willemsen V, Terlouw M, Lawson E, Dean C, Weisbeek P (1994) Embryonic origin of the *Arabidopsis* primary root and root meristem initials. Development 120: 2475–2487

Seth CS (2012) A review on mechanisms of plant tolerance and role of transgenic plants in environmental cleanup. Bot Rev 78(1):32–62

Shahid M, Pourrut B, Dumat C, Nadeem M, Aslam M, Pinelli E (2014) Heavy-metal-induced reactive oxygen species: phytotoxicity and physicochemical changes in plants. Rev Environ Contam 232:1–44

Shao H, Chu L, Jaleel CA, Zhao C (2008) Water-deficit stress-induced anatomical changes in higher plants. C R Biol 331(3):215–225. https://doi.org/10.1016/j.crvi.2008.01.002

Sharp RE, Wu Y, Voetberg GS, Aab IN, LeNoble ME (1994) Confirmation that abscisic acid accumulation is required for maize primary root elongation at low water potentials. J Exp Bot 45:1743–1751

Shen J, Yuan L, Zhang J, Li H, Bai Z, Chen X, Zhang W, Zhang F (2011) Phosphorus dynamics: from soil to plant. Plant Physiol 156:997–1005

Siddiqi KS, Husen A (2017) Plant response to strigolactones: current developments and emerging trends. Appl Soil Ecol 120:247–253. https://doi.org/10.1016/j.apsoil.2017.08.020

Siddiqi KS, Husen A (2019) Plant response to jasmonates: current developments and their role in changing environment. Bull Natl Res Cent 43(1):153. https://doi.org/10.1186/s42269-019-0195-6

Siddiqi KS, Husen A (2021) Significance of brassinosteroids and their derivatives in the development and protection of plants under abiotic stress. Biologia 76:2837–2857. https://doi.org/10.1007/s11756-021-00853-3

Singh M, Gupta A, Laxmi A (2017) Striking the right chord: signaling enigma during root. Front Plant Sci 2017:8

Sirrenberg A, Göbel C, Grond S, Czempinski N, Ratzinger A, Karlovsky P, Santos P, Feussner I, Pawlowski K (2007) *Piriformospora indica* affects plant growth by auxin production. Physiol Plant 131:581–589. https://doi.org/10.1111/j.1399-3054.2007.00983.x

Spollen WG, Lenoble ME, Samuels TD, Bernstein N, Sharp RE (2000) Abscisic acid accumulation maintains maize primary root elongation at low water potentials by restricting ethylene production. Plant Physiol 122:967–976

Street IH, Aman S, Zubo Y, Ramzan A, Wang X, Shakeel SN, Kieber JJ, Eric Schaller G (2015) Ethylene inhibits cell proliferation of the *Arabidopsis* root meristem. Plant Physiol 169:338–350

Sun T, Li M, Shao Y, Yu L, Ma F (2017) Comprehensive genomic identification and expression analysis of the phosphate transporter (PHT) gene family in apple. Front Plant Sci 8:426. https://doi.org/10.3389/fpls.2017.004266

Sunitha MS, Prashant S, Kumar SA, Rao S, Narasu ML, Kishor PK (2013) Cellular and molecular mechanisms of heavy metal tolerance in plants: a brief overview of transgenic plants overexpressing phytochelatin synthase and metallothionein genes. Plant Cell Biotechnol Mol Biol 14(1–2):33–48

Wachsman G, Sparks EE, Benfey PN (2015) Genes and networks regulating root anatomy and architecture. New Phytol 208(1):26–38. https://doi.org/10.1111/nph.13469

Wang M, Ding L, Gao L, Li Y, Shen Q, Guo S (2016) The interactions of aquaporins and mineral nutrients in higher plants. Int J Mol Sci 17(8):1229. https://doi.org/10.3390/ijms17081229

Wang S-Q, Zhao H-H, Zhao L-M, Gu C-M, Na Y-G, Xie B, Cheng S-H, Pan G-J (2020) Application of brassinolide alleviates cold stress at the booting stage of rice. J Integr Agric 19(4):975–987. https://doi.org/10.1016/S2095-3119(19)62639-0

Wang W, Bai M-Y, Wang Z-Y (2014) The brassinosteroid signaling network—a paradigm of signal integration. Curr Opin Plant Biol 21:147–153. https://doi.org/10.1016/j.pbi.2014.07.012

Wang Y-T, Chen Z-Y, Jiang Y, Duan B-B, Xi Z-M (2019) Involvement of ABA and antioxidant system in brassinosteroid-induced water stress tolerance of grapevine (*Vitis vinifera* L.). Sci Hortic 256:108596. https://doi.org/10.1016/j.scienta.2019.108596

Yeo AR, Flowers SA, Rao G, Welfre K, Senanayake N, Flowers TJ (1999) Silicon reduces sodium uptake in rice (*Oryza sativa* L.) in saline conditions and this is accounted for by a reduction in the transpirational bypass flow. Plant Cell Environ 22:559–565

Yurchenko O, Kimberlin A, Mehling M, Koo AJ, Chapman KD, Mullen RT, Dyer JM (2018) Response of high leaf-oil *Arabidopsis thaliana* plant lines to biotic or abiotic stress. Plant Signal Behav 13(5):e1464361. https://doi.org/10.1080/15592324.2018.1464361

Zheng D, Han X, An Y, Guo H, Xia X, Yin W (2013) The nitrate transporter NRT2.1 functions in the ethylene response to nitrate deficiency in *Arabidopsis*. Plant Cell Environ 36:1328–1337

Zhu J, Ingram PA, Benfey PN, Elich T (2011) From lab to field, new approaches to phenotyping root system architecture. Curr Opin Plant Biol 14:310–317. https://doi.org/10.1016/j.pbi.2011.03.020

Water Logging Tolerance and Crop Productivity

10

Varucha Misra and Mohammad Israil Ansari

Abstract

Water logging is a frequently occurring event, which is accompanied by heavy rainfall and has a negative impact on crop productivity by reducing productivity by 80%. Higher losses in productivity are seen in sensitive crops than tolerant crops in respect to water logging stress. Plant growth and development (at different growth stages) respond differently to water logging stress. At times, a longer time duration of water logging causes plant death. Nutrient uptake is highly hampered in plants under such stress. Carbon assimilation and transpiration rate are also reduced in plants exposed to water logging. Water logging stress creates hypoxia or anoxia condition for the plant due to which alterations in different traits is seen. Switch in plant biochemical and metabolic traits are commonly observed in plants exposed to water logging. Roots are the first part of the plant, which is exposed to this stress, and rooting adaptations under this condition help in plant survival. Formation of aerial roots, aerenchyma development, and higher production of ethylene are some characteristics of tolerant cultivars against water logging conditions. We focus on plant responses toward water logging condition, how the hypoxia or anoxia condition is induced, the mechanism involved in tolerant plant cultivars, and various strategies that a plant adopt for its survival under this stress.

Keywords

Water logging · Adaptation · Plant · Hypoxia · Anoxia

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10.1 Introduction

Water logging is a concerning problem all over the world due to the changing climate, which has emerged out in the recent past. The problem of water logging is affecting various soils to a less or greater extent. In Russia, agricultural lands are being affected by water logging by 10%, while in the United States, it is 16% and in India, Bangladesh, Pakistan, and China, soils are affected by water logging by 10% (Food and Agriculture Organization 2015; Yaduvanshi et al. 2014). Furthermore, water logging also causes a strong impact on the yield of various agricultural crops like lentils, barley, etc. (Solaiman et al. 2007; Romina et al. 2018). Hossain and Uddin (2011) had revealed that ten million hectares to 15 million hectares of land were being affected annually by water logging, and loss in wheat yield ranges between 20% and 50%. Marashi and Chinchanikar (2010) had illustrated that the average yield loss in wheat crop due to water logging was 71.6 kg per hectare implying that for every one day of water logging, 1.5% loss in yield was reported. Also, apparent yield losses in wheat crop due to water logging was known to range between 0% and 38% along with the reduction in nitrogen uptake by the crop (0%–40%) (Robertson et al. 2019). In soybean crops, productivity is affected by water logging by 17%–43% at the vegetative stage while 50%–56% at the reproductive stage (Oosterhuis et al. 1990). Shannon et al. (2005) had also reported that variation in yield in tolerant and sensitive soybean varieties was seen under water logging conditions. In tolerant varieties, reduction in yield was 39%, while in sensitive ones, the yield was reduced by 77% at the R_1 stage of growth, while Rhine et al. (2010) had shown that at the R_5 growth stage, reduction in yield loss was of 20%–39% under water logging condition. In corn crop, reduction in yield was seen by 0.57 Mg ha^{-1} d^{-1} under water logging condition at V_6 stage of crop; however, Urban et al. (2015) had revealed that water logging caused the decline of 1%–3% in the yield during spring season in 62 years study report. Besides, in cereal crops, several studies had showed that yield loss due to water logging ranges from 0% to <80% (MacEwan et al. 1992; Setter 2000). In the sugarcane crops, reduction in yield due to water logging was reported by 15%–45% (Gomathi et al. 2015). Misra et al. (2016) had reported that in postharvest deterioration aspect under waterlogging condition, reduction in sucrose percentage by 2.82 units, and 1.51 units in November and March harvest. This decline causes a strong impact on the yield of the crop.

Water is a necessary commodity for plant growth and development, but excess water is harmful to it. When the excess amount of water present in soil restricts the diffusion of gas, it is termed as water logging condition (Setter and Waters 2003), and the plant grown under such condition is known as a waterlogged plant. There is often a misconception of flooding and water logging conditions to be more or less the same but in fact both the terms though define excess amount of water; however, they are completely different. Flooding or submergence is the one where either some parts or whole shoot is submerged or covered underwater (Sasidharan et al. 2017), while water logging implies that the root system of the plant inside the soil is affected by an excess of water. Further, in flooding condition, depletion of the oxygen concentration rapidly occur leading to hypoxia conditions (Lee et al. 2011; Vashisht et al. 2011). This causes no proper exchange of oxygen and carbon dioxide through stomata, which results in a hindrance of heterotrophic energy production in mitochondria. Besides, reduced carbon dioxide content also causes a reduction in photosynthesis. Armstrong (1979) had illustrated that oxygen deficiency created by water logging conditions is due to reduce solubility and oxygen diffusion rate. Occurrence of water logging is affecting agricultural crops worldwide annually wherein major constraints are imposed on roots causing a negative effect on yield and production (Jackson 2004). The occurrence of water logging condition is due to heavy monsoon rainfall, poor drainage system, and irrigation practices. Under such a situation, oxygen diffusivity in water is nearly 10,000 times much slower compared with oxygen diffusivity in air, while flux of oxygen is also reduced to nearly 3,20,000 times when soil pores contain water rather than when it contains gas (Colmer and Flowers 2008; Armstrong and Drew 2002a, b). Inadequate supply of oxygen to submerge tissues of the plant under such conditions is the main reason for harm in plants. This is resulted due to the combination of speedy consumption of oxygen by the microorganisms present in soil and slow diffusion of gases. The anaerobic environment is known to initiate within a few hours of water logging under some cases. Besides, the anaerobic environment also causes the stimulation of toxic substances like H_2S and Mn^{2+} (Drew and Lynch 1980). A decrease in reduction potential is another reason by which plants under water logging condition are damaged (Setter et al. 2009). Rapid changes in soil conditions are also observed in water logging condition.

Water logging condition in plant also refers to as soil water logging, which is a transient condition that may be caused due to hindrance in water flow through different layers of soil or by the troubles created with a high amount of water entering into the soil. In waterlogged soils, water content is one of the factors that affect the plant growth by either restriction in water flow in the soil profile or its heavy intake or mixture of both the problems. Soil provides a medium for plant growth, and so any alteration in its chemical and physical characteristics will cause a strong impact on root biomass and vegetative growth of the plant (Pierret et al. 2007). For the good growth of plants, an important aspect is the quantity of water content and its balance. Anthropogenic and natural activities can alter this balance. This includes the poor irrigation supply and compaction of soil due to human activities, while excessive rainfall causes impact by natural flooding or water logging (Irfan et al. 2010). The oxygen deficiency occurring under such a condition causes a poor supply in roots and most of the plants need a good amount of oxygen (maybe above 0.21 L^{-1}) for their survival by fulfilling the needs of shoots by water and nutrients (Brady and Weil 2008). In general, soil is considered poorly aerated when the soil O_2 concentration is less than 10% by volume. Sojka and Scott (2000) had shown that the composition of many other gases like CO_2, ethylene, and methane can affect the soil oxygen concentration.

This chapter describes the plant response under water logging condition, induction of hypoxia or anoxia conditions, the mechanism of tolerance, and adaptive strategies for plants to survive under water logging condition.

10.2 Plant Response Toward Water Logging Condition

Different plants respond differently under water logging conditions. Some plants show a tolerance response, while some are sensitive toward it. The slow gas diffusion in water logging conditions is the major aspect by which physiological changes are seen in plants and the majorly affected portions are roots and shoots of the plant (Vartapetian and Jackson 1997). This low gas diffusion condition speeds up the accumulation of phytotoxic products of anaerobic metabolism like carbon dioxide, ethanol, nitrogen, lactic acid, etc. These products, later on, build up in cells or are released in soil solution, which causes alteration in the chemical properties of soil. Other compounds such as organic acids of reduced volatile property may also produce and accumulate in such conditions (Bailey-Serres and Voesenek 2008). This change in the amount of oxygen also induces more production of reactive oxygen species like hydrogen peroxide, superoxide, etc. (Blokhina et al. 2003). Besides alteration in soil quality in water logging, the nutrient requirement is also affected. For instance, nitrogen and phosphorus uptake are hampered by the plant, whereas the amount of iron and manganese are enhanced due to reduction in soluble form (Drew 1997). Drew (1997) further revealed that root metabolism is severely influenced either by sudden availability or sudden restriction of various elements required for plant growth (Ferreyra et al. 2011). Nitrogen assimilation was also reported to be hampered via poor capacity for symbiotic nitrogen fixation in leguminous crops (Pucciariello et al. 2019). Gibbs and Greenway (2003) had revealed that reduction in ATP (high-energy compound-bearing phosphate group) was seen up to 37.5% in plants that are affected by water logging. Furthermore, reduction in cellular energy, elongation of stem and shoots, formation of adventitious roots, and cytoplasmic pH were some other responses, which a plant under water logging condition demonstrates (Pedersen et al. 2009; Yang et al. 2011). A significant reduction in fresh and dry biomass in water logging conditions was also seen in plants (Shabala et al. 2014).

10.3 Induction of Hypoxia or Anoxia Condition

Hypoxia and anoxia environmental stress is generally being observed in water logging or submergence condition. Hypoxia condition implies that when limitation of oxygen level causes a restriction in aerobic respiration of plants and occurs when the plant is exposed to shorter duration of flooding where shoots remain in the atmosphere but roots are submerged with water (Loreti and Perata 2020), whereas anoxia condition implies when there is a complete absence of oxygen in the environment where the plant is grown. An anoxic condition occurs when there is long-term flooding and all the parts of the plant are submerged in water. Shift in microorganisms from aerobic to anaerobic conditions is also seen under long-term flooding conditions where anaerobic microbes use alternative electron acceptors (Ponnamperuma 1972). This causes a higher accumulation of reduced phytotoxic forms of mineral ions such as ferrous, reduced form of ferric ion (Ponnamperuma

1972). In higher plants, there is a need for the continuous supply of oxygen levels for the proper functioning of respiration and other oxidation processes. The hypoxic or anoxic condition induced by water logging in roots of plant is inadequate to sustain the physiological activities in plant shoots for their right functioning. In barley and wheat plants, nutrient absorption and its transportation through the xylem are hindered resulting in a shortage of ion uptake for the development of tissues and its expansion. Senescence is observed in mature leaves as the mobile nutrients are relocated to younger leaves through the phloem (Taiz and Zeiger 2010). The hypoxic condition so induced by water logging in plant roots further enhances the production of 1-aminocyclopropane-1-carboxylic acid (ACC), an ethylene precursor. In tomato plants, this ACC moves toward buds via xylem sap where oxygen converts this ACC to ethylene by ACC oxidase. But in other plants like peas, water logging induces closure of stomata, which could be associated with more production of abscisic acid in premature leaves that transports ABA to the turgid young leaves, which stimulates stomatal closure (Zhang and Zhang 1994).

In anoxic conditions, the oxidative phosphorylation process stops, and the only available source for ATP production left is glycolysis for the plants to respire, wherein 2–3 molecules of ATP are produced per mole of glucose (Gibbs and Greenway 2003). But each glucose molecule yielded 1/10 of the ATP produced in the process of oxidative phosphorylation, which is not enough for the fulfillment of the energy demand generated by the plant. This causes the rapid decline in ATP due to which lower cellular ATP levels also occur. Overall, it causes an impact on ion pump activity by ceasing the activity leading to a loss in ion homeostasis (Armstrong and Drew 2002b). Furthermore, Drew (1997) had illustrated that during such conditions induced in water logging, fermentation processes are the other major events, which supports reoxidation and recycling of NADH.

10.4 Water Logging Mechanism Tolerance in Different Crops

In low-lying areas, water logging is a crucial problem. Under such a situation, the deficit of oxygen supply is the key basis for the damage to the plant by affecting the supply of nutrients and water in the plant. This causes wilting in the plant. A shift in mode from aerobic to anaerobic condition is seen in plants under such situations. Plant surviving under such conditions with good growth and development and having a relatively higher growth rate than in well-irrigated conditions is termed as water logging tolerant plants. Setter and Waters (2003) had defined water logging plant tolerance as the capability of plants to maintain good and increased yields in water logging conditions with respect to normal conditions. The development of morphological traits and metabolic activities as a response to the low oxygen content in water logging provides the plant with tolerance capability, which helps in the proper growth and development of the plant. Various mechanisms are known for water logging tolerance in plants. Armstrong et al. (1994) had reported that the development of aerenchymatous tissues (for high internal aeration) and oxidized zone in roots (particularly at root tips) of waterlogged plants helps in providing

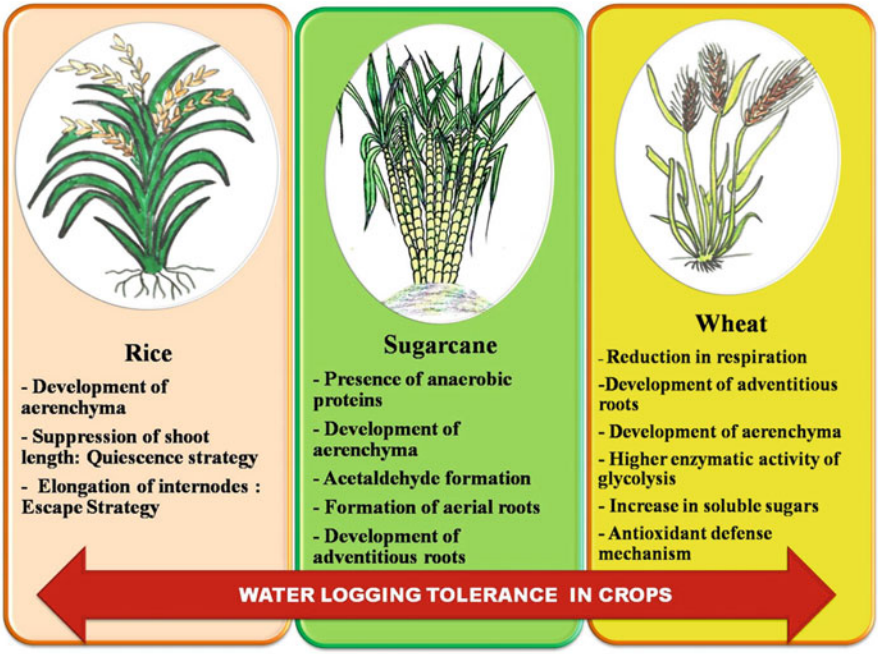

Fig. 10.1 Water logging tolerance in crops. Tolerant traits in rice, sugarcane, and wheat under water logging condition

tolerance to plant. Brandle and Crawford (1987) had revealed another tolerance mechanism where an alteration in metabolic activity under hypoxia conditions is seen in tolerant waterlogged plants; however, Brandle (1991) had reported of significant amount of carbohydrate production and accumulation under hypoxia conditions in waterlogged tolerant plants. Some of the important crops and their morphological traits are mentioned in brief that provides tolerance to water logging (Fig. 10.1).

Sugarcane being a large water consumer for high yield and productivity (Misra et al. 2016), sugarcane even needs to adapt under water logging conditions (Avivi et al. 2020). When the genes coding for anaerobic proteins (ANPs protein) sense oxygen deficiency, they begin to regulate upstream of genes either at transcriptional or post-transcriptional levels. The presence of ANPs is essential for the acclimation (Jackson et al. 2003). Besides, the development of the aerenchyma system in the cortex region increased levels of alcohol dehydrogenase (ADH) activity and ethanol production; high level of fermentative metabolism in the roots, acetaldehyde accumulation, and formation of adventitious roots (aerial roots) (Misra et al. 2020) are various ways by which sugarcane crop cope up with the problem of water logging. The aerenchymatous cells facilitate the transportation of gases, while combined effects of auxins and ethylene enhance the formation of adventitious roots, whereas ethylene solely promotes aerenchyma development under such conditions (Gomathi et al. 2015).

In the case of wheat under such conditions, the tissues of the wheat plant had reduced respiration rate in roots irrespective of whether the cultivar is tolerant or sensitive (Lambers 1976; Drew 1990). The tolerant cultivars are known to manage such conditions by the adaptation in metabolic activities involved in oxygen deficiency, viz., anaerobic respiration, and development of defense system having antioxidative properties, carbohydrate preservation, and avoidance of cytoplasmic acidification (Hossain and Uddin 2011). The cultivars tolerant to such sort of condition are able to survive by altering their morphological traits and some metabolic processes. Development of adventitious roots and aerenchyma cells are the tolerant characteristics in wheat under water logging conditions, and this is often accompanied by radial oxygen loss (ROL) barrier. The deficiency of oxygen in water logging conditions in wheat plants induces the roots to shift their energy mode from aerobic to anaerobic mode. Furthermore, the main metabolic changes, which provide tolerance in wheat plant, are higher activities of enzymes involved in glycolysis and fermentation, increase in the availability of soluble sugars, and antioxidant defense mechanism to post oxidative stress in the wheat plant (Alamgir and Nasir 2011).

Rice has several adaptive traits that help the plant to cope up with water logging conditions. These are the formation of gas spaces known as aerenchyma and leaf gas films. The aerenchyma functions as aeration between roots and shoots (Colmer 2003), while gas film contributes to the internal aeration between leaves and water (Pedersen et al. 2009, b). It is known that some of the low-land rice cultivars possess distinctive strategies to cope up with the problem of submergence. The quiescence and escape are the two strategies involved in rice for submergence tolerance, based on ethylene-responsive transcription factors (Hattori et al. 2009; Xu et al. 2006). In quiescence strategy, the length of the shoot is suppressed so that carbohydrates can be stored for a longer duration of 10–14 days. This carbohydrate preservation will help the plant cultivar to revive their growth and development when such condition of submergence is over (Colmer and Voesenek 2009). In escape strategy, internodes get elongated to grow above the water level and cope up with such conditions (Bailey-Serres and Voesenek 2008).

10.5 Survival/Adaptive Crop Strategies for Water Logging Condition

Majorly for plants to survive under water logging conditions, avoidance of oxygen deficiency by plant tissues and adaptation to this deficiency are the two ways. These have been described below in detail:

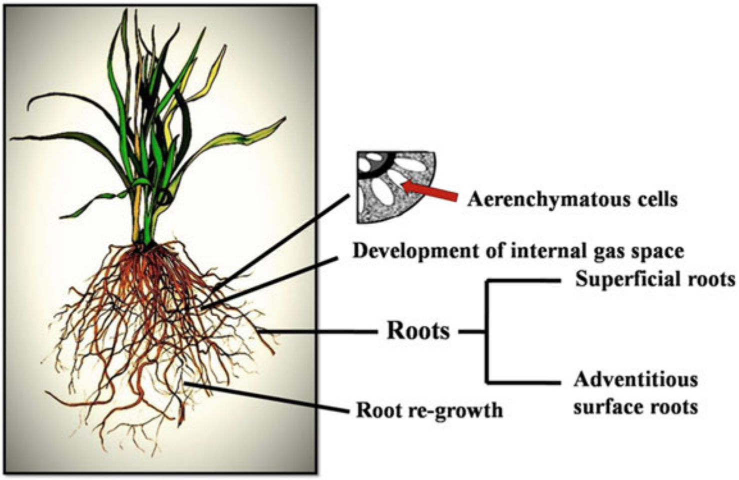

Fig. 10.2 Rooting survival strategies under water logging condition. Aerenchyma development, superficial rooting, and development of internal gas space are the rooting strategies under water logging by plant for its survival

10.5.1 Avoidance of Oxygen Deficiency with the Aid of Using Crop Tissues

The anatomical and morphological alterations is the first strategy by which water logging plants try to overcome the stress as it helps in improving the gaseous exchange with the environmental conditions (Voesenek et al. 2015; Yamauchi et al. 2018), wherein the role of ethylene hormone plays by higher accumulation under such condition (Sasidharan et al. 2015). Rooting in the plant has a special role in water logging condition (Fig. 10.2). The important modification in the rooting system is the aerenchyma formation so that gaseous transport and its distribution can be improved. The development of aerenchyma occurs in the root cortex, stems, and leaves (Colmer et al. 2009; Colmer 2003). In roots of wetland plants like rice, the development of barrier also occurs as radial oxygen loss that surrounds the tissue, which consists of aerenchyma (Yamauchi et al. 2018; Shiono et al. 2014). The development of aerenchyma has two functions, firstly reduction in a diffusive resistance to longitudinal gaseous transport and secondly decline in demand of oxygen per unit volume leading to enhancement in oxygen supply to apical portions of the plant (Armstrong 1979).

In conditions when the plant is under submergence, certain plants have the capability to move their leaves toward the surface of the water where the plant can regain the oxygen lost. This phenomenon is known as hyponastic growth, which implies that leaves of the plant change their angle to move upright position such as in *Arabidopsis thaliana* (Mustroph 2018). However, in certain plants rather than the movement of leaves, movement of the shoot is involved wherein the shoots try to elongate so that the leaves reach the water surface. This is termed as an escape strategy where rapid increase in the growth of petioles or stem is being observed, for example, rice (Van Veen et al. 2013; Vriezen et al. 2003). Studies had revealed that when there is internal oxygen transport, loss in radial oxygen supply from root to soil also occurs. This in turn causes oxidative removal of soil-borne phytotoxins, an additional factor for survival (Wheeler et al. 1985; Marschner 1986).

10.5.2 Crop Adaptation Toward Oxygen Deficiency

Under conditions when a plant is not able to induce modifications in morphological characters or when water levels had increased so much that they need to survive under a restricted gaseous environment under that condition, metabolism adaptation by certain plants is seen. The fermentation is the first metabolic change observed in plants under an oxygen deficit environment. This metabolic change is seen due to lesser production of mitochondrial ATP production, and so the plant need to fulfill its ATP requirement by glycolysis wherein accumulation of NADH occurs along with reoxidation to NAD. The process of reoxidation to NAD requires lactic acid fermentation (majorly involving ethanolic fermentation through two enzymes, viz., pyruvate decarboxylase and alcohol dehydrogenase). Oxygen-labile transcription factors play an important role in regulating transcription genes that encode fermentative enzymes (Mustroph 2018). The oxygen-labile transcription factors include group VII of the ethylene-response factor family. Under water logging conditions, when the fermentation process is stimulated, the availability of carbohydrates and energy production is reduced (Mustroph 2018). This in turn hinders the productivity and survival of plants under such a condition. Plants sensitive to water logging often die due to the deficiency of energy. This energy deficiency is responsible for exhaustion of fermentable substrates prior to the end of this phase (Van Dongen et al. 2015). Some plants use carbohydrate, which is derived from sources like starch. The carbohydrates are otherwise difficult to access under oxygen deficiency. The carbohydrates are available by the presence of specific amylases and manipulation in regulatory pathways (Kretzschmar et al. 2015) and facilitate elongation of shoots applying escape strategy. In some plants, this strategy is not used rather another strategy termed as quiescence strategy is applied where growth and metabolism are affected (Mustroph et al. 2014). The plants are able to survive for a longer duration under limited carbohydrate supply (Atwell et al. 2015).

10.6 Development of Aerenchyma in Waterlogged Plants

The formation of aerenchyma is the chief morphological and physiological trait of plants adapted to water logging conditions (Jiang et al. 2011). Aerenchyma roots are formed either lysigenously or schizogenously. In lysiogenous manner, aerenchyma formation occurs by concomitant cell separation and delayed collapse at times, while in schizogenous manner, aerenchyma formation occurs by cell separation mainly without collapse and is often followed by cell division. The aerenchyma tissues function as air conductors between roots and aerial parts of the plant (Williams and Barber 1961). Yamasaki (1952) had shown that the association of water tolerance and aerenchyma tissues formed during water logging conditions.

Prior researches assumed that due to oxygen deficiency, these aerenchymatous tissues in roots are produced, but actually, researches revealed that the hormone ethylene plays role in the formation of these aerenchymatous tissues (Armstrong and Armstrong 1991). Many studies in wheat had shown that this hormone stimulates the formation of aerenchyma in roots, while its nonpresence or inhibition causes inhibition in aerenchyma production as well (Konings 1982; Drew et al. 1981; Jackson et al. 1981). The production of ethylene in plant roots is a normal process, but the higher accumulation of this hormone results in inducing aerenchyma development. This increase in accumulation is mostly seen when plants are exposed to flooding and roots partially trap gas within itself (Konings and Jackson 1979). A high concentration of ethylene in waterlogged roots also triggers cellulose activity and is often observed that it increases under water logging conditions, thus contributing to aerenchyma formation (Kawase 1978, 1979). Aerenchyma formation in mesophytic angiosperms exposed to water logging condition possesses big irregular air cavities in the cortex region of roots cells. Studies had illustrated that the air spaces produced in plants exposed to water logging condition are relatively larger than the roots developed in normal condition (Beals 1917; Dunn 1921; McPherson 1939). This is also related to the poor aeration system of the plant under water logging condition (Bryant 1934). Shiono et al. (2011) had further stated that the aerenchyma formation is increased when the water logging condition in soil increases. For example, in plants that are nonaquatic (such as wheat and maize), the development of aerenchyma occurs via lysis and programmed cell death (Gladish et al. 2006; Drew et al. 1989). However, when a certain plant variety is tolerant to water logging, aerenchyma production is more. For instance in soybean water logging tolerant plants when plants are exposed to such conditions for 7 days, 20% aerenchyma is more produced (Thomas et al. 2005; Shimamura et al. 2010).

10.7 Conclusion

The excess amount of water due to heavy monsoon rainfall, poor drainage system, and irrigation practices cause water logging or flooding condition to occur. Water logging and flooding though demonstrate excess water, but they are completely different from each other. Water logging in agricultural crops causes a strong impact on productivity. In wheat crop, reduction in yield by 0%–38% was seen, while in sugarcane, cereal, and soybean crop, reduction in yield by 15%–45%, 0%–80%, and 39%–77% (depending on tolerant and sensitive cultivars), respectively, due to water logging. Water logging results in constrain in gaseous diffusion and oxygen diffusivity in water is relatively much slower compared with the one occurring in the air. The slower rate of gas diffusion is the key aspect by which physiological alterations are seen in plants. Water logging causes a rapid accumulation of phytotoxic products and reactive oxygen species. Hypoxia or anoxia condition prevails under water logging, and the plant needs to either adapt to such environment for survival or if not then the plant undergoes wilting and eventually death. The anatomical and morphological alterations are the first strategy by which plants try to overcome this stress by improving their gaseous exchange. The formation of aerenchyma is the chief morphological and physiological trait of plants under such conditions. Raised bed cultivation, subsurface tile drainage, crop management practices like the use of tolerant varieties, adjusting planting dates, etc., precision agriculture, adjustment of fertilizer application rate are some of the management measures, which may be adopted by crops to cope up with water logging problem.

References

Alamgir HM, Nasir USS (2011) Mechanisms of water logging tolerance in wheat: morphological and metabolic adaptations under hypoxia or anoxia. Australian J Crop Sci 5:1094–1101

Armstrong J, Armstrong W (1991) A convective through-flow of gases in *Phragmites australis*. Aquat Bot 39:73–86

Armstrong W (1979) Aeration in higher plants. In: Woolhouse HW (ed) Advances in botanical research. Academic Press, London, pp 225–232

Armstrong W, Drew M (2002a) Root growth and metabolism under oxygen deficiency. Plant Root 3:729–761

Armstrong W, Drew MC (2002b) Root growth and metabolism under oxygen deficiency. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half, 3rd edn. Marcel rd Dekker, New York, pp 729–761

Armstrong W, Strange ME, Cringle S, Beckett PM (1994) Microelectrode and modelling study of oxygen distribution in roots. Ann Bot 74:287–299

Atwell BJ, Greenway H, Colmer TD (2015) Efficient use of energy in anoxia-tolerant plants with focus on germinating rice seedlings. New Phytol 206:36–56

Avivi S, Arnin SFM, Soeparjono S, Restanto DP, Fanata WID, Widjaya KA (2020) Tolerance screening of sugarcane varieties toward water logging stress. E3S Web Conf 142(03007):1–6

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

Beals CC (1917) The effect of aeration on the roots of *Zea mays*. I Proc Indiana Acad Scii 7:177–180

Blokhina O, Virolainen E, Fagerstedt KV (2003) Antioxidants, oxidative damage and oxygen deprivation stress: a review. Ann Bot 91:179–194

Brady NC, Weil RR (2008) The nature and properties of soil, 14th edn. Prentice-Hall, Upper Saddle River, New Jersey

Brandle R, Crawford RMM (1987) Rhizome anoxia tolerance and habitat socialization in wetland plants. In: RMM C (ed) Plant life in aquatic and amphibious habitats. Blackwell, Oxford, pp 397–410

Brandle RA (1991) Flooding resistance of rhizomatous amphibious plants. In: Jackson MD, Davies DD, Lambers H (eds) Plant life under oxygen deprivation. Academic Publisher, The Hague, pp 35–46

Bryant AE (1934) Comparison of anatomical and histological differences between roots of barley grown in aerated and in non-aerated culture solutions. Plant Physiol 9:389–391

Colmer TD (2003) Long distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. Plant Cell Environ 26:17–36

Colmer TD, Flowers TJ (2008) Flooding tolerance in halophytes. New Phytol 179:964–974

Colmer TD, Voesenek LACJ (2009) Flooding tolerance: suites of plant traits in variable environments. Funct Plant Biol 36:665–681

Drew MC (1990) Sensing soil oxygen. Plant Cell Environ 13:681–693

Drew MC (1997) Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Annu Rev Plant Physiol Plant Mol Biol 48:223–250

Drew MC, He CJ, Morgan PW (1989) Decreased ethylene biosynthesis, and induction of aerenchyma, by nitrogen or phosphate-starvation in adventitious roots of *Zea mays* L. Plant Physiol 91:266–271

Drew MC, Jackson MB, Giffard SC, Campbell R (1981) Inhibition by silver ions of gas space (aerenchyma) formation in adventitious roots of *Zea mays* L. subjected to exogenous ethylene or to oxygen deficiency. Planta 153:217–224

Drew MC, Lynch JM (1980) Soil anaerobiosis, microorganisms and root function. Annu Rev Phytopathol 18:37–66

Dunn GA (1921) Note on the histology of grain roots. Amer J Bot 8:207–211

Ferreyra R, Selles G, Pinto M, Morales M, Seguel O (2011) Effect of soil air capacity on water relations and vegetative growth of ‘Thompson seedless’ grafted on different rootstocks. Preliminary results. Acta Hortic 889:145–150

Food and Agriculture Organization (2015) Food and Agriculture Organization of the United Nations. http://www.fao.org/3/abc600e.pdf

Gibbs J, Greenway H (2003) Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. Funct Plant Biol 30:1–47

Gladish DK, Xu JP, Niki T (2006) Apoptosis-like programmed cell death occurs in procambium and ground meristem of pea (*Pisum sativum*) root tips exposed to sudden flooding. Ann Bot 97: 895–902

Gomathi R, Rao PNG, Chandran K, Selvi A (2015) Adaptive responses of sugarcane to water logging stress: an overview. Sugar Tech 17(4):325–338

Hattori Y, Nagai K, Furukawa S, Song XJ, Kanwano R, Sakakibara H, Wu J, Matsuoka T, Yoshimura A, Kitano H, Matsuoka M, Mori H, Ashikari M (2009) The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt deep water. Nature 460:1026–1030

Hossain MA, Uddin SN (2011) Mechanisms of water logging tolerance in wheat: morphological and metabolic adaptations under hypoxia or anoxia. Aust J Crop Sci 5(9):1094–1101

Irfan M, Hayat S, Hayat Q, Afroz S, Ahmad A (2010) Physiological and biochemical changes in plants under waterlogging. Protoplasma 241:3–17. https://doi.org/10.1007/s00709-009-0098-8

Jackson MB (2004) The impact of flooding stress on plants and crops. http://www.plantstress.com/Articles/waterlogging_i/waterlog_i.htm

Jackson MB, Drew MC, Giffard SC (1981) Effects of applying ethylene to the root system of *Zea mays* on growth and nutrient concentration in relation to flooding tolerance. Physiol Plant 52: 23–28

Jackson MB, Saker LR, Crisp CM, Else MA, Janowiak F (2003) Ionic and pH signalling from roots to shoots of flooded tomato plants in relation to stomatal closure. Plant and Soil 253:103–113

Jiang Z, Hu Z, Zeng L, Lu W, Zhang H, Li T, Xiao H (2011) The role of the Golgi apparatus in oxidative stress: is this organelle less significant than mitochondria? Free Radic Biol Med 50: 907–917

Kawase M (1978) How plants adapt to water logging. Ohio Rep Ohio Agric Res Dev Center 63:14–15

Kawase M (1979) Role of cellulase in aerenchyma development in sunflower. Amer J Bot 66:183–190

Konings H (1982) Ethylene-promoted formation of aerenchyma in seedling roots of *Zea mays* L. under aerated and non-aerated conditions. Physiol Plant 54:119–124

Konings H, Jackson MB (1979) A relationship between rates of ethylene production by roots and the promoting or inhibiting effects of exogenous ethylene and water on root elongation. Z Pflanzenphysiol 92:385–397

Kretzschmar T, Pelayo MAF, Trijatmiko KR, Gabunada LFM, Alam R, Jimenez R, Mendioro MS, Slamet-Loedin IH, Sreenivasulu N, Bailey-Serres J, Ismail AM, Mackill DJ, Septiningsih EM

(2015) A trehalose-6-phosphate phosphatase enhances anaerobic germination tolerance in rice. Nat Plants 1:15124

Lambers H (1976) Respiration and NADH oxidation of the root of flood-intolerant *Senecio* species as affected by anaerobiosis. Plant Physiol 37:117–122

Lee SC, Mustroph A, Sasidharan R, Vashisht D, Pedersen O, Oosumi T, Voesenek LACJ, Bailey-Serres J (2011) Molecular characterization of the submergence response of the *Arabidopsis thaliana* ecotype Columbia. New Phytol 190:457–471

Loreti E, Perata P (2020) The many facets of hypoxia in plants. Plan Theory 9(6):745–759

MacEwan R, Gardner W, Ellington A, Hopkins D, Bakker A (1992) Tile and mole drainage for control of waterlogging in duplex soils of South-Eastern Australia. Aust J Exp Agric 32:865–878

Marashi SK, Chinchanikar GS (2010) Effect of waterlogging on yield and yield components of wheat (*Triticum aestivum* L.). Int J Appl Agric Res 5(4):561–567

Marschner H (1986) Mineral nutrition of higher plants. Academic Press, London, 674

Mcpherson DC (1939) Cortical air spaces in the roots of *Zea mays* L. New Phytol 38:190–202

Misra V, Solomon S, Singh P, Prajapati CP, Ansari MI (2016) Effect of water logging on post harvest sugarcane deterioration. Agri 5(2):119–132

Misra V, Solomon S, Mall AK, Prajapati CP, Hasheem A, Abdallah EF, Ansari MI (2020) Morphological assessment of water stressed sugarcane: a comparison of waterlogged and drought affected crop. Saudi J Biol Sci 27(5):1228–1236

Mustroph A (2018) Improving flooding tolerance of crop plants. Agronomy 8:160–185

Mustroph A, Hess N, Sasidharan R (2014) Hypoxic energy metabolism and PPi as an alternative energy currency. In: van Dongen JT, Licausi F (eds) Low-oxygen stress in plants. Springer, Vienna, pp 165–184

Oosterhuis DM, Scott RE, Hampton RE, Wullschleger SD (1990) Physiological responses of two soyabean (*Glycine max*. (L.) Merr) cultivars to short-term flooding. Environ Exp Bot 30 (1):85–92

Pedersen O, Rich SM, Colmer TD (2009) Surviving floods. Leaf gas films improve O_2 and CO_2 exchange, root aeration, and growth of completely submerged rice. Plant J 58:147–156

Pierret A, Doussan C, Capowiez Y, Bastardie F, Pages L (2007) Root functional architecture: a framework for modeling the interplay between roots and soil. Vadose Zone J 6:269–281

Ponnamperuma PN (1972) The chemistry of submerged soils. Adv Agron 24:29–96

Pucciariello C, Boscari A, Tagliani A, Brouquisse R, Perata P (2019) Exploring legume rizobia symbiotic models for water logging tolerance front. Plant Sci 10:578. https://doi.org/10.3389/fpls.2019.00578

Rhine MD, Stevens G, Shannon G, Wrather A, Sleper D (2010) Yield and nutritional responses to waterlogging of soybean cultivars. Irrig Sci 28:135–142

Robertson F, Suraweera D, McCaskill M, Christy B, Armstrong R, Zollinger R, Byron J, Partington D, Clark S (2019) Waterlogging effects on soils and wheat crops in the high rainfall zone of Victoria. In: Proceedings of the 2019 agronomy Australia conference, 25–29 August 2019, Wagga Wagga, Australia

Romina P, Abeledo LG, Miralles DJ (2018) Physiological traits associated with reductions in grain number in wheat and barley under waterlogging. Plant and Soil 429:1–13

Sasidharan R, Bailey-Serres J, Ashikari M, Atwell BJ, Colmer TD, Fagerstedt K, Fukao T, Geigenberger P, Hebelstrup KH, Hill RD, Holdsworth MJ, Ismail AM, Licausi F, Mustroph A, Nakazono M, Pedersen O, Perata P, Sauter M, Shih MC, Sorell BK, Striker GG, Dongen JTV, Whelan J, Xiao S, Visser EJW, Voesenek LACJ (2017) Community recommendations on terminology and procedures used in flooding and low oxygen stress research. New Phytol 214:1403–1407

Sasidharan R, Voesenek LACJ (2015) Ethylene-mediated acclimations to flooding stress. Plant Physiol 169:3–12

Setter TL (2000) Farming systems for waterlogging prone sand-plain soils of the south coast. Department of Agriculture, Western Australia

Setter TL, Waters I (2003) Review of prospects for germplasm improvement for water logging tolerance in wheat, barley and oats. Plant and Soil 253:1–34

Setter TL, Waters I, Sharma SK, Singh KN, Kulshreshtha N, Yaduvanshi NPS, Ram PC, Singh BN, Rane J, McDonald G, Khabaz-Saberi H, Biddulph TB, Wilson R, Barclay I, McLean R, Cakir M (2009) Review of wheat improvement for water logging tolerance in Australia and India: the importance of anaerobiosis and element toxicities associated with different soils. Ann Bot 103: 221–235

Shabala S, Shabala L, Barcelo J, Poschenrieder C (2014) Membrane transporter mediating root signaling and adaptive responses to oxygen deprivation and soil flooding. Plant Cell Environ 37: 2216–2233

Shannon JG, Stevens WE, Wiebold WJ, McGraw RL, Sleper DA (2005) Breeding soybeans for improved tolerance to flooding. In: Proceedings of 35th soybean seed research conference, American Seed Trade Association, Chicago

Shimamura S, Yamamoto R, Nakamura T, Shimada S, Komatsu S (2010) Stem hypertrophic lenticels and secondary aerenchyma enable oxygen transport to roots of soybean in flooded soil. Ann Bot 106:277–284

Shiono K, Oga FLS, Yamazaki S, Isoda H, Fujimura T, Nakazono M, Colmer TD (2011) Contrasting dynamics of radial O_2- loss barrier induction and aerenchyma formation in rice roots of two lengths. Ann Bot 107:89–99

Shiono K, Yamauchi T, Yamazaki S, Mohanty B, Malik AI, Nagamura Y, Nishizawa NK, Tsutsumi N, Colmer TD, Nakazono M (2014) Microarray analysis of laser-microdissected tissues indicates the biosynthesis of suberin in the outer part of roots during formation of a barrier to radial oxygen loss in rice (*Oryza sativa*). J Exp Bot 65:4795–4806

Sojka RE, Scott HD (2000) Aeration measurement. In: Lal R (ed) Encyclopedia of soil science. Marcel Dekker, New York, pp 27–29

Solaiman Z, Colmer T, Loss S, Thomson B, Siddique K (2007) Growth responses of cool-season grain legumes to transient waterlogging. Aust J Agr Res 58:406–412

Taiz L, Zeiger E (2010) Plant physiology, 5th edn. Sinauer Associates, Sunderland

Thomas AL, Guerreiro SMC, Sodek L (2005) Aerenchyma formation and recovery from hypoxia of the flooded root system of nodulated soybean. Ann Bot 96:1191–1198

Urban DW, Roberts MJ, Schlenker W, Lobell DB (2015) The effects of extremely wet planting conditions on maize and soybean yields. Climate Change 130:247–260

Van Dongen JT, Licausi F (2015) Oxygen sensing and signaling. Annu Rev Plant Biol 66:345–367

Van Veen H, Mustroph A, Barding GA, Vergeer-van EM, Welschen-Evertman RAM, Pedersen O, Visser EJW, Larive CK, Pierik R, Bailey-Serres J, Laurentius ACJ, Voesenek RS (2013) Two Rumex species from contrasting hydrological niches regulate flooding tolerance through distinct mechanisms. Plant Cell 25:4691–4707

Vartapetian BB, Jackson MB (1997) Plant adaptations to anaerobic stress. Ann Bot 79:3–20

Vashisht D, Hesselink A, Pierik R, Ammerlaan JMH, Bailey-Serres J, Visser EJW, Pedersen O, van Zanten M, Vreugdenhil D, Jamar DCL, Voesenek LACAJ, Sasidharan R (2011) Natural variation of submergence tolerance among *Arabidopsis thaliana* accessions. New Phytol 190: 299–310

Voesenek LACJ, Bailey-Serres J (2015) Flood adaptive traits and processes: an overview. New Phytol 206:57–73

Vriezen WH, Zhou Z, Van der Straeten D (2003) Regulation of submergence-induced enhanced shoot elongation in *Oryza sativa* L. Ann Bot 91:263–270

Wheeler BD, Al-Farraj M, Cook RED (1985) Iron toxicity to plants in base-rich wetlands: comparative effects on the distribution and growth of *Epilobium hirsutum* L. and *Juncus subnodulosus* Schrank. New Phytol 100:653–669

Willaims WT, Barber DA (1961) The functional significance of aerenchyma in plants. Soc Exp Biol Symp 15:132–144

Xu K, Xu X, Fukao T, Canlas P, Maghirang-Rodriguez R, Heuer S, Ismial AM, Bailey-Serres J, Ronald PC, Mackill DJ (2006) Sub1A is an ethylene responsive-factor-like gene that confers submergence tolerance to rice. Nature 442:705–708

Yaduvanshi N, Setter T, Sharma S, Singh K, Kulshreshtha N (2014) Influence of waterlogging on yield of wheat (*Triticum aestivum*), redox potentials, and concentrations of microelements in different soils in India and Australia. Soil Res 50:489–499

Yamasaki T (1952) Studies on the "excess moisture injury" of upland crops in over-moist soil from the viewpoint of soil chemistry and plant physiology. Bull Nat Inst Agric Sci 1:1–92

Yamauchi T, Colmer TD, Pedersen O, Nakazono M (2018) Regulation of root traits for internal aeration and tolerance to soil water logging-flooding stress. Plant Physiol 176:1118–1130

Yang CY, Hsu FC, Li JP, Wang NN, Shih MC (2011) The AP2/ERF transcription factor AtERF73/HRE1 modulates ethylene responses during hypoxia in *Arabidopsis*. Plant Physiol 156:202–212

Zhang J, Zhang X (1994) Can early wilting of old leaves account for much of the ABA accumulation in flooded pea plants? J Exp Bot 45:1335–1342

Crop Adaptability to Excess Salt

11

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and Saurabh Singh Rathore

Abstract

High salt concentration in arable soil/soil salinization poses an increasing agricultural problem all over the world. Such salt accrual is resulting from the sea water mixing with irrigation supply and naturally high content of salts in water used for agricultural irrigation. Further, concerning plants, the stress generated by salt salinization of the soil can be divided into two stages: (i) early osmotic imbalance disturbing water uptake by the plant roots and (ii) the stress created by Na^+ and Cl^- ions that disturb the metabolism together with the productivity of photosynthesis. Plants moderate these stresses by developing certain mechanisms for enhancing water retention (decrease in the loss of water with increase in its uptake) and preventing the detrimental effects of Na^+ ions by their vacuolar entrapment together with exclusion from the tissues of the leaves. However, even after employing the tolerant mechanisms, plants are adversely affected, and this is specially observed as a decrease in crop productivity/yields that ultimately resulting in continuous decrease in arable land resources. Factors of rapid expansion of population size and continuously improving quality of life are exerting a great pressure upon the agriculture resources. Therefore, managing the salt stress in agricultural plants and developing varieties with such mechanisms

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can play a pivotal role in addressing the challenge of rapidly increasing demand of agribusiness. This chapter focuses on the mechanisms of salt tolerance in plants, sensory, and signaling networks associated with salinization, Na^+ transport, gene expression regulatory responses toward salt stress, and the approaches toward designing salt tolerant crops.

Keywords

Salt stress · Crop plants · Salt tolerance · Osmolytes · Gene regulation · Sodium/ potassium transfer

11.1 Introduction: Salt-Induced Stress

Plants employ two strategies to cope up with stress created by soil salinization, i.e., sensory mechanism is for recognizing increased osmotic potential and second is for the enhanced presence of Na^+ ions (Fig. 11.1). Responses of the aforementioned two mechanisms are sometimes mutually exclusive of one another, thereby proving the two distinct mechanisms against salt stress. Till date, the precise identification of the key players of these two sensory mechanisms has not been successful. However, there have been some successful attempts in which it has been demonstrated that histidine kinase receptor protein HK1 of *Arabidopsis thaliana* has a functional role in sensing osmotic imbalances (Urao et al. 1999). Some of the physiological responses by plants toward salt-induced osmotic stress are changed in HK1 mutants, while others are unchanged depicting the role of protein entities, excluding HK1, responding to osmotic stress in mutants (Kumar et al. 2013). A quick increase in the Ca^{2+} ion concentration in the cytosol on a brief NaCl/mannitol exposure suggested

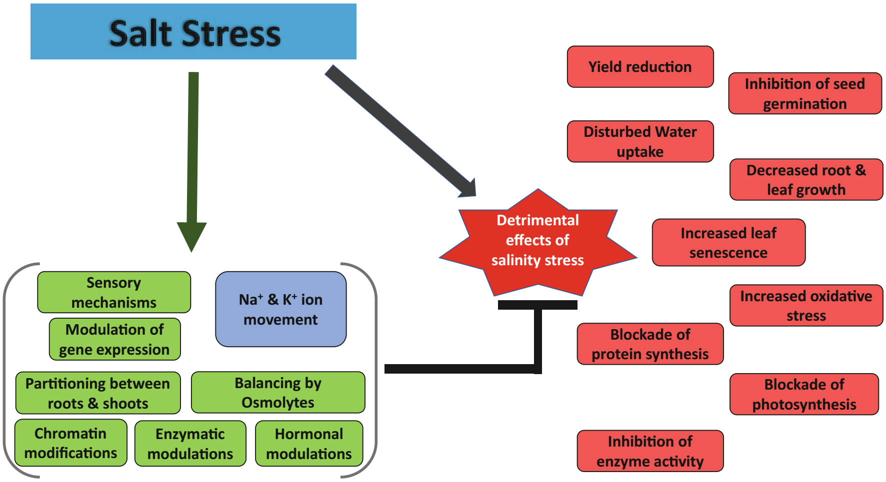

Fig. 11.1 Adverse effects of salt stress and their management in plants

the coupling of the Ca^{2+} ion channel with hyperosmotic sensory apparatus of plants (Knight et al. 1997). The origin of Ca^{2+} ion response in plant's roots and in many types therein possibly implicates sensing by a mechanical ion channel gate structure (Kiegle et al. 2000; Tracy et al. 2008; Kurusu et al. 2013; Marti et al. 2013). Proper cuticle development builds the structural strength of the cellular envelope and supports the mechanical osmo-sensors. Mutations disturbing cuticle development can result in weakened osmotic potential that governed responses and thereby altered water diffusion (Wang et al. 2011b). Consequently, cuticle is a prime factor in altering the mechanical properties of cellular water stress.

Reactive oxygen species (ROS) and annexins are the secondary messengers mediating the salt-induced and ROS-induced responses (Laohavisit et al. 2012, 2013). These secondary messengers work in conjunction with Ca^{2+} ion signaling machinery and get induced by presence of excess salt or osmotic stress (Jiang et al. 2013b). Some kinases can be activated and pass the salt stress/hyperosmotic signal to further activity of proteins through gene expression mechanism (Weinl and Kudla 2009). The Ca^{2+} ions/calmodulin can direct the activation of transcription factors (Weng et al. 2012). Though a quick rise in the Ca^{2+} ion concentration characterizes the osmotic stress response, but other sensory mechanisms that are not governed by Ca^{2+} ions are also found in plants. Identifying the genetic basis of these sensory networks is essential in deciphering the code of plants osmo-sensory response toward increased ionic concentrations and salt stress.

11.2 Modulation of Gene Regulation in Plant Roots Under Salt Stress

The sensory pathways related to increased salt concentrations are linked to several salt tolerance responses by many transcription factors. Groups of transcription family genes are expressed to different degrees when an increased salt concentration is sensed by the salt stress sensory mechanisms (Jiang et al. 2009; Cui et al. 2013). Expression of the genes affecting the salt tolerance response of plants is in turn regulated by these transcription factors. Some of the genes are upregulated or downregulated, depending on their roles in supporting or countering the salt stress, correspondingly. The osmotic constituent of enhanced salinity causes a lowering of the water potential, and therefore, to balance this, uptake of inorganic ions and synthesis of osmolytes must be enhanced. As a result, genes responsible for such responses are upregulated (Geng et al. 2013). Dynamic shift in the synthesis of hormones also plays a role to some extent in the regulation of the transcription of the stress responsive genes (Dinneny et al. 2008; Geng et al. 2013). Initial stress phase is followed first by a short dormant and later growth recovery period. The two phases of dormancy and growth recovery are associated with the corresponding levels of plant hormones. Data mining has shown a secondary signaling network controlling the salt affected plant growth (Kilian et al. 2007; Geng et al. 2013). Majority of the stress-mediated variations are observed after around 3 h of exposure to high salt concentrations (Geng et al. 2013). Cells of the root cortex in the seedlings of

Arabidopsis thaliana show highest amounts of transcriptional activity (Geng et al. 2013). In salt-stressed conditions, lateral growth in roots has been shown to be most significantly caused by the endodermal cellular layers of the roots. Some plant hormones like ABA can affect the directional growth of roots to avoid high salinity areas (Duan et al. 2013). This spatial circumvention to evade high salt microenvironment by directional root growth is defined as halotropism and is found to be mainly caused by another plant hormone auxin under the influence of salt (Galvan-Ampudia et al. 2013). Discovering the molecular pathways underlying halotropism can further clear our understanding regarding plant's capabilities of bearing the high salt load around its roots. Instead of all the findings till now, our understanding of this subject is still incomplete. An interesting study has deciphered that ethylene, along with ABA and auxin, improves the shoot Na^+/K^+ ratio and makes *Arabidopsis* more capable of bearing the salt stress load (Jiang et al. 2013a). Ethylene levels are increased when *ETO1* (ethylene over producer 1) gene is knocked out. The increased ethylene triggers the RBOHF (respiratory burst oxidase homolog F) for ROS synthesis in root stele. Buildup of the ROS inside stele lowers the accumulation of Na^+ in xylem including flow of Na^+ and holding of K^+ in roots. All these changes lead to increased tolerance of salt (Jiang et al. 2013a).

11.3 Role of Na^+ and K^+ Transporters in Salt Stress Tolerance

Control of influx and efflux of ions across plasma membrane has a very significant role in various biotic/abiotic stress tolerant mechanisms. Specifically, the Na^+/K^+ membrane transporters are involved in the resistance against salt stress (Schroeder et al. 2013). The roots contain pathways for the transportation of Na^+ ions across the plasma membrane through their transporters or via the channels for nutrient uptake. In plant leaves, the mutation in some of these transporters and channels can decrease the Na^+ ions intake. Nevertheless, only a few of these channels when present in defective forms can hamper the Na^+ ions uptake into the roots in mutants. Some nonselective cation channels are also found in plant roots to serve as a gateway for Na^+ ions movement (Tapken and Hollmann 2008). Apart from these nonselective channels, specific antiporters for cation/proton exchange are also found in root epidermis for transporting Na^+ ions to stele from cells of the endodermal layer (Hall et al. 2006). The K^+ starvation has been shown to enhance Na^+ ions intake to the roots in *Oryza sativa* through a plant high affinity K^+ ion transporter, OsHKT2;1 (Horie et al. 2007). Another K^+ ion transporter OsHAK5 in *Oryza sativa* is not very permeable for Na^+ ions and provides salt stress bearing ability to tobacco cells when present in overexpressed state (Horie et al. 2011).

Stellar cells transfer the Na^+ ions to the xylem for their further transport to distant plant parts. The cargo of Na^+ ions is set up in the xylem through a control of few K^+ ion channels (de Boer and Wegner 1997). Further removal of Na^+ ions from the xylem is dome by separate low affinity transporters (Ren et al. 2005). During salt stress management, ionic movement in plants is done in such a manner that ion homeostasis is maintained. For this K^+ ions are acquired and distributed in a stable manner with an added advantage of their balancing of Na^+ ions buildup-related toxic effects (Schroeder et al. 1994). The K^+ ion channels that precisely put K^+ ions selectively inside or outside the plant cells have been shown to reduce the levels of toxicity associated with elevated Na^+ ions (Schroeder et al. 1987).

11.4 NHX and SOS-Mediated Maintenance of Low Na^+ Ion Levels in Cytoplasm

Na^+/H^+ exchanger 1 (NHX1) of tonoplast and Salt Overly Sensitive 1 (SOS1/NHX7) antiporters of plasma membrane are the two key factors for lowering the plant cell's Na^+ ion concentrations (Blumwald and Poole 1985; Qiu et al. 2002). The mode of lowering of the Na^+ ion levels by the two mechanisms differs from one another. While NHX detoxifies the Na^+ ions by their sequestration in the vacuoles, the SOS mediates efflux of Na^+ ions from the cell. Plants' enhanced salt tolerance is associated with the overexpression of NHX proteins (Apse et al. 1999). NHX like proteins probably work by causing vacuolar restriction of K^+ ions and maintaining the pH stability (Barragan et al. 2012). Advantageous functioning of NHX type protein AtNHX1 is observed with its overexpression leading to increased vacuolar K^+ ion retention and its transport from roots to shoots in tomato (Leidi et al. 2010). In this manner, overexpressed AtNHX1 reduces Na^+ ion stress by increasing the K^+/Na^+ ratios inside the cell. Mapping of LeNHX3 to a leaf Na^+ ion accrual QTL locus relates the NHX type proteins with Na^+ ion stress management (Villalta et al. 2008). NHX antiporters in vacuoles significantly affect osmolarity balance, cellular growth, and, as a result, development of plant (Bassil et al. 2011). Processing of proteins, vesicle-mediated trafficking, and conveyance of the cargo have potential contribution from the NHX antiporters of the endosomes (Krebs et al. 2010). NHX and other transporters of endosomes have potential roles in salt tolerance through their ability to regulate pH and ionic balance inside organelles of plant cells (Krebs et al. 2010). Involvement of NHX proteins in trafficking of proteins has been shown in double knockout plants for *nhx5* and *nhx6* genes wherein a significant reduction in salt tolerance was observed (Leidi et al. 2010). Moreover, in *Arabidopsis thaliana*, no change in salt tolerance was observed at the cost of H^+-ATPase inside the vacuoles. The H^+-ATPase is also known as V-ATPase and its functionality in trans-Golgi network/early endosome (TGN/EE) is required for maintaining salt tolerance (Villalta et al. 2008). Vacuolar upregulated expression of type 1 H^+-pyrophosphatase AVP1 causes Na^+ ions to be confined inside vacuoles (Undurraga et al. 2012). Practical application of improving salt tolerance under artificially maintained greenhouse environment is successful after overexpression of H^+-pyrophosphatase in crop plants. This significantly increases the biomass production and grain yields in crops (Schilling et al. 2014).

11.5 Partitioning of Na^+ Ions from Roots to Shoots in Combating Salt Stress

Plant high affinity potassium transporter (HKT) plays an important role in Na^+/K^+ cation transport in plants, and many *HKT* genes have been successfully characterized, e.g., *TaHKT1* (*Triticum aestivum HKT 1*), *AtHKT1* (*Arabidopsis thaliana HKT1*), and OsHKT1 (*Oryza sativa HKT 1*) (Rubio et al. 1995). HKT transporters are classified into two groups: class I HKT transporters are mostly involved in selective transfer of Na^+ ions, and the class II HKT transporters mediate the transport of both Na^+ and K^+ ions (Rubio et al. 1995; Uozumi et al. 2000). Examples of the functions of HKTs have been provided by the studies showing buildup of Na^+ ions in leaves on salt stress exposure with associated depletion of Na^+ ions in roots (Berthomieu et al. 2003). Active role of OsHKT1;1 and AtHKT1;1 has been demonstrated in exiting Na^+ ions out of deeper xylem tissues to prevent toxicity of Na^+ ions (Davenport et al. 2007; Horie et al. 2011). Plants with overexpressed *AtHKT1*; one have more salt tolerating ability over plants with normal expression of *AtHKT1*;1. Role of *AtHKT1*;*1* in passive control of Na^+ ion transfer has already been established by the in vivo patch clamping electrophysiological study on root cells (Xue et al. 2011). Stress generation by high Na^+ ions in leaves is countered by their removal by AtHKT1;1. External rectifier channels for K^+ ions help to load xylem vessels with potassium ions leading to increase in the ratio of Na^+ and K^+ ions. Increased K^+/Na^+ ratio counters the salt stress and helps plants to sustain themselves in soils having higher salt concentration. Varied crop plants have common Na^+ countering mechanisms, e.g., wheat and rice. Results from QTL analysis have revealed that in both wheat and rice plants, the main salt tolerance mechanism is linked to certain common genomic landscapes that are responsible for production of highly effective transporters for Na^+ ions, e.g., Nax1 and Na^+-selective class I HKT transporter (James et al. 2006; Byrt et al. 2007). Some of these QTL identified regions encode the proteins for both Na^+ ion clearance and HKT transporters to give a protection to leaf sheaths against Na^+ ions overaccumulation (Huang et al. 2006). When HKT transporter is introduced into a commercial wheat variety from a wild variety, grain yields were significantly increasing instead of the crop plant growing in salt stressed environment (Munns et al. 2012). All these findings confirm the importance of HKT transporters as an effective counter measure against the damaging effects of salt stress in form of high Na^+ loads.

The mechanisms of maintaining a high K^+/Na^+ ion ratio in plant leaves is important for plant's ability to resist the salt stress. Contradictory to the above importance, high Na^+ ion accumulation is observed in leaves of the plants typically growing in salt rich soils. A weak allele of *AtHKT1;1* is found to be associated with its reduced expression in plant roots (Baxter et al. 2010). This weak allele still confers a slight functionality of removing Na^+ ions, and thus, toxic concentrations are avoided. Osmotic tuning according to the load of salt stress is not a single factor mechanism. For instance, in plants, where weak allele of *HKT1* is in effect, there may be higher alterations in other salt tolerance pathways like vacuolar sodium ion sequentializations. Thus, knowledge of such cooperative effects that working together to cope up with salt stress could aid in designing crop varieties with more salt tolerance. Class 2 HKT transporters in *Hordeum vulgare* also depict transport of Na^+ ions, from roots to xylem, even with more intensity when overexpressed and thereby confer higher salt tolerance. Plants employ some regulatory mechanisms pertaining to expression of K^+ ion transporters to modulate their activity, e.g., *AtHKT1;1* of *Arabidopsis thaliana* roots that is depressed by cytokinin negative regulators ARR1 and 2. When salinity is sensed, cytokinin levels fall leading to enhanced expression of *AtHKT1;1* (Mason et al. 2010). ABI4 (ABA-Insensitive 4) is another transcription factor acting negatively for expression of *AtHKT1;1*. ABI4 expression is found to correlate with the expression of *AtHKT1;1* that impart salt tolerance in case when its gene is mutated. When ABI4 is overexpressed, *AtHKT1;1* is lowered in expression, and plants become highly sensitive for the presence of salts (Shkolnik-Inbar et al. 2013). Positive regulators or enhancers of *AtHKT1;1* expression is not discovered yet. A complex network of signals from many *cis*- and *trans*-acting elements control the expression of *AtHKT1;1* in salt induced stress.

11.6 Epigenetic Modifications Induced by Salt Stress

Plants adapt to various environmental conditions by modifications at the level of chromatin. Epigenetic chromatin modifications in plants growing under salinity stress have been demonstrated by their presence in the same generation on exposure to the stress. In an experiment done on *Arabidopsis* plants, two groups were differently and consecutively treated for salt stress. First group was given mild salt treatment in their seedling stage and then grown later in desalted normal conditions. The second group of seedlings was not pretreated with salt and was grown under normal condition. During the stress-free normal condition growth of the seedlings, no differences were observed between the two groups. However, when further salt stress was applied on the two groups of plants, the first group was found to be more tolerant for the salt stress than the second group, which was initially untreated with salt stress. It was speculated that this high salt tolerance was due to the epigenetic histone modifications affecting transcription factor expression (Zhu 2008). Previously stress exposed plants show strongly induced expression of *HKT1* over the unexposed plants. That is why Na^+ ions accumulate differently in the two groups (Sani et al. 2013).

Methylation of target sites at genomic regions is another influential aspect for salt tolerance. The salt stress hypersensitivity is found to be associated with altered *AtHKT1;1* promoter activity (Baek et al. 2011). This alteration was due to unsuccessful methylation at a target site on the promoter. Evidence of salt affected DNA methylation, of transcription factor coding regions along with their promoters, indicated the potential of chromatin modifications in ever-increasing salt tolerance of plants (Song et al. 2012). Under salt stress, temporal variations of gene expression between plants of different genotypes have led to speculations about the involvement of an epigenetic component of chromatin modification and methylation-induced responses (Wang et al. 2011a). However, there is no clear understanding of the epigenetic influence on salt tolerant mechanisms and its inheritance through generations. Differences in ploidy levels can also affect salt tolerance, particularly the hold up of potassium in *Arabidopsis* (Chao et al. 2013).

11.7 Role of Osmolytes

Lower osmotic potential is maintained in plant cells by accumulation of osmolytes to combat the salt-induced stress. Therefore, to completely decipher the code of salt tolerant mechanisms, it is very important to get an understanding of the mechanisms controlling the activity and presence of osmolytes. Presence of salt stress enhances synthesis of osmolytes, while in the normal conditions when salt stress is not present, osmolytes are catabolized. Proline is one such osmolyte that functions as an important signaling mediator for various cellular activities in the recovery phase (Szabados and Savoure 2010). Blocking proline synthesis in *Arabidopsis* knockout plants caused hypersensitivity to salt and this observation confirms the role of osmolytes in management of salt stress (Szekely et al. 2008). Initially, proline was considered to play a role as an osmolyte only. Later, many other roles of proline were discovered, for instance as ROS, buffering agent, molecular chaperon, and structural component under stress. Another osmolyte, glycine betaine, is produced for osmotic balancing by many plant species (Jain et al. 2021). It is also a protective agent for many enzymes and membrane components. ROS rummaging enzyme activities are maintained by glycine betaine, but proof of its direct role as a ROS scavenger is still lacking (Chen and Murata 2008).

11.8 Other Regulators of Salt Tolerance Response in Plants

The salt response network in plants is constituted by many different genes. The genes guide the salt response network to influence salt tolerance in plants. Therefore, to develop salt tolerant crop varieties, it is very important to have knowledge of these machineries of salt tolerance network (Al-Khayri et al. 2021). In *Arabidopsis*, a serine/threonine protein phosphatase negatively regulates the signaling of ABA, and plant's increased salt tolerance is associated with its decreased transcripts levels. Moreover, expression of the protein phosphatase is downregulated by a transcription factor, *AtMYB20* (Merlot et al. 2001; Cui et al. 2013). Interestingly, aforesaid association is proved from the demonstration of plants with overexpressed *AtMYB20* to be more salt tolerant over wild types and vice versa (Cui et al. 2013). Another protease involved in balancing of Na^+ and salt tolerance is the ubiquitin-specific protease 16 (UBP16). Its expression is induced by the presence of salt, and its presence plays a stabilizing role for the Na^+/H^+ antiporter activity. UBP16 acts in opposition to proteasomal degradation of proteins through deubiquitylation and thus helps in protein stability (Zhou et al. 2012).

11.9 Developing Salt-Tolerant Plant Varieties

Conventional breeding methods are very time consuming, so it is essential to look for alternative and comparatively rapid methods of crop improvements. Genetically diverse germplasm are used to cross the existing varieties, and phenotypes of the offspring generation are looked for improved characteristics. Gene manipulation for salt tolerance has been attempted in *Arabidopsis*, where transcription factor (*bZIP24*) was identified in a comparative study conducted in halo-tolerant plant and *Arabidopsis* (Popova et al. 2008). This transcription factor is responsible for the induction of many stress responsive genes. When *bZIP24* is knocked down by RNAi methods, salt tolerance increases. This was further strengthened by the observation that *bZIP24* targets to depress expression of *AtHKT1;1* (Yang et al. 2009). Thus, halophilic plants can be used as a model for discovery of potential target of salt tolerance regulation. Negative regulators of *AtHKT1;1* have been well studied and serve as targets for gene manipulations for inducing salt tolerance. However, positive regulatory mechanisms of *AtHKT1;1* are not so well identified. Studies in the crop plant species have also revealed insights of salt tolerance networks. In rice, transcription factor *SERF1* (Salt Responsive ERF 1) triggers the ROS-activated MAP kinase cascade in salt-rich conditions (Schmidt et al. 2013). Under high salt concentration, roots show enhanced expression of *SERF1*. When *SERF1* expression is blocked in rice plants, gene expression of salt stress fighting genes is negatively affected. *SERF1* has a definite role in maintaining high Na^+/K^+ ratios in leaves as shown by high salt tolerance in case of its overexpression (Schmidt et al. 2013).

11.10 Conclusion and Future Directions

A comprehensive understanding of the factors and players of salt tolerance mechanisms in plants have been achieved in around the last 20 years. Still, there are many things unclear and need further exploration. More investigations are needed to elucidate the gene expression and regulatory networks of many more Na^+ and K^+ transporters in different plant species. Moreover, the present knowledge about the described mechanisms of salt tolerance must be used to develop newer more capable crop varieties for salt-rich soils currently considered inarable. Modern biotechnological methods need to be used in combination with molecular breeding techniques for developing such varieties. The potential targets for these developments can be the genes, in exclusion or in combination, for ion transporters, ROS scavenging pathways, salt homeostatic systems, and those influencing the plant's salt tolerating ability in any way.

References

Al-Khayri JM, Ansari MI, Singh AK (2021) Nanobiotechnology: mitigation of abiotic stress in plants, 1st edn. Springer, Cham, pp 1–593

Apse MP, Aharon GS, Snedden WA, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar Na^+/H^+ antiport in *Arabidopsis*. Science 285:1256–1258

Baek D, Jiang J, Chung JS, Wang B, Chen J, Xin Z, Shi H (2011) Regulated AtHKT1 gene expression by a distal enhancer element and DNA methylation in the promoter plays an important role in salt tolerance. Plant Cell Physiol 52:149–161

Barragan V, Leidi EO, Andres Z, Rubio L, De Luca A, Fernandez JA, Cubero B, Pardo JM (2012) Ion exchangers NHX1 and NHX2 mediate active potassium uptake into vacuoles to regulate cell turgor and stomatal function in *Arabidopsis*. Plant Cell 24:1127–1142

Bassil E, Ohto MA, Esumi T, Tajima H, Zhu Z, Cagnac O, Belmonte M, Peleg Z, Yamaguchi T, Blumwald E (2011) The *Arabidopsis* intracellular Na+/H+ antiporters NHX5 and NHX6 are endosome associated and necessary for plant growth and development. Plant Cell 23:224–239

Baxter I, Brazelton JN, Yu D, Huang YS, Lahner B, Yakubova E, Li Y, Bergelson J, Borevitz JO, Nordborg M, Vitek O, Salt DE (2010) A coastal cline in sodium accumulation in *Arabidopsis thaliana* is driven by natural variation of the sodium transporter AtHKT1;1. PLoS Genet 6: e1001193

Berthomieu P, Conejero G, Nublat A, Brackenbury WJ, Lambert C, Savio C, Uozumi N, Oiki S, Yamada K, Cellier F, Gosti F, Simonneau T, Essah PA, Tester M, Very AA, Sentenac H, Casse F (2003) Functional analysis of AtHKT1 in *Arabidopsis* shows that $Na^{(+)}$ recirculation by the phloem is crucial for salt tolerance. EMBO J 22:2004–2014

Blumwald E, Poole RJ (1985) Na/H Antiport in isolated tonoplast vesicles from storage tissue of *Beta vulgaris*. Plant Physiol 78:163–167

Byrt CS, Platten JD, Spielmeyer W, James RA, Lagudah ES, Dennis ES, Tester M, Munns R (2007) HKT1;5-like cation transporters linked to Na+ exclusion loci in wheat, Nax2 and Kna1. Plant Physiol 143:1918–1928

Chao DY, Dilkes B, Luo H, Douglas A, Yakubova E, Lahner B, Salt DE (2013) Polyploids exhibit higher potassium uptake and salinity tolerance in *Arabidopsis*. Science 341:658–659

Chen TH, Murata N (2008) Glycinebetaine: an effective protectant against abiotic stress in plants. Trends Plant Sci 13:499–505

Cui MH, Yoo KS, Hyoung S, Nguyen HT, Kim YY, Kim HJ, Ok SH, Yoo SD, Shin JS (2013) An *Arabidopsis* R2R3-MYB transcription factor, AtMYB20, negatively regulates type 2C serine/threonine protein phosphatases to enhance salt tolerance. FEBS Lett 587:1773–1778

Davenport RJ, Munoz-Mayor A, Jha D, Essah PA, Rus A, Tester M (2007) The Na+ transporter AtHKT1;1 controls retrieval of Na+ from the xylem in *Arabidopsis*. Plant Cell Environ 30:497–507

de Boer AH, Wegner LH (1997) Regulatory mechanisms of ion channels in xylem parenchyma cells. J Exp Bot 48:441–449

Dinneny JR, Long TA, Wang JY, Jung JW, Mace D, Pointer S, Barron C, Brady SM, Schiefelbein J, Benfey PN (2008) Cell identity mediates the response of *Arabidopsis* roots to abiotic stress. Science 320:942–945

Duan L, Dietrich D, Ng CH, Chan PM, Bhalerao R, Bennett MJ, Dinneny JR (2013) Endodermal ABA signaling promotes lateral root quiescence during salt stress in *Arabidopsis* seedlings. Plant Cell 25:324–341

Galvan-Ampudia CS, Julkowska MM, Darwish E, Gandullo J, Korver RA, Brunoud G, Haring MA, Munnik T, Vernoux T, Testerink C (2013) Halotropism is a response of plant roots to avoid a saline environment. Curr Biol 23:2044–2050

Geng Y, Wu R, Wee CW, Xie F, Wei X, Chan PM, Tham C, Duan L, Dinneny JR (2013) A spatio-temporal understanding of growth regulation during the salt stress response in *Arabidopsis*. Plant Cell 25:2132–2154

Hall D, Evans AR, Newbury HJ, Pritchard J (2006) Functional analysis of CHX21: a putative sodium transporter in *Arabidopsis*. J Exp Bot 57:1201–1210

Horie T, Costa A, Kim TH, Han MJ, Horie R, Leung HY, Miyao A, Hirochika H, An G, Schroeder JI (2007) Rice OsHKT2;1 transporter mediates large Na+ influx component into K+-starved roots for growth. EMBO J 26:3003–3014

Horie T, Sugawara M, Okada T, Taira K, Kaothien-Nakayama P, Katsuhara M, Shinmyo A, Nakayama H (2011) Rice sodium-insensitive potassium transporter, OsHAK5, confers increased salt tolerance in tobacco BY2 cells. J Biosci Bioeng 111:346–356

Huang S, Spielmeyer W, Lagudah ES, James RA, Platten JD, Dennis ES, Munns R (2006) A sodium transporter (HKT7) is a candidate for Nax1, a gene for salt tolerance in durum wheat. Plant Physiol 142:1718–1727

Jain P, Pandey B, Singh P, Singh R, Singh SP, Sonkar S, Gupta R, Rathore SS, Singh AK (2021) Plant performance and defensive role of glycine betaine under environmental stress. In: Husen A (ed) Plant performance under environmental stress. Springer, pp 225–248

James RA, Davenport RJ, Munns R (2006) Physiological characterization of two genes for Na+ exclusion in durum wheat, Nax1 and Nax2. Plant Physiol 142:1537–1547

Jiang C, Belfield EJ, Cao Y, Smith JA, Harberd NP (2013a) An *Arabidopsis* soil-salinity-tolerance mutation confers ethylene-mediated enhancement of sodium/potassium homeostasis. Plant Cell 25:3535–3552

Jiang Y, Yang B, Deyholos MK (2009) Functional characterization of the *Arabidopsis* bHLH92 transcription factor in abiotic stress. Mol Genet Genomics 282:503–516

Jiang Z, Zhu S, Ye R, Xue Y, Chen A, An L, Pei ZM (2013b) Relationship between NaCl- and H_2O_2-induced cytosolic Ca2+ increases in response to stress in *Arabidopsis*. PLoS One 8: e76130

Kiegle E, Moore CA, Haseloff J, Tester MA, Knight MR (2000) Cell-type-specific calcium responses to drought, salt and cold in the *Arabidopsis* root. Plant J 23:267–278

Kilian J, Whitehead D, Horak J, Wanke D, Weinl S, Batistic O, D'Angelo C, Bornberg-Bauer E, Kudla J, Harter K (2007) The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. Plant J 50:347–363

Knight H, Trewavas AJ, Knight MR (1997) Calcium signalling in *Arabidopsis thaliana* responding to drought and salinity. Plant J 12:1067–1078

Krebs M, Beyhl D, Gorlich E, Al-Rasheid KA, Marten I, Stierhof YD, Hedrich R, Schumacher K (2010) *Arabidopsis* V-ATPase activity at the tonoplast is required for efficient nutrient storage but not for sodium accumulation. Proc Natl Acad Sci U S A 107:3251–3256

Kumar MN, Jane WN, Verslues PE (2013) Role of the putative osmosensor *Arabidopsis* histidine kinase1 in dehydration avoidance and low-water-potential response. Plant Physiol 161:942–953

Kurusu T, Kuchitsu K, Nakano M, Nakayama Y, Iida H (2013) Plant mechanosensing and Ca2+ transport. Trends Plant Sci 18:227–233

Laohavisit A, Richards SL, Shabala L, Chen C, Colaco RD, Swarbreck SM, Shaw E, Dark A, Shabala S, Shang Z, Davies JM (2013) Salinity-induced calcium signaling and root adaptation in *Arabidopsis* require the calcium regulatory protein annexin1. Plant Physiol 163:253–262

Laohavisit A, Shang Z, Rubio L, Cuin TA, Very AA, Wang A, Mortimer JC, Macpherson N, Coxon KM, Battey NH, Brownlee C, Park OK, Sentenac H, Shabala S, Webb AA, Davies JM (2012) *Arabidopsis* annexin1 mediates the radical-activated plasma membrane ca(2)+− and K+-permeable conductance in root cells. Plant Cell 24:1522–1533

Leidi EO, Barragan V, Rubio L, El-Hamdaoui A, Ruiz MT, Cubero B, Fernandez JA, Bressan RA, Hasegawa PM, Quintero FJ, Pardo JM (2010) The AtNHX1 exchanger mediates potassium compartmentation in vacuoles of transgenic tomato. Plant J 61:495–506

Marti MC, Stancombe MA, Webb AA (2013) Cell- and stimulus type-specific intracellular free Ca2+ signals in *Arabidopsis*. Plant Physiol 163:625–634

Mason MG, Jha D, Salt DE, Tester M, Hill K, Kieber JJ, Schaller GE (2010) Type-B response regulators ARR1 and ARR12 regulate expression of AtHKT1;1 and accumulation of sodium in *Arabidopsis* shoots. Plant J 64:753–763

Merlot S, Gosti F, Guerrier D, Vavasseur A, Giraudat J (2001) The ABI1 and ABI2 protein phosphatases 2C act in a negative feedback regulatory loop of the abscisic acid signalling pathway. Plant J 25:295–303

Munns R, James RA, Xu B, Athman A, Conn SJ, Jordans C, Byrt CS, Hare RA, Tyerman SD, Tester M, Plett D, Gilliham M (2012) Wheat grain yield on saline soils is improved by an ancestral Na(+) transporter gene. Nat Biotechnol 30:360–364

Popova OV, Yang O, Dietz KJ, Golldack D (2008) Differential transcript regulation in *Arabidopsis thaliana* and the halotolerant *Lobularia maritima* indicates genes with potential function in plant salt adaptation. Gene 423:142–148

Qiu QS, Guo Y, Dietrich MA, Schumaker KS, Zhu JK (2002) Regulation of SOS1, a plasma membrane Na+/H+ exchanger in *Arabidopsis thaliana*, by SOS2 and SOS3. Proc Natl Acad Sci U S A 99:8436–8441

Ren ZH, Gao JP, Li LG, Cai XL, Huang W, Chao DY, Zhu MZ, Wang ZY, Luan S, Lin HX (2005) A rice quantitative trait locus for salt tolerance encodes a sodium transporter. Nat Genet 37: 1141–1146

Rubio F, Gassmann W, Schroeder JI (1995) Sodium-driven potassium uptake by the plant potassium transporter HKT1 and mutations conferring salt tolerance. Science 270:1660–1663

Sani E, Herzyk P, Perrella G, Colot V, Amtmann A (2013) Hyperosmotic priming of *Arabidopsis* seedlings establishes a long-term somatic memory accompanied by specific changes of the epigenome. Genome Biol 14:R59

Schilling RK, Marschner P, Shavrukov Y, Berger B, Tester M, Roy SJ, Plett DC (2014) Expression of the *Arabidopsis* vacuolar H(+)-pyrophosphatase gene (AVP1) improves the shoot biomass of transgenic barley and increases grain yield in a saline field. Plant Biotechnol J 12:378–386

Schmidt R, Mieulet D, Hubberten HM, Obata T, Hoefgen R, Fernie AR, Fisahn J, San Segundo B, Guiderdoni E, Schippers JH, Mueller-Roeber B (2013) Salt-responsive ERF1 regulates reactive oxygen species-dependent signaling during the initial response to salt stress in rice. Plant Cell 25:2115–2131

Schroeder JI, Delhaize E, Frommer WB, Guerinot ML, Harrison MJ, Herrera-Estrella L, Horie T, Kochian LV, Munns R, Nishizawa NK, Tsay YF, Sanders D (2013) Using membrane transporters to improve crops for sustainable food production. Nature 497:60–66

Schroeder JI, Raschke K, Neher E (1987) Voltage dependence of K channels in guard-cell protoplasts. Proc Natl Acad Sci U S A 84:4108–4112

Schroeder JI, Ward JM, Gassmann W (1994) Perspectives on the physiology and structure of inward-rectifying K+ channels in higher plants: biophysical implications for K+ uptake. Annu Rev Biophys Biomol Struct 23:441–471

Shkolnik-Inbar D, Adler G, Bar-Zvi D (2013) ABI4 downregulates expression of the sodium transporter HKT1;1 in *Arabidopsis* roots and affects salt tolerance. Plant J 73:993–1005

Song Y, Ji D, Li S, Wang P, Li Q, Xiang F (2012) The dynamic changes of DNA methylation and histone modifications of salt responsive transcription factor genes in soybean. PLoS One 7: e41274

Szabados L, Savoure A (2010) Proline: a multifunctional amino acid. Trends Plant Sci 15:89–97

Szekely G, Abraham E, Cseplo A, Rigo G, Zsigmond L, Csiszar J, Ayaydin F, Strizhov N, Jasik J, Schmelzer E, Koncz C, Szabados L (2008) Duplicated P5CS genes of *Arabidopsis* play distinct roles in stress regulation and developmental control of proline biosynthesis. Plant J 53:11–28

Tapken D, Hollmann M (2008) *Arabidopsis thaliana* glutamate receptor ion channel function demonstrated by ion pore transplantation. J Mol Biol 383:36–48

Tracy FE, Gilliham M, Dodd AN, Webb AA, Tester M (2008) NaCl-induced changes in cytosolic free Ca2+ in *Arabidopsis thaliana* are heterogeneous and modified by external ionic composition. Plant Cell Environ 31:1063–1073

Undurraga SF, Santos MP, Paez-Valencia J, Yang H, Hepler PK, Facanha AR, Hirschi KD, Gaxiola RA (2012) *Arabidopsis* sodium dependent and independent phenotypes triggered by H(+)-PPase up-regulation are SOS1 dependent. Plant Sci 183:96–105

Uozumi N, Kim EJ, Rubio F, Yamaguchi T, Muto S, Tsuboi A, Bakker EP, Nakamura T, Schroeder JI (2000) The *Arabidopsis* HKT1 gene homolog mediates inward Na(+) currents in *Xenopus laevis* oocytes and Na(+) uptake in *Saccharomyces cerevisiae*. Plant Physiol 122:1249–1259

Urao T, Yakubov B, Satoh R, Yamaguchi-Shinozaki K, Seki M, Hirayama T, Shinozaki K (1999) A transmembrane hybrid-type histidine kinase in *Arabidopsis* functions as an osmosensor. Plant Cell 11:1743–1754

Villalta I, Reina-Sanchez A, Bolarin MC, Cuartero J, Belver A, Venema K, Carbonell EA, Asins MJ (2008) Genetic analysis of Na(+) and K (+) concentrations in leaf and stem as physiological components of salt tolerance in tomato. Theor Appl Genet 116:869–880

Wang W, Zhao X, Pan Y, Zhu L, Fu B, Li Z (2011a) DNA methylation changes detected by methylation-sensitive amplified polymorphism in two contrasting rice genotypes under salt stress. J Genet Genomics 38:419–424

Wang ZY, Xiong L, Li W, Zhu JK, Zhu J (2011b) The plant cuticle is required for osmotic stress regulation of abscisic acid biosynthesis and osmotic stress tolerance in *Arabidopsis*. Plant Cell 23:1971–1984

Weinl S, Kudla J (2009) The CBL-CIPK ca(2+)-decoding signaling network: function and perspectives. New Phytol 184:517–528

Weng H, Yoo CY, Gosney MJ, Hasegawa PM, Mickelbart MV (2012) Poplar GTL1 is a Ca2+/calmodulin-binding transcription factor that functions in plant water use efficiency and drought tolerance. PLoS One 7:e32925

Xue S, Yao X, Luo W, Jha D, Tester M, Horie T, Schroeder JI (2011) AtHKT1;1 mediates nernstian sodium channel transport properties in *Arabidopsis* root stelar cells. PLoS One 6:e24725

Yang O, Popova OV, Suthoff U, Luking I, Dietz KJ, Golldack D (2009) The *Arabidopsis* basic leucine zipper transcription factor AtbZIP24 regulates complex transcriptional networks involved in abiotic stress resistance. Gene 436:45–55

Zhou H, Zhao J, Yang Y, Chen C, Liu Y, Jin X, Chen L, Li X, Deng XW, Schumaker KS, Guo Y (2012) Ubiquitin-specific protease16 modulates salt tolerance in *Arabidopsis* by regulating Na (+)/H(+) antiport activity and serine hydroxymethyltransferase stability. Plant Cell 24:5106–5122

Zhu JK (2008) Epigenome sequencing comes of age. Cell 133:395–397

Plant Scavenging Potential to Heavy Metals

12

Azzreena Mohamad Azzeme

Abstract

Rapid urbanization and industrialization contribute to accumulation of heavy metals (HMs) like Hg, Cd, Pb, As, Fe, Cu, and Zn in environment. The accumulation may negatively influence plant growth and development, therefore affecting plant productivity. Therefore, through evolution, plants develop two mechanisms to scavenge HMs, the root uptakes and foliar uptakes. Both mechanisms induce accumulation of HMs in root and aerial parts of plants, but percentage of accumulation is species dependent. The plants that are responding to HMs are further categorized into two categories, the hyperaccumulator and non-hyperaccumulator species. Both groups require ion transporters to uptake and remove metal ions. Involvement of phytohormones is also crucial in increasing tolerance toward HMs. Therefore, this chapter summarizes the mechanisms in scavenging HMs and role of ion transporters and phytohormones in hyperaccumulator and non-hyperaccumulator plants.

Keywords

Foliar uptake · Heavy metals · Plant development and productivity · Metal scavenging

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12.1 Introduction

Heavy metals (HMs) are collective term for metals and metalloids that have high atomic weight and density compared with water. Most of them are harmful to humans even at low concentration like arsenic (As) and mercury (Hg) (Kinuthia et al. 2020). On earth, HMs naturally exist in the form of parent rocks and metallic minerals, but the geogenic and anthropogenic activities have released them to the environment, therefore contaminating the soil. The anthropogenic activities that contribute to HMs pollution are agricultural, metallurgy, industrial, pharmaceutical, domestic effluents, and atmospheric activities (Ali et al. 2019; Vareda et al. 2019). The pollution is at worrying state because the persistence characteristic of HMs in the environment, which they can contaminate the food chain through bioaccumulation and bioaugmentation processes (Rai et al. 2019). Present report has shown that the toxicity of HMs toward humans, plants, and animals is ranged from 0.1 to 0.3 mg/L, in which this range is considered as low concentration.

Some of the HMs are classified as essential micronutrient for plant growth and development. For instances, Fe is a component of heme proteins (e.g. cytochrome and Fe-S proteins), Cu is an integral component of certain electron transfer proteins in photosynthesis (e.g. plastocyanin) and respiration (e.g. cytochrome c oxidase), and Zn is a non-redox-active but has a key structural and/or catalytic role in many proteins and enzymes. Metal deficiency symptoms may appear when these HMs are lacking (Hall and Williams 2003). But at excess amounts, the plant may receive toxic effects, which can result in low biomass accumulation, chlorosis, inhibition of growth and photosynthesis, altered water balance and nutrient assimilation, senescence, and plant death (Singh et al. 2016; Atabaki et al. 2020).

Plants scavenge HMs through root and/or foliar uptakes (Shahid et al. 2017). Plant root can sense and scavenge the HMs present in the soil, but the scavenging capability depends on the dose-dependent manner because at high concentration, the HMs may interfere plant growth and development. Once HMs enter the root tissue, the HMs are accumulated and translocated in the cell wall system, which ultimately change the root appearance (Gomes et al. 2011).

The plants use foliar system to scavenge HMs in the ambient air like Cd, Pb, Mn, Hg, Ni, and As. These metals accumulate on the leaves surface, and latter enter the plant system through stomata, cuticular cracks, lenticels, ectodesmata, and aqueous pores. Similar to root uptake, the deposition of HMs through foliar system is also dose-dependent manner (Shahid et al. 2017). The ability of plants to uptake a large amount of HMs from soils without phytotoxicity symptoms is known as hyperaccumulators, wherein they have greater ability in uptaking HMs, translocating HMs from root- to-shoot, and detoxification and sequestration of HMs. Examples of hyperaccumulator species are *Thlaspi caerulescens* and *Arabidopsis halleri* (Singh et al. 2016). The non-hyperaccumulators accumulate lower amount of HMs when compared with hyperaccumulators, but they can produce high biomass; hence they are able to accumulate HMs at higher amount comparable to hyperaccumulator species (Souza et al. 2013).

Scavenging of HMs through hyperaccumulator and non-hyperaccumulator plant systems involves different physiological and biochemical mechanisms. Reduction of chlorophyll, shoots, and roots are common strategies when they are exposed to HMs; however the changes are species dependent (Both et al. 2020). Involvement of calcium signaling, hormone signaling, and mitogen activated protein kinase (MAPK) to alleviate toxicity in both hyperaccumulators and non-hyperaccumulators has also been reported (Jalmi et al. 2018). The phytohormones like cytokinins, auxins, salicylic acids, gibberellic acids, brassinosteroids, and strigolactones also play important role in remediating the toxicities (Sytar et al. 2019). Apart from that, the ability of hyperaccumulators and non-hyperaccumulators in scavenging HMs is also due to tolerance mechanism developed by them such as immobilization, plasma membrane exclusion, restriction of uptake and transport, synthesis of specific HM transporters, chelation and sequestration of HMs by particular ligands (PCs and MTs), induction of mechanisms contrasting the effects of reactive oxygen species (ROS) and methylglyoxal (MG) (such as upregulation of antioxidant and glyoxalase system), induction of stress proteins, and the biosynthesis of proline, polyamines, and signaling molecules such as salicylic acid and nitric oxide (Hossain et al. 2012). Therefore, these hyperaccumulator and non-hyperaccumulator species can be used in phytoremediation. In this chapter, the HMs scavenging mechanisms of hyperaccumulators and non-hyperaccumulators are further discussed.

12.2 Roots and Foliar Uptakes of HMs in Plants

The HMs uptake or absorption into plants occurs through two routes, the roots and foliar uptakes (Fig. 12.1). As sessile organism, some plants have established their ability to uptake HMs without impairing their metabolism through various processes that are known as phytoextraction, phytoaccumulation, phytovolatilization, phytostabilization, and phytotransformation. Phytoextraction or also known as phytoaccumulation is a process wherein plants absorb inorganic and organic contaminants through the stem and roots. Meanwhile, phytovolatization is capability of plants to absorb and subsequently volatilize the contaminant into the atmosphere. Phytostabilization is a process to store and immobilize HMs by binding them with biomolecules. This process prevents metal transport, either remain in the root or rhizosphere. Also, plants can convert them into less toxic substances, and then mobilize them into plant system. Phytotransformation is a HMs degradation process, which involves plant metabolic pathways (Tangahu et al. 2011; Raza et al. 2020).

Root is highly specified and well-organized plant organ. These properties make the root the main organ that can uptake HMs present in the contaminated soil. The penetration of HMs into root can accumulate about 95% of total HMs or more. The penetration mechanism involves an adsorption of HMs onto root surface followed by HMs binding to rhizodermal polysaccharides like pectin or carboxyl group of mucilage uronic acid. It involves complex mechanism between microbiome in the rhizosphere. The HMs are then passively penetrated the root, and afterwards, they

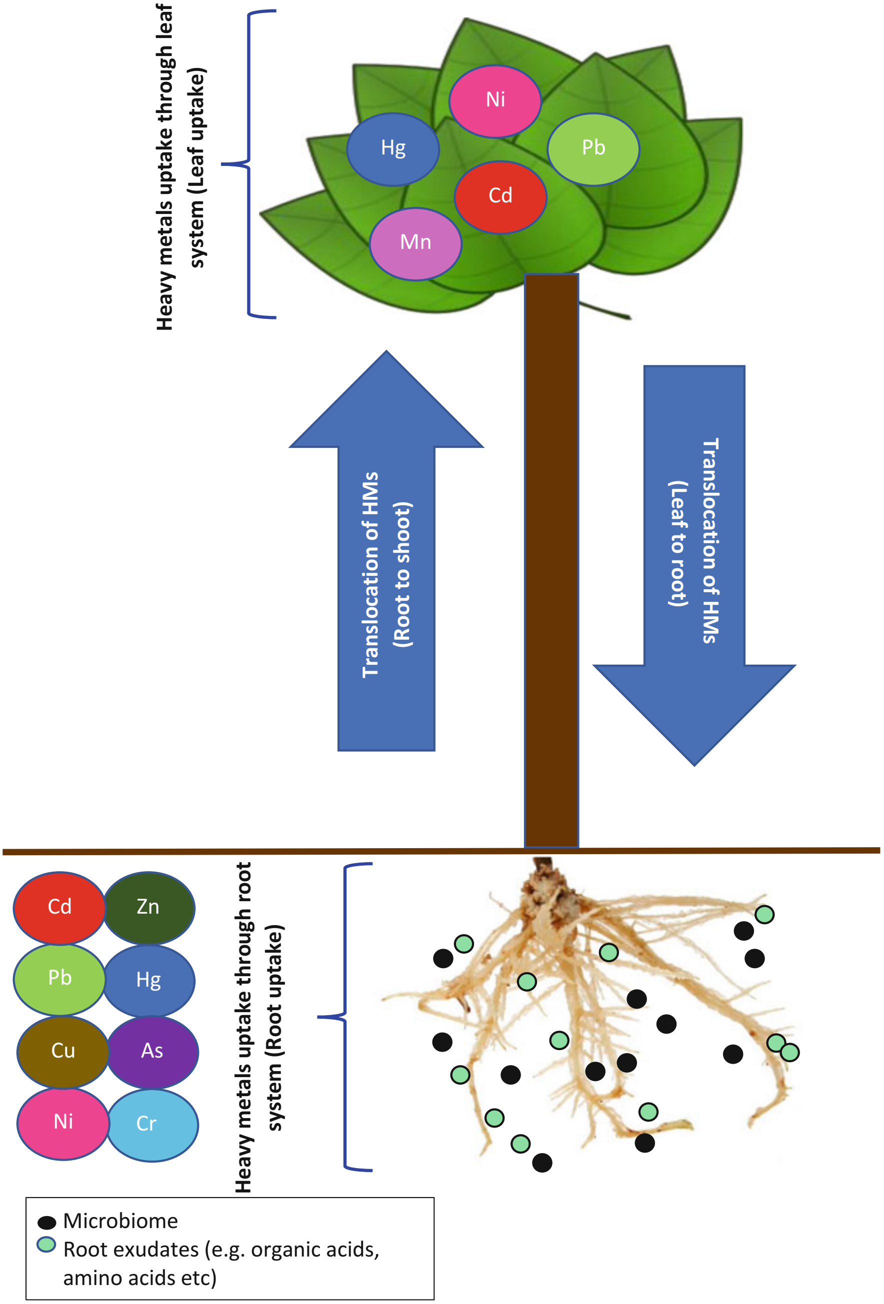

Fig. 12.1 General mechanism of heavy metal (HM) transportation from root to leaf and leaf to root

are diffused through water streams and further transported to the aerial parts through xylem loading (Shahid et al. 2017). The presence of root exudates can also increase HMs uptake by the roots. Apart from that, the organic acids present in root exudates are able to bind metal ions, therefore affecting metal mobility, solubility, and bioavailaibility in soil (Ma 2016). For instance, root of *A. halleri* releases nicotianamine (NA), a main chelator that has beneficial effect on improving solubilization and accumulation of Zn. Furthermore, the roots of *Hordeum vulgare* and *Lolium perenne* L. release organic molecules that can form complexes with Zn, hence promoting Zn mobility (Balafrej et al. 2020). Once enter the root, the plants develop strategy to prevent excess translocation to the shoot by increasing root thickness and increase lignin production (Gomes et al. 2011).

Deposition of atmospheric HMs on the leaves surface can activate foliar uptake either through diffusion for lipophilic compounds via cuticle or via aqueous pores of the stomata and cuticle for hydrophilic compounds, therefore increase level of HMs in the leaves. This scenario has been recorded for plants and leafy vegetables that are grown near to mining and smelting areas. Types of HMs that are commonly found in these plants are Fe, Mn, Zn, Cu, Cd, Pb, As, and Cr (Shahid et al. 2017). A report published by Nabulo et al. (2006) showed that the presence of Pb, Zn, and Cd in *Amaranthus dubius* (red spinach), a leafy vegetable that was grown near to the road. Out of total HMs in the shoots, less than 1% is transported to the root (Shahid et al. 2017). As reported by Leitenmaier and Küpper (2013), there are three groups of plants that have different abilities to cope with HMs exposure. First is indicator plants, in which they are usually sensitive to heavy metals, second is excluders, in which they are a type of plants that can tolerate heavy metals in the soil up to a threshold concentration by preventing the accumulation of metal in the cells (i.e., hyperaccumulator), and third is plants that can not only tolerate high concentrations of specific elements but also actively take up and accumulate HMs to several percent of the dry mass of their above-ground parts (i.e., non-hyperaccumulator).

12.3 Metal Ion Transporters in Plants

Transportation and translocation of HMs between root and shoots involve metal transporters, the transporters that introduce metals into the cytosol and transporters that remove metals out from the cytosol (Table 12.1). The proteins are located across the cell membrane, tonoplast, and other subcellular membrane bounded organelles, and they are specific to HMs. When HMs enter the plant cell, the localization of metal transporters is controlled by the availability of the metal ions and trafficking mechanism. This system, therefore, can regulate the metal ion uptake into the plant cells. As an example, the ZIPs are synthesized on ribosomes attached to the endoplasmic reticulum (ER) and then trafficked to different intracellular compartments. Many ZIPs are available on the cell surface coexisting with availability of Zn. The depletion of Zn causes a decrease in endocytosis and degradation of ZIPs, in which increase the Zn uptakes (Bowers and Srai 2018). The ATPase, however, is normally located at the Golgi apparatus. High availability of Cu

Table 12.1 Type of metal ion transporters and metal ion specificity

Transporters that introduce metals into the cytosol	
Heavy metal transporter	Metal ion specificity
ZIP (zinc-regulated transporter iron-regulated transporter proteins)	Fe^{2+}, Zn^{2+}, Ni^{2+}, and Mn^{2+}
Ctr/COPT transporters (copper transporter)	Cu^{+}
NRAMP transporters	Fe^{2+}, Mn^{2+}, Co^{2+}, Zn^{2+} and Ni^{2+}
YSL transporters (yellow stripe-like proteins)	Fe^{2+}-Nicotianamine
MOT1 (molybdate transporter type 1)	Mo
Transporters that remove metals out of the cytosol	
Heavy metal transporter	Metal ion specificity
P1b-ATPases	$P_{1b\text{-}1}$ for cu^{+}, $P_{1b\text{-}2}$ for Zn^{2+}
CDF transporters (cation diffusion facilitator)	Fe^{2+}, Zn^{2+}, and Mn^{2+}
Ferroportins	Fe^{2+}, Ni^{2+}, and Co^{2+}
VIT1/CCC1	Fe^{2+} and Mn^{2+}

Source: González-Guerrero et al. (2016).

redistributes the ATPase to the plasma membrane (Williams et al. 2000). Apart from that, the involvement of choline transporter regulator, CTL1 has also been reported to regulate the expression pattern of different ion transporters through modulation of vesicle trafficking. Loss of function of CTL1 in the root was reported to significantly disrupt the leaf homeostasis of Na, Mn, Fe, Zn, and Mo (Gao et al. 2017).

At the transcriptional level, the expression of ion transporters in the root is coordinated by a series of transcription factors (TFs) after the protein receiving signal from MAPK cascade. The TFs include MYB (myeloblastosis), WRKY (containing a conserved WRKYGQK domain and a zinc finger-like motif), ZAT (C2H2-type zinc finger transcription factor), bZIP (basic region leucine ZIPper), AP2 (Activating Protein 2), ERF (ethylene-responsive factor), and DREB (dehydration responsive element-binding protein) (Jalmi et al. 2018). Upon exposure to Cd, *A. thaliana*, *A. halleri*, and *Brassica juncea* induced accumulation of bZIP, ERF1, and ERF5 (Singh et al. 2016).

The P-type ATPase, RAN1 (responsive to antagonist 1), has been reported to involve in transporting Cu^{2+}, in which the metal ion is involved in helping the perception between ethylene and its receptor (Williams et al. 2000). Characterization of RAN1 using engineered *Saccharomyces cerevisiae* expressing ETR1 (ethylene receptor 1) but lacking RAN1 homolog Ccc2p (Δccc2) further showed deficiency in ethylene-binding activity. The ethylene activity was restored when Cu^{2+} were added to the Δccc2 mutants. A study on plants carrying loss-of-function mutations in ran1 was also shown to have lacked ethylene-binding activity (Binder et al. 2010). Hence, in plants, P-type ATPase is important in activation of plant ethylene signaling pathway.

12.4 HMs Uptake in Hyperaccumulator and Non-Hyperaccumulator Plant Species

Many plants can accumulate HMs without giving harms to their metabolism. These plant species are recognized as hyperaccumulator and non-hyperaccumulator. More than 450 plant species, including trees, crops, vegetables, and weeds belong to hyperaccumulators. These species are capable in translocating HMs from roots to the aerial parts at concentration of 100 to 1000-fold higher than that of non-hyperaccumulators from the same plant genus without showing visible toxicity symptoms (Singh et al. 2016; Chandra et al. 2018). The hyperaccumulator species and their capacity in translocating different types of HMs are summarized in Table 12.2.

The non-hyperaccumulators (Table 12.3) is a low HM accumulating plants, but the species produce high biomass. Examples of non-hyperaccumulator plants are willow, poplar, and Brazilian leguminous trees (*Mimosa caesalpiniaefolia*, *Erythrina speciosa*, and *Schizolobium parahyba*) (Souza et al. 2013). In non-hyperaccumulator species, strong ligands function to complex with metal ion, while formation of transient binding between ligand and metal ion is found in hyperaccumulators species. The transient binding allows metal transportation to storage site that is usually located at leaf epidermis (Leitenmaier and Küpper 2013). A number of ligands produced by plants such as organic acids (e.g., mugineic acid, avenic acid, citric acid, and nicotianamine,), amino acids (e.g., histidine), and

Table 12.2 Hyperaccumulator species and its heavy metals specificity

Plant species	Family	Metal (s) that accumulate	Concentration of heavy metal accumulated in aerial parts	References
Cardamine violifolia	Brassicaceae	Se	2000 and 2700 mg/kg DW of se in leaves of 100 and 200 μM selenate treated seedling	Both et al. (2020)
Arabidopsis halleri	Brassicaceae	Zn	4000 μg g − 1 DW in shoots of plant grown on soil containing 100 μg g^{-1} Zn	Peer et al. (2006)
Thlaspi caerulescens	Brassicaceae	Zn	2000 μg g^{-1} in shoots of plant grown on soil containing 100 μg g^{-1} Zn and 100 μg g^{-1} Ni	Peer et al. (2006)
Thlaspi praecox	Brassicaceae	Cd	2700 μg g-1 dry weight of cd in shoots	Tolra et al. (2006)
Senecio conrathii	Compositae	Ni	1695 μg g^{-1} DW of Ni in leaves	Siebert et al. (2018)
Berkheya zeyheri	Asteraceae	Ni	1793 μg g^{-1} DW of Ni in leaves	Siebert et al. (2018)
Viola baoshanensis	Violaceae	Cd	456–2310 mg kg^{-1} DW of cd in the shoots	Liu et al. (2004)

Table 12.3 Non-hyperaccumulator species and its heavy metal specificity

Plant species	Family	Metal (s) that accumulate	Concentration of heavy metal accumulated in aerial parts	References
Cardamine pratensis	Brassicaceae	Se	500 mg kg^{-1} DW of se in leaves of 100 uM selenate-treated seedling	Both et al. (2020)
Brassica juncea	Brassicaceae	Se	2000 mg kg^{-1} DW of se in leaves	Harris et al. (2014)
Thlaspi arvense	Brassicaceae	Cd	>4000 ug g^{-1} DW of cd in root	Tolra et al. (2006)
Senecio coronatus	Asteraceae	Ni	30 μg g^{-1} of Ni in root	Mesjasz-Przybyłowicz et al. (2007)
Pteris ensiformis L.	Pteridaceae	As	69 mg kg^{-1} of as in root	Singh and Ma (2006)

peptides and proteins (e.g., phytochelatins) (Callahan et al. 2006). Some hyperaccumulator species such as *Noccaea goesingense* and *Alyssum lesbiacum* accumulate high levels of free His in their root tissues compared with non-hyperaccumulators, suggesting its role as ion chelator (Ingle et al. 2005; Kozhevnikova et al. 2014). Meanwhile, the nicotianamine is the main ligand found in genus *Noccaea*, and it is mainly for chelating Ni (van der Pas and Ingle 2019).

The mechanisms in uptaking and translocating HMs in hyperaccumulator species involve transportation of metal ions across the plasma membrane of root cells, xylem loading and translocation of HMs in shoot, detoxification, and finally sequestration of HMs at the whole plant and cellular levels (Yang et al. 2005). The translocation of HMs in the xylem occurs due to transpiration (Hossain et al. 2012).

In hyperaccumulators species, expression of *yellow strip 1-like proteins* (*YSL*), aluminum-activated malate transporter (*ALMT*), *zinc-regulated transporter iron-regulated transporter proteins* (*ZIP*), *multidrug and toxin efflux* (*MATE*), *heavy metal transporting ATPases* (*HMA*), *metal transporter proteins* (*MTP*), and *ATP-binding cassette* (*ABC*) families are observed (Dar et al. 2020). *YSL* gene is responsible in producing plasma-localized transporters that are involved in transporting HM-nicotianamine (NA) complex. The complex metal elements include Fe(II)-NA, Cu-NA, Zn-NA, and Cd-NA (Shu et al. 2019). *A. halleri* is known to hyperaccumulate Zn and Cd. For Zn transportation, there are four genes that are reported to highly express during Zn uptakes. The genes are *HMA4*, *ZIP9*, *ZIP6*, and *ZIP3*. The ZIP proteins are involved in cytoplasmic metal influx in roots, while HMA4 protein is involved in Zn root-to-shoot transportation (Grennan 2009). Differential expression of ZIP genes family (*TcIRT1*, *TcIRT2*, *TcZNT1*, and *TcZNT5*) was observed in the *Thlaspi caerulescens* roots ecotype Ganges and Prayon when the plants were grown in hydroponic system with and without addition of Fe and Cd. The upregulation of *TcIRT1* expression was observed in plants grown in Fe deficiency media and Cd containing media. *TcIRT2* expression was stimulated by Fe deficiency, and the gene was not expressed in Cd-treated plants (Plaza et al. 2007). These findings suggest the involvement of *TcIRT2* in Fe homeostasis in *T. caerulescens*. The increment of Cd uptake during Fe deficiency was also reported by Lombi et al. (2002). They reported an increase of V_{max} of Cd in Fe-deficient Ganges, which was three times higher than Fe-sufficient plants. Apart from transporting Zn and Cd, ZIP transporter is reported to transport Mn^{2+}, Fe^{2+}, Co^{2+}, Cu^{2+}, and Ni^{2+}. Meanwhile, the iron-regulated transporters (IRTs) are reported to be members of the ZIP family transporters as they have been proven to involve in Fe^{2+} uptake and transport in *Arabidopsis* (Krishna et al. 2020). Overexpression studies showed that *ZmIRT1* enhanced Fe and Zn uptakes in roots and seeds of *Arabidopsis*, while *ZmZIP3* increased Zn accumulation only in the *Arabidopsis* roots. The findings show selectivity mechanism of different ZIP genes from maize (Li et al. 2015). In rice, *OsZIP1* functions as efflux transporter when the plant grows under excess concentration of Zn, Cu, and Cd, and it can work as metal uptake when the rice is under HMs deficiency. Overexpression of *OsZIP1* in rice decreased concentration of Zn, Cu, and Cd when the transgenic rice plants were exposed to excess concentration of HMs. The efflux activity of OsZIP1, therefore, showed growth improvements of the rice plants (Liu et al. 2019).

Large gene copy number of ion transporter has also been observed in non-hyperaccumulator species. For instances, *Sedum alfredii* showed to have high copy number of *heavy metal transporting ATPases* (*HMAs*) gene as compared with its non-hyperaccumulator ecotype (Huang et al. 2020). Northern analysis toward hyperaccumulator and non-hyperaccumulator species of Zn further showed an abundant of zinc transporter ZNT1 in *T. caerulescens* compared with that of *T. arvense* (Guerinot 2000). The finding shows different ability of plants to accumulate Zn even though both of them are from the same genus. However, efflux transporter that involved in metal effluxion from the cytoplasm found to be involved in transporting Zn^{2+}, Mn^{2+}, Fe^{2+}, Cd^{2+}, Co^{2+}, and Ni^{2+} in both non-hyperaccumulators (e.g., *A. thaliana*) and hyperaccumulators (e.g., *A. halleri* and *N. caerulescens*) (Ricachenevsky et al. 2013).

12.5 Involvement of Phytohormones in Response to HMs Exposure

Phytohormones (e.g., auxins, cytokinins, abscisic acid, salicylic acids, gibberellic acids, and brassinosteroids) play important role in transmitting signal when plants responding to low and high level of HMs. The interaction between phytohormones and DNA elements located at promoter can activate the expression of HMs responsive genes (Pál et al. 2018). In response to accumulation of HMs, expression of auxin-related genes like *phosphoribosyl anthranilate transferase 1* (*PAT1*), *CYP79B2* and *CYP79B3*, *YUCCA* (*YUC*), *Gretchen Hagen* (*GH3*), and *PINFORMED1* (*PIN1*) was observed in plants. The expression of these genes is associated with high level of endogenous auxins (Jalmi et al. 2018). However, depletion of endogenous auxin and other phytohormones may also occur when plants responding to toxic HMs. Many researchers found that exogenous application of auxins may alleviate HM toxicity through regulation of the endogenous phytohormone levels. Piotrowska-Niczyporuk et al. (2020) reported that exogenous application of auxin and cytokinin alleviated Pb toxicity through regulation of the endogenous phytohormones levels.

Accumulation of abscisic acid (ABA) increases after HMs exposure. The increment suggests an involvement of ABA in protective mechanisms against HMs toxicity. Previous studies showed that ABA accumulation was increased when plants responding to Cd, Cu, Ni, Zn, and Pb (Bücker-Neto et al. 2017). Elevated of endogenous ABA was determined in *Oryza sativa*, *Solanum tuberosum*, *Brassica napus*, and many plant species exposed to Cd. The findings were paralleled with upregulation of genes involved in ABA biosynthesis (Hu et al. 2020). Expression of *OsNCED3*, *OsNCED4*, and *OsNCED5* was observed in rice when the plants were exposed to Cd (Tan et al. 2017).

Salicylic acid, however, interacts with other plant hormones such as auxin, gibberellic acids, and abscisic acids to promote stimulation of antioxidant compounds and enzymes. This interaction leads to increasing of plant tolerance and adaptation (Sharma et al. 2020). The content of glutathione, non-protein thiol, and phytochelatins increased in *Nymphaea tetragona* in response to Cd. The activities of antioxidant enzymes such as superoxide dismutase, peroxidase, and ascorbate peroxidase were also increased (Gu et al. 2018). Furthermore, exogenous application of salicylic acid ameliorated toxic effects of HMs in cauliflower (Sinha et al. 2015). Application of GA_3 was also alleviated the inhibitory effect of Cd and Mo on seed germination of barley (Amri et al. 2016). Also, the exogenous GA_3 can upregulate salicylic acid biosynthesis, therefore enhancing the HMs tolerance (Emamverdian et al. 2020).

12.6 Conclusion and Future Prospects

HMs pollution has become serious problem due to anthropogenic activities. The harmful HMs can contaminate food chain and therefore can lead to serious ailments in humans. Understanding plants scavenging activities toward HMs is crucial in order to find the best plant system to remediate HMs from the environment. Hyperaccumulator can uptake high amount of HMs; however due to low plant biomass, the hyperaccumulator species is reported not very efficient to be used in phytromediation. Non-hyperaccumulator is therefore suggested due to high biomass produced, even though the plants can just uptake low amount of HMs. Hence, understanding scavenging mechanisms including ligands and ion transporters activities in hyperaccumulator and non-hyperaccumulator species can help in transgenic plants development. The gene candidate from hyperaccumulator species can be used for development of transgenic non-hyperaccumulators with high biomass. Hence, the future focus is to find the gene candidate from hypoaccumulator species and the non-hyperaccumulator species for development of transgenic plants. Apart from that, application of genome editing technique can also be applied to produce superior plants that increase tolerance toward HMs and at the same time can uptake high amount of HMs and produce high biomass.

References

Ali H, Khan E, Ilahi I (2019) Environmental chemistry and ecotoxicology of hazardous heavy metals: environmental persistence, toxicity, and bioaccumulation. J Chem 2019:1–14

Amri B, Khamassi K, Ali MB, da Silva JA, Kaab LB (2016) Effects of gibberellic acid on the process of organic reserve mobilization in barley grains germinated in the presence of cadmium and molybdenum. S Afr J Bot 106:35–40

Atabaki N, Shaharuddin NA, Ahmad SA, Nulit R, Abiri R (2020) Assessment of water mimosa (*Neptunia oleracea* Lour.) Morphological, physiological, and removal efficiency for phytoremediation of arsenic-polluted water. Plan Theory 9:1500

Balafrej H, Bogusz D, Triqui Z-E A, Guedira A, Bendaou N, Smouni A, Fahr M (2020) Zinc hyperaccumulation in plants: a review. Plan Theory 9:1–22

Binder BM, Rodríguez FI, Bleecker AB (2010) The copper transporter RAN1 is essential for biogenesis of ethylene receptors in *Arabidopsis*. J Biol Chem 285:37263–37270

Both EB, Stonehouse GC, Lima LW, Fakra SC, Aguirre B, Wangeline AL, Xiang J, Yin H, Jokai Z, Soos A, Dernovics M, Pilon-Smits EAH (2020) Selenium tolerance, accumulation, localization and speciation in a *Cardamine* hyperaccumulator and a non-hyperaccumulator. Sci Total Environ 703:1–27

Bowers K, Srai SKS (2018) The trafficking of metal ion transporters of the Zrt- and Irt-like protein family. Traffic 19:813–822

Bücker-Neto L, Paiva AL, Machado RD, Arenhart RA, Margis-Pinheiro M (2017) Interactions between plant hormones and heavy metals responses. Genet Mol Biol 40:373–386

Callahan DL, Baker AJ, Kolev SD, Wedd AG (2006) Metal ion ligands in hyperaccumulating plants. J Biol Inorg Chem 11:2–12

Chandra R, Kumar V, Singh K (2018) Hyperaccumulator versus nonhyperaccumulator plants for environmental waste management. In: Chandra R, Dubey NK, Kumar V (eds) Phytoremediation of environmental pollutants. CRC Press, Florida, pp 43–74

Dar FA, Pirzadah TB, Malik B (2020) Accumulation of heavy metals in medicinal and aromatic plants. In: Aftar T, Hakeem KR (eds) Plant micronutrients deficiency and toxicity management. Springer, Cham, pp 113–127

Emamverdian A, Ding Y, Mokhberdoran F (2020) The role of salicylic acid and gibberellin signaling in plant responses to abiotic stress with an emphasis on heavy metals. Plant Signal Behav 15:7

Gao Y-Q, Chen J-G, Chen Z-R, An D, Lv Q-Y, Han M-L, Wang Y-L, Salt DE, Chao D-Y (2017) A new vesicle trafficking regulator CTL1 plays a crucial role in ion homeostasis. PLoS Biol 15: e2002978

Gomes MP, Marques TCLLSM, Nogueira MOG, Castro EM, Soares AM (2011) Ecophysiological and anatomical changes due to uptake and accumulation of heavy metal in *Brachiaria decumbens*. Sci Agric 68:566–573

González-Guerrero M, Escudero V, Saéz A, Tejada-Jiménez M (2016) Transition metal transport in plants and associated endosymbionts: arbuscular mycorrhizal fungi and rhizobia. Front Plant Sci 7:1–21

Grennan AK (2009) Identification of genes involved in metal transport in plants. Plant Physiol 149: 1623–1624

Gu CS, Yang YH, Shao YF, Wu KW, Liu ZL (2018) The effects of exogenous salicylic acid on alleviating cadmium toxicity in *Nymphaea tetragona* Georgi. S Afr J Bot 114:267–271

Guerinot ML (2000) The ZIP family of metal transporters. Biochim Biophys Acta 1-2:190–198

Hall JL, Williams LE (2003) Transition metal transporters in plants. J Exp Bot 54:2601–2613

Harris J, Schneberg KA, Pilon-Smits EAH (2014) Sulfur–selenium–molybdenum interactions distinguish selenium hyperaccumulator *Stanleya pinnata* from non-hyperaccumulator *Brassica juncea* (Brassicaceae). Planta 239:479–491

Hossain MA, Piyatida P, Silva JAT, Fujita M (2012) Molecular mechanism of heavy metal toxicity and tolerance in plants: central role of glutathione in detoxification of reactive oxygen species and methylglyoxal and in heavy metal chelation. Int J Chem Eng 2012:1–37

Hu B, Deng F, Chen G, Chen X, Gao W, Long L, Xia J, Chen ZH (2020) Evolution of abscisic acid signaling for stress responses to toxic metals and metalloids. Front Plant Sci 11:909

Huang X, Duan S, Wu Q, Yu M, Shabala S (2020) Reducing cadmium accumulation in plants: structure–function relations and tissue-specific operation of transporters in the spotlight. Plan Theory 9:223

Ingle RA, Mugford ST, Rees JD, Campbell MM, Smith JA (2005) Constitutively high expression of the histidine biosynthetic pathway contributes to nickel tolerance in hyperaccumulator plants. Plant Cell 17:2089–2106

Jalmi SK, Bhagat PK, Verma D, Noryang S, Tayyeba S, Singh K, Sharma D, Sinha AK (2018) Traversing the links between heavy metal stress and plant signalling. Front Plant Sci 9:12

Kinuthia GK, Ngure V, Beti D, Lugalia R, Wangila A, Kamau L (2020) Levels of heavy metals in wastewater and soil samples from open drainage channels in Nairobi, Kenya: community health implication. Sci Rep 10:1–13

Kozhevnikova AD, Seregin IV, Erlikh NT, Shevyreva TA, Andreev IM, Verweij R, Schat H (2014) Histidine-mediated xylem loading of zinc is a species-wide character in *Noccaea caerulescens*. New Phytol 203:508–519

Krishna TPA, Maharajan T, Roch GV, Ignacimuthu S, Ceasar SA (2020) Structure, function, regulation and phylogenetic relationship of ZIP family transporters of plants. Front Plant Sci 11:1–18

Leitenmaier B, Küpper H (2013) Compartmentation and complexation of metals in hyperaccumulator plants. Front Plant Sci 4:374

Li S, Zhou X, Li H, Liu Y, Zhu L, Guo J, Liu X, Fan Y, Chen J, Chen R (2015) Overexpression of *ZmIRT1* and *ZmZIP3* enhances iron and zinc accumulation in transgenic *Arabidopsis*. PLoS One 10:1–21

Liu W, Shu W, Lan C (2004) *Viola baoshanensis*, a plant that hyperaccumulates cadmium. Chin Sci Bull 49:29–32

Liu XS, Feng SJ, Zhang BQ, Wang MQ, Cao HW, Rono JK, Chen X, Yang ZM (2019) OsZIP1 functions as a metal efflux transporter limiting excess zinc, copper and cadmium accumulation in rice. BMC Plant Biol 19:1–16

Lombi E, Tearall KL, Howarth JR, Zhao F-J, Hawkesford MJ, McGrath SP (2002) Influence of iron status on cadmium and zinc uptake by different ecotypes of the hyperaccumulator *Thlaspi caerulescens*. Plant Physiol 128:1359–1367

Ma Y, Oliveira RS, Freitas H, Zhang C (2016) Biochemical and molecular mechanisms of plant-microbe-metal interactions: relevance for phytoremediation. Front Plant Sci 7:1–19

Mesjasz-Przybyłowicz J, Barnabas A, Przybyłowicz W (2007) Comparison of cytology and distribution of nickel in roots of Ni-hyperaccumulating and non-hyperaccumulating genotypes of *Senecio coronatus*. Plant and Soil 293:61–78

Nabulo G, Oryem-Origa H, Diamond M (2006) Assessment of lead, cadmium, and zinc contamination of roadside soils, surface films, and vegetables in Kampala City, Uganda. Environ Res 101:42–52

Pál M, Janda T, Szalai G (2018) Interactions between plant hormones and thiol-related heavy metal chelators. Plant Growth Regul 85:173–185

Peer WA, Mahmoudian M, Freeman JL, Lahner B, Richards EL, Reeves RD, Murphy AS, Salt DE (2006) Assessment of plants from the Brassicaceae family as genetic models for the study of nickel and zinc hyperaccumulation. New Phytol 172:248–260

Piotrowska-Niczyporuk A, Bajguz A, Kotowska U, Zambrzycka-Szelewa E, Sienkiewicz A (2020) Auxins and cytokinins regulate phytohormone homeostasis and thiol-mediated detoxification in the green alga *Acutodesmus obliquus* exposed to lead stress. Sci Rep 10:1–4

Plaza S, Tearall KL, Zhao F-J, Buchner P, McGrath SP, Hawkesford MJ (2007) Expression and functional analysis of metal transporter genes in two contrasting ecotypes of the hyperaccumulator *Thlaspi caerulescens*. J Exp Bot 58:1717–1728

Rai PK, Lee SS, Zhang M, Tsang YF, Kim K-H (2019) Heavy metals in food crops: health risks, fate, mechanisms, and management. Environ Int 125:365–385

Raza A, Habib M, Kakavand SN, Zahid Z, Zahra N, Sharif R, Hasanuzzaman M (2020) Phytoremediation of cadmium: physiological, biochemical, and molecular mechanisms. Biol 9:1–47

Ricachenevsky FK, Menguer PK, Sperotto RA, Williams LE, Fett JP (2013) Roles of plant metal tolerance proteins (MTP) in metal storage and potential use in biofortification strategies. Front Plant Sci 4:144

Shahid M, Dumat C, Khalid S, Schreck E, Xiong T, Niazi NK (2017) Foliar heavy metal uptake, toxicity and detoxification in plants: a comparison of foliar and root metal uptake. J Hazard Mater 325:36–58

Sharma A, Sidhu GP, Araniti F, Bali AS, Shahzad B, Tripathi DK, Brestic M, Skalicky M, Landi M (2020) The role of salicylic acid in plants exposed to heavy metals. Molecules 25:540

Shu H, Zhang J, Liu F, Bian C, Liang J, Liang J, Liang W, Lin Z, Shu W, Li J, Shi Q, Liao B (2019) Comparative transcriptomic studies on a cadmium hyperaccumulator *Viola baoshanensis* and its non-tolerant counterpart *V. inconspicua*. Mol Sci 20:1–20

Siebert SJ, Schutte NC, Bester SP, Komape DM, Rajakaruna N (2018) *Senecio conrathii* N.E.Br. (Asteraceae), a new hyperaccumulator of nickel from serpentinite outcrops of the Barberton Greenstone Belt, South Africa. Ecol Res 33:651–658

Singh N, Ma LQ (2006) Arsenic speciation, and arsenic and phosphate distribution in arsenic hyperaccumulator *Pteris vittata* L. and non-hyperaccumulator *Pteris ensiformis* L. Environ Pollut 141:238–246

Singh S, Parihar P, Singh R, Singh VP, Prasad SM (2016) Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics, and ionomics. Front Plant Sci 6:1143

Sinha P, Shukla AK, Sharma YK (2015) Amelioration of heavy-metal toxicity in cauliflower by application of salicylic acid. Commun Soil Sci Plant Anal 46:1309–1319

Souza LA, Piotto FA, Nogueirol RC, Antunes A (2013) Use of non-hyperaccumulator plant species for the phytoextraction of heavy metals using chelating agents. Sci Agric 70:290–295

Sytar O, Kumari P, Yadav S, Brestic M, Rastogi A (2019) Phytohormone priming: regulator for heavy metal stress in plants. J Plant Growth Regul 38:739–752

Tan M, Cheng D, Yang Y, Zhang G, Qin M, Chen J et al (2017) Co-expression network analysis of the transcriptomes of rice roots exposed to various cadmium stresses reveals universal cadmium-responsive genes. BMC Plant Biol 17:194

Tangahu BV, Abdullah SRS, Basri H, Idris M, Anuar N, Mukhlisin M (2011) A review on heavy metals (As, Pb, and Hg) uptake by plants through phytoremediation. Int J Chem Eng 2011:1–33

Tolra R, Pongrac P, Poschenrieder C, Vogel-Mikuš K, Regvar M, Barcelo J (2006) Distinctive effects of cadmium on glucosinolate profiles in Cd hyperaccumulator *Thlaspi praecox* and non-hyperaccumulator *Thlaspi arvense*. Plant and Soil 288:333–341

van der Pas L, Ingle R (2019) Towards an understanding of the molecular basis of nickel hyperaccumulation in plants. Plan Theory 8:11

Vareda JP, Valente AJM, Duraesa L (2019) Assessment of heavy metal pollution from anthropogenic activities and remediation strategies: a review. J Environ Manage 246:101–118

Williams LE, Pittman JK, Hall JL (2000) Emerging mechanisms for heavy metal transport in plants. Biochim Biophys Acta Biomembr 1465:104–126

Yang X, Fenga Y, He Z, Stoffella PJ (2005) Molecular mechanisms of heavy metal hyperaccumulation and phytoremediation. J Trace Elem Med Biol 18:339–353

Role of Plant Microbiome Under Stress Environment to Enhance Crop Productivity

13

Swati Sachdev and Mohammad Israil Ansari

Abstract

Plants during their life cycle often come across multiple biotic and abiotic stress that mutilates their growth and productivity. As the world's population is increasing gradually and the climate is changing at an alarming rate, the need for global food security has become the priority. Therefore, addressing approaches that can enhance food productivity sustainably and safeguard food availability in the future is the need of the hour. Plants possess an intrinsic defense mechanism to combat stressful environmental conditions but in severe conditions are unable to overcome persisting situations. To strengthen their defense system plants recruit associated beneficial microbiome that alleviates stresses and promotes plant growth. Plants select particular microorganisms mainly through the production of varied compounds via root exudates. The plant microbiome lives either as epiphytes in the rhizosphere and phyllosphere or as endophytes within living tissues and caters multiple beneficial effects. The plant microbiome shows resilience toward stress and promotes plant productivity through various mechanisms. These mechanisms include the production of antioxidants, antibiotics, phytohormones, exopolysaccharides, and cell wall degrading enzymes that lead to inhibition of pathogens, bioremediation of toxic metals, acquisition of nutrients, tolerance toward abiotic stress, and enhanced plant growth parameters. Engineering plant microbiome to enhance stress tolerance and plant growth may be the most sustainable approach that can ensure food security for the growing

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population. Thus, understanding and deciphering mechanisms employed by the plant microbiome is important to harness their potential.

Keywords

Root exudates · Antioxidants · Cell wall degrading enzymes · Exopolysaccharides · Endophytes · Rhizosphere

13.1 Introduction

Plants are the primary producer and chief energy driving sources for other living organisms on earth. Flourished plant growth and productivity are therefore essential to sustain life. Plant in nature encounters number of unfavorable environmental conditions encompassing both biotic and abiotic stresses (Ali and Baek 2020). Incidence of diseases caused by living organisms such as pests (insects) and pathogenic microorganisms (fungi, bacteria, viruses, and oomycetes) trigger biotic stresses (Bulgari et al. 2019; Iqbal et al. 2021). The biotic stress occurs frequently, however, becomes a matter of grave concern when losses incurred surpass the plant's ability to recover the losses (Sachdev and Singh 2016a). Similarly, abiotic stresses including all abiotic adversities such as heat shock, chilling/freezing, drought, water-logging, salinity, heavy metals, pesticides, ozone, nutrient redundancy, or deficiency induce negative responses and toxicity in plants, impinging their growth and yield (Jalil and Ansari 2018; Ali and Baek 2020). It has been estimated that approximately 64% of the total global land area is affected by drought. Similarly, abiotic factors including cold, soil alkalinity, anoxia, mineral deficiency, and salinity have affected nearly 57%, 15%, 13%, 9%, and 6% of land cover, respectively. Around 3.6 billion ha of the world's agricultural dryland has been documented to be influenced by the problems of soil erosion, degradation, and salt stress (Jalil and Ansari 2018).

Incidence of particular stress has been often noticed to enhance plants' susceptibility toward other stresses. In particular, high soil moisture content or water-logging condition may increase the risk of pathogenic diseases in the plant (Sachdev and Singh 2016b). Manifestation of stress(es) either singularly or in concert severely affects a plant's growth and development throughout its life cycle spanning germination to fruit setting stage (Bulgari et al. 2019). Under influence of stress, plant shows loss of photosynthetic activity, reduce stomatal conductance, poor root development, abridge seed germination and seedling vigor, senescence, necrosis, development of cankers, wilting, leaf spot, functional loss of protein and enzymes, nutrient deficiency, stunted growth, reduced plant biomass and productivity, excess ethylene production, over-production of reactive oxygen species (ROS), and even death under severe conditions (Ansari and Lin 2010; Lopes et al. 2021; Iqbal et al. 2021; Sachdev et al. 2021).

Plants are anchored in the soil and therefore cannot escape from stresses, but are capable to manage their growth under unfavorable conditions by deploying intrinsic

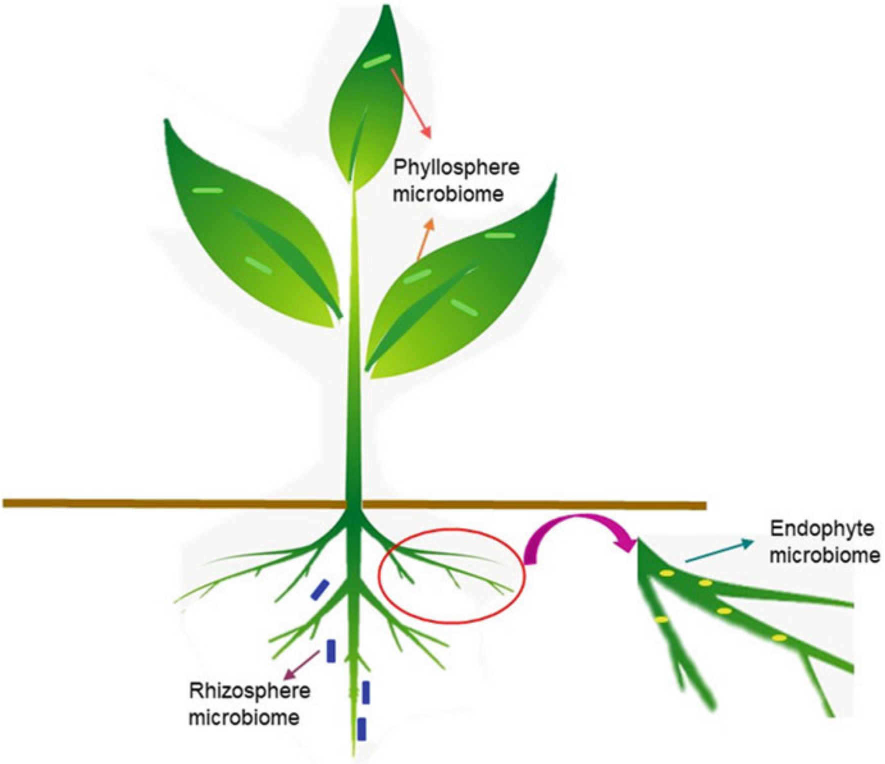

Fig. 13.1 Microbiota colonizing different parts of the plant

defense mechanisms may be at the physiological level or molecular level (Ali and Baek 2020). However, many times, plant innate defense system is not enough to provide complete protection. Plants are holobionts (i.e., the assemblage of host and other species) (Schlaeppi and Bulgarelli 2015) and, under severe conditions, in addition to innate defense mechanisms, hire associated microorganisms to facilitate tolerance and improve productivity. Plant microbiota (plant-associated microbial communities) include highly complex microbial structures (including bacteria, fungi, archaea, virus, protozoa, and algae) inhabiting in episphere (rhizosphere and phyllosphere) and/or endosphere of the plant (Compant et al. 2019) (Fig. 13.1). The genomic constituent of plant microbiota in a particular habitat is referred to as plant microbiome according to Bulgarelli et al. (2013); however, some use the term microbiome to designate the sum of all plant-associated microbial communities (del Carmen Orozco-Masqueda et al. 2018). Plant's host-specific microbiome exhibits either mutualistic, pathogenic, or commensalism association with the meta-organism (Turner et al. 2013; Schlaeppi and Bulgarelli 2015). Many plant-linked microorganisms or plant probiotics execute plant growth and confer tolerance against stress by exploiting number of mechanisms (Kim and Anderson 2018;

Kumar and Verma 2018; Subiramani et al. 2020). In addition to their natural microbiome, plant also recruits or attracts other beneficial microorganisms to fortify their protection. This phenomenon of attracting beneficial microbes from the environment to cope with adverse conditions is termed as "cry for help" strategy (Liu et al. 2020). The volatile organic compounds (VOCs) secreted by plants, released through root exudates aids in attracting specific microbes (Liu and Brettell 2019). For instance, VOCs produced by *Carex arenaria* after being infected by *Fusarium culmorum* were greatly different from VOCs secreted by noninfected plant and observed to attract beneficial bacteria from a distance of more than 12 cm (Schulm-Bohm et al. 2018). Elucidating and understanding the role of plants in recruiting selective microbiome as well as deciphering mechanisms displayed by plant microbiome can facilitate their comprehensive utilization in crop protection and strengthening food security in a sustainable modus operandi (Turner et al. 2013). Realizing the importance and viability of plant microbiome in determining plant's health, productivity, and stress resilience, this chapter has been composed to consolidate the information's on the status of plant microbiomes in stress management and plant fitness.

13.2 Rhizospheric Microbiome

The rhizosphere is a narrow zone of soil surrounding plant roots and a tempting denizen for millions of microbial communities (Sachdev and Singh 2018a). The microbiome assemblage at the rhizosphere is the overall function of host genetics, the growth stage of the plant, root phenotypes, root exudate composition, soil types, and environmental conditions (Li et al. 2018; Qu et al. 2020). A large number of microorganisms are attracted toward the rhizosphere due to the presence of root exudates. Root exudates improve the nutrient level in the rhizosphere that makes this zone a striking ecological niche for the growth and activity of soil microbiota (Compant et al. 2019). The root exudates primarily constitute approximately 5%–20% of photosynthetically fixed carbon and plant nitrogen, along with organic acids, sugars, amino acids, fatty acids, phenolics, proteins, vitamins, and polysaccharides (Walker et al. 2003; Turner et al. 2013) that shape the microbial assemblage in the rhizosphere, termed as rhizospheric effect (Compant et al. 2019; Qu et al. 2020). The rhizospheric effect represents diverse microbial communities in the rhizosphere compared with bulk soil (Qu et al. 2020). In the wheat rhizosphere, the abundance of bacterial communities (pseudomonads, oligotrophs, actinobacteria, and copiotrophs) is reported higher than the bulk soil (Donn et al. 2015). Changes in dynamics of microbial communities over time were also noticed in the rhizosphere that remained unaltered in bulk soil. The composition of root exudates depends on plant species, genotype, developmental stage, and diurnal cycle, determining peculiar microbial assemblage (Qu et al. 2020). The tomato root exudate that comprises sugars and organic acid promoted colonization of antifungal *Pseudomonads* (Kravchenko et al. 2003). Similarly, different amino acids in the root exudate of *Arabidopsis thaliana* facilitate colonization of *Bacillus subtilis* (Massalha et al.

2017). Likewise, leguminous plants under nitrogen-deficient conditions release flavonoids in the soil to attract nitrogen-fixing bacteria (Hassan and Mathesius 2012). The common microbial spp. inhabiting in rhizosphere includes plant growth-promoting bacteria (PGPB) such as *Bacillus* and *Pseudomonas*; arbuscular mycorrhizal fungi (AMF); biocontrol and plant growth-promoting fungi (PGPF) like *Trichoderma* spp.; nitrogen-fixing bacteria (*Rhizobium* spp.); and protozoa that facilitate good health and luxurious plant growth (Mendes et al. 2013).

13.3 Phyllosphere Microbiome

Phyllosphere harbors a diverse array of microbiomes commonly bacteria, fungi, and yeast that influence plant growth and activity (Stone et al. 2018). However, phyllosphere microbiota is less varied than rhizospheric microbiota. The microbial composition of the phyllosphere is also influenced by various factors such as environmental conditions such as moisture, nutrition, etc., plant genotype, leaf topography, and geographical location (Copeland et al. 2015; Stone et al. 2018). In the phyllosphere, majority of the microbiome are found in areas that are comparatively less affected by environmental conditions, in particular, stomatal opening, leaf veins, and base of trichome (Stone et al. 2018). Moisture is the key determinant that restricts microbial growth in the phyllosphere. Microbiota colonizing the phyllosphere prevents desiccation by secreting biosurfactant and/or exopolysaccharides (EPS), which aid in biofilm formation (Stone et al. 2018). The phyllosphere microbiome tolerates UV radiation by synthesizing more pigment, enzymes to scavenge ROS, and DNA protective protein (Stone et al. 2018). The production of EPS also protects microbiota from harmful UV radiation (Stone et al. 2018).

13.4 Endophytic Microbiome

Microbiota inhabiting within plant tissues may be in leaves, roots, and/or stems and colonizing intercellular and intracellular spaces are called endophytic microbiota (Turner et al. 2013; Ghiasian 2020). Endophytic microbes may include bacterial or fungal species that live inside living tissue for all or part of their life cycle (Lata et al. 2018). Endophytes are considered as subpopulation of rhizospheric microbiota; however, not all rhizospheric microbes are endophytes (Turner et al. 2013). The distribution of endophytes inside plants depends upon their colonization ability and availability of nutrients (Gaiero et al. 2013). For instance, the colonization of *Pseudomonas* spp. in potato stem was higher as compared with roots. The endophytic microbiome has been reported to promote plant growth and protect from a number of pathogenic infections (Doty 2017). Endophytes enter inside plants through natural openings like stomata, through wounds or cracks caused by mechanical abrasion and pathogens, and the formation of lateral roots (Lata et al. 2018). Endophytic microbiome to enter within host tissues produces several hydrolytic enzymes such as lignin-peroxidase, pectinase, cellulase, and many others that cause degradation of the plant cell wall and facilitate movement of endophytes inside host (Shubha and Srinivas 2017; Lata et al. 2018). These hydrolytic enzymes also referred as cell wall degrading enzymes (CWDEs) support the growth of the host plant and provide protection against pathogenic microorganisms (Shubha and Srinivas 2017).

13.5 Microbiome-Mediated Mechanisms for Plant Growth Under Stress

Plant beneficial microbiota or probiotics either directly or indirectly promote plant growth and enhance resilience against both biotic and abiotic stresses (del Carmen Orozco-Masqueda et al. 2018; Lopes et al. 2021). Different plant microbiome documented in the literature to display activity in amelioration of stress and plant growth has been listed in Table 13.1. Root growth stimulation, improved nutrients and water status of the plant, alleviation of oxidative stress, removal of toxicants from the vicinity of plants, induced local and systemic resistance, fortifying plant defense mechanism and signaling via production of phytohormones, certain enzymes like 1-aminocyclo-propane-1-carboxylate (ACC) deaminase, CWDE, exopolysaccharides, antioxidants, siderophores, volatile compounds, accumulation of osmolytes, and up- and downregulation of stress-responsive genes by the phytomicrobiome assist plant growth and support survival under adverse environmental conditions (Mendes et al. 2013; Vurukonda et al. 2016; del Carmen Orozco-Masqueda et al. 2018; Kim and Anderson 2018; Kumar and Verma 2018; Subiramani et al. 2020). The various mechanisms displayed by the plant microbiome that promote plant growth under stress are shown in Fig. 13.2.

13.5.1 Nutrition: Acquisition and Competition

Root nodules formation by bacteria including *Rhizobium* and *Bradyrhizobium* that are capable to fix atmospheric nitrogen has been reviewed as an important mechanism to accomplish the nitrogen requirement of leguminous plants and promote growth (Mendes et al. 2013; Pascale et al. 2020). Similarly, AMF uptake inorganic orthophosphate has low solubility, from soil and transport inside the plant roots (Pascale et al. 2020). Microorganisms also synthesize iron-chelating siderophores that alleviate the iron deficiency of plants (Lurthy et al. 2020). *Pseudomonad*-derived siderophores have been reported to maintain an iron status of several plant species like pea and many more (Lurthy et al. 2020). Thus, the assemblage of beneficial microorganisms in or around plant tissues facilitates the acquisition of nutrient and maintains nutritional status under adverse conditions. In addition to nutrient uptake, the plant microbiome eliminates pathogenic microorganisms from the plant growth zone by introducing competition for food and space (Rai et al. 2019). Certain beneficial microorganisms with the capacity to synthesize

Table 13.1 Different plant microbiome with ability to confer tolerance against stresses and increase plant growth

Microbe(s)	Plant	Stress	Remarks	References
Rhizobacteria strain YAS 34	Sunflower	Water-deficit	The exopolysaccharide (EPS) producing bacterium improved plant growth parameters under stress condition, improved soil structure in the vicinity of plant root, and improved nitrogen uptake	Alami et al. (2000)
Pseudomonas mendocina and arbuscular mycorrhizal fungi *(Glomus intraradices* and *G. mosseae)*	Lettuce	Water-deficit	Increased antioxidants and reduced oxidative stress	Kohler et al. (2008)
Burkholderia phytofirmans PsJN	Wheat	Water- deficit	Increased photosynthesis, chlorophyll content, grain yield, and improved water use efficiency	Naveed et al. (2014)
Trichoderma harzianum	*Brassica juncea*	Salinity	Improved oil content and nutrient acquisition, increased accumulation of osmolytes and antioxidant, and reduce sodium ion uptake	Ahmad et al. (2015)
T. Harzianum and *Serratia proteamaculans*	Tomato seedling	Fungal pathogen *Rhizoctonia solani*	Protected against pathogen by reducing oxidative burst via an increase in activity of enzymatic antioxidants, viz., catalase, ascorbate peroxidase, superoxide dismutase, and guaiacol peroxidase during the early stage of infection and also improved plant growth parameters	Youssef et al. (2016)
T. Harzianum and *T. atroviride*	Grape	Fungal pathogen *Uncinula necator*	*Trichoderma* produced secondary metabolites harzianic acid and 6PP that suppressed	Pascale et al. (2017)

(continued)

Table 13.1 (continued)

Microbe(s)	Plant	Stress	Remarks	References
			pathogen growth, enhanced crop yield, increased antioxidant activity, and accumulation of polyphenols	
Bacillus megaterium MCR-8	*Vinca rosea*	Nickel	Auxin synthesized by the bacteria promote root and shoot growth and alleviated nickel stress	Khan et al. (2017)
T. asperellum	Maize	Fungal pathogen *Fusarium graminearum* and *F. verticillioides*	Reduced severity of stalk rot and ear rot by 49.83 and 39.63%, modified endophytic microbiome and reduced the accumulation of mycotoxins produced by the pathogen	He et al. (2019)
Aneurinibacillus aneurinilyticus and *Paenibacillus* sp.	French bean seedling	Salinity	The isolate with the ability to synthesize ACC deaminase on inoculation through seed bacterization increased plant growth, chlorophyll content, and ameliorated salinity stress	Gupta and Pandey (2019)
B. cereus	Tomato	Heat	ACC deaminase and EPS production by bacteria increased cleavage of ACC and significantly reduced heat stress and improved plant growth	Mukhtar et al. (2020)

siderophores prevent pathogenic infection by increasing competition for iron, present in limited quantity and essentially required for the growth of pathogenic strains (Sachdev and Singh 2018b). Siderophores bind with iron and reduce their availability to pathogenic microbes, resulting in starvation and elimination (Kumar and Verma 2018; Rai et al. 2019). *Trichoderma* spp.–mediated production of

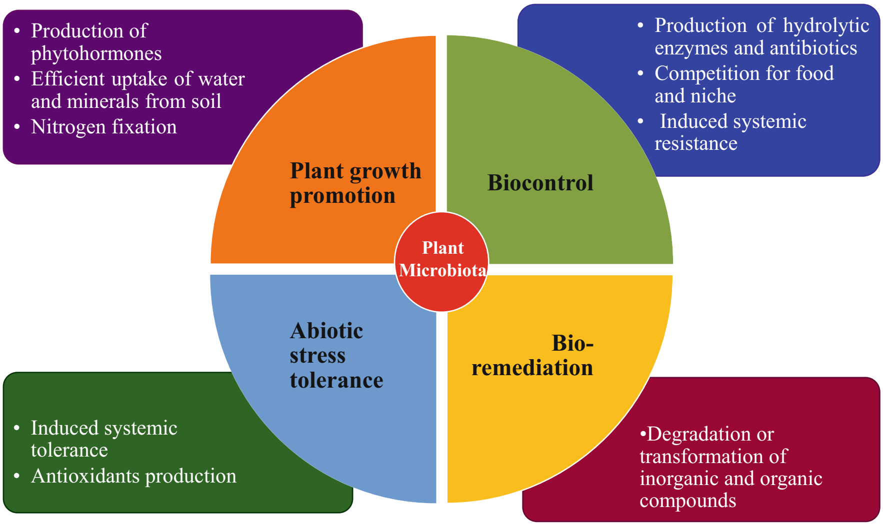

Fig. 13.2 The multiple mechanisms involved by the plant microbiome that confer stress resilience and promote plant growth

siderophores has been reported to suppress the growth of pathogenic fungus *Fusarium lycopersici* causal agent of Fusarium wilt in tomato (Segarra et al. 2009). Likewise, suppression of pathogen *Erwinia carotovora* by an endophytic bacteria *P. fluorescens* by competing for bioavailable iron (Latha et al. 2019).

13.5.2 Production of Phytohormones

Phytohormones including indole acetic acid (IAA), gibberellins, cytokinins, etc., play an instrumental role in conferring tolerance against environmental stress (Jalil and Ansari 2018). Production of IAA by plant-associated microorganisms can alter the architecture of plants' roots, enhancing the number of root tips and surface area (Kaushal and Wani 2016). This modification facilitates deep root anchorage and assists in the improved acquisition of nutrients and water from the soil, thereby promoting growth and alleviating nutrient deficiency and water-deficit stress (Sachdev and Singh 2018b). Seed treatment of clover (*Trifolium repens* L.) with IAA producing *Pseudomonas putida* and *Bacillus megaterium* improved plant biomass under drought (Marulanda et al. 2009). IAA has been shown to induce tolerance in plants against heavy metal stress, which may be due to increased plant biomass that enhances phytoextraction of metals from soil (Egamberdieva et al. 2017). Abscisic acid (ABA) is another important phytohormone that protects plants from stress and regulates their growth (Egamberdieva et al. 2017). ABA mediates signaling that regulates the expression of stress-responsive genes eliciting tolerance against stress (Sah et al. 2016). ABA-producing bacteria *B. licheniformis* and

P. fluorescens promoted the growth of grapevine under drought conditions (Salomon et al. 2014). Likewise, *B. aryabhattai* strain SRB02 with ABA producing ability significantly stimulated biomass of soybean and increased number of nodules in root and trigger drought resilience through stomatal closure under elevated temperature (Park et al. 2017). Cytokinins produced by the plant microbiome have been reported to induce resistance in plants against biotic stress (Akhtar et al. 2020). Priming of *Arabidopsis* with *P. fluorescens* G20–18 that can produce cytokinin has been found to efficiently control bacterial pathogen *P. syringae* (Grosskinsky et al. 2016).

13.5.3 ACC Deaminase Activity

Plants under stress conditions trigger the production of ethylene, which is detrimental to the plant's health (Sapre et al. 2019). The certain microorganism can synthesize ACC deaminase that can cleave ACC, the precursor of ethylene production, and thus abridges ethylene level, alleviates damages incurred by biotic and abiotic stresses, and improves plant growth (Hussain et al. 2018). Plant growth-promoting bacteria (PGPB) *Achromobacter piechauddi* ARV8 have been reported to alleviate the drought stress in pepper and tomato seedling by synthesizing ACC deaminase and significantly improved the growth of the seedlings (Mayak et al. 2004). The rhizobacteria associated with rice root were reported to produce ACC deaminase that induced tolerance against salinity and improved plant growth and development under saline conditions (Bal et al. 2013).

13.5.4 Antibiotics and Cell Wall Degrading Enzymes

Plant-associated microbe's mediate tolerance against biotic stress by synthesizing enzymes and antibiotic compounds that restrict the growth of pests and pathogens. Several microorganisms have also been reported to synthesize CWDEs like chitinase, protease, and β-glucanase that aids disintegration of pathogen cell wall polysaccharides leading to entry into pathogen cytoplasm and parasitic relation for nutrition and ultimately death of pathogen (Sachdev and Singh 2020). Several beneficial fungal species, in particular *Trichoderma* spp., have displayed mycoparasitism and facilitated elimination of pathogens through the production of CWDEs (Sachdev and Singh 2018b). Overgrowth of *T. harzianum* and *T. viride* invading in the colony of plant pathogen *Verticillium dahlia* was reported to reduce the growth of the pathogen (Jabnoun-Khiareddine et al. 2009). Similarly, mycoparasitism and production of CWDEs by *T. harzianum* caused enzymatic lysis of the pathogen *Aspergillus*, inhibiting the growth (Braun et al. 2018).

Several microorganisms have been recorded to secrete low-molecular-weight diffusible nonvolatile and volatile metabolites known as antibiotics or secondary metabolites, which are deleterious to other microbes and inhibit their growth (Vinale et al. 2014a; Kohl et al. 2019). Antimicrobial metabolites are synthesized by bacteria belonging to *Bacillus*, *Pseudomonas*, *Serratia*, *Streptomyces,* and many other genera and fungal genera including *Trichoderma* spp. (Kohl et al. 2019). Iturin, surfactin, and fengycin are some common antibiotics produced by *Bacillus* spp. Similarly, members of *Pseudomonas* genera synthesize pyrrolnitrin, phenazine, and 2,4-Diacetylphloroglucinol (DAPG) (Kohl et al. 2019). *Trichoderma* spp.-derived metabolites harzianic acid, viridin, viridiol, gliovirin, gliotoxin, 6-pentyl-α-pyrone, and terpenoids observed to be capable of suppressing pathogen growth (Ghorbanpour et al. 2018; Sachdev and Singh 2020). The volatile metabolites 6n-pentyl-α-pyrone (6PP) and 6n-pentenyl-α-pyrone synthesized by *T. harzianum* have been reported by Claydon et al. (1987) to show inhibitory effect on the growth of pathogen *Rhizoctonia solani* that causes damping-off in lettuce seedlings. Other secondary metabolites such as harzianic acid, harzianolide, T39 butenolide, T-22 azaphilone, harzianopyridone, and peptaibols biosynthesized by *T. harzianum* have demonstrated a significant inhibitory effect on fungal pathogens *Botrytis cinerea*, *Fusarium oxysporum* f. sp. *conglutinans*, *Gaeumannomyces graminis* var. *tritici*, *Pythium ultimum*, *Pythium irregular*, *Rhizoctonia solani*, and *Sclerotinia sclerotiorum* (Vinale et al. 2006, 2009, 2014b; Palyzova et al. 2019). Plants constituting microbiome that show antibiotic production ability facilitate the alleviation of biotic stress by inhibiting the growth of pathogens. The microbial antibiotic has also shown the ability to assist in nutrition acquisition, thereby enhancing plant growth and reducing nutritional stress in plants. *Pseudomonas* spp. synthesizing DAPG can upregulate the nitrogen fixation ability of *Azospirillum brasilense* and facilitates the mobilization of nutrients such as iron and manganese (Kohl et al. 2019).

13.5.5 Antioxidants and Osmolyte Accumulation

Unfavorable environmental conditions trigger the production of ROS such as hydroxyl ions, singlet oxygen, superoxide radicals, and hydrogen peroxide in plants that act as both signaling and damaging molecules causing cellular injuries depending on their concentration (Baltruschat et al. 2008; Kerchev et al. 2020). Generally, plants recruit intrinsic antioxidants such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POX), ascorbic acid, glutathione, etc. that maintain redox homeostasis of a plant cell by scavenging excessive ROS (Kaushal and Wani 2016). However, in extremely adverse conditions, this equilibrium disturbs resulting in oxidative stress (Baltruschat et al. 2008; Kerchev et al. 2020). The plant microbiome has been observed to modulate the level of both enzymatic and nonenzymatic antioxidants and increase the accumulation of osmolytes that mediates tolerance against oxidative stress (Vurukonda et al. 2016). *Pseudomonas fluorescens* has been reported to promote plant growth under water stress by enhancing the activity of enzymes like CAT and POX and increasing the accumulation of proline (Saravanakumar et al. 2011). The maize seedlings inoculated with *Pseudomonas putida* strain GAP-P45 promoted resilience to water-deficit condition; improved plant growth; increased accumulation of compatible solutes such as proline, free amino acids, and sugars; abridged water loss from leaves; and lowered electrolyte leakage (Sandhya et al. 2010). The phosphate-solubilizing fungal isolate *Penicillium* sp. EU-FTF-6 mitigated negative effects of water-deficit stress in foxtail millet by enhancing the accumulation of osmolytes and reducing lipid peroxidation (Kour et al. 2020). Similarly, the endophytic fungus *Piriformospora indica* alleviated salinity stress in barley by increasing the activity of enzymatic antioxidants such as CAT, ascorbate peroxidase (APX), and others and ascorbic acid in plant roots (Baltruschat et al. 2008). Root colonization by the fungus also improved plant growth and reduced lipid peroxidation. The plant-associated microbiome can reduce oxidative stress triggered due to pathogenic stress. Pretreatment of wheat seedlings with *Trichoderma viride* on subsequent infection with *Fusarium oxysporum* Schlect. improved plant growth parameters and activated antioxidant enzymes (CAT, APX, SOD, and guaiacol peroxidase (GPX)), which imparted resistance against pathogen by reducing H_2O_2 level (Mohapatra and Mittra 2017).

13.5.6 Production of Exopolysaccharides

EPS is the major component of the biofilm and consists of 97% water in the polymer matrix, hence protect from desiccation (Kaushal and Wani 2016). Microbial EPS can improve soil aggregation that helps plants to grow well under water-deficit conditions due to better water and nutrients uptake (Kaushal and Wani 2016). The maize plants inoculated with EPS-producing microbes have displayed resistance toward drought stress (Naseem and Bano 2014). *Pseudomonas* spp. produce alginate, a major form of EPS that helps in maintaining hydration of biofilms by reducing evaporation loss and abridge oxidative stress (Halverson 2009; Kaushal and Wani 2016). In another study, the bacterial strain *P. putida* GAP-P45 was reported to improve drought tolerance in sunflower seedling through the production of EPS and biofilm formation that improved soil aggregation and root-soil adhesion and elevated leave water content (Sandhya et al. 2009).

13.6 Conclusion and Future Perspectives

Plants harbor a variety of microorganisms throughout their life, inhabiting either on the surface or within living tissues. These plant-associated microorganisms are known as plant microbiomes that show a mutualistic, parasitic, or commensal relationship with their host. Plant under the emergency condition of stress hires selective microbes to strengthen their defense system to enhance stress tolerance and growth. Root exudates of plants have been shown to play a very important role in catering to the interaction between plants and their selective microbiome. Plant-associated microbiota showing mutualistic relationship with the plants have tremendous potential to enhance plant productivity under both biotic and abiotic stress. Understanding the factors that regulate plant and microbe interaction and the mechanisms mediated by these beneficial microbes that facilitate growth under individual and multiple stress conditions can be helpful to manipulate plant microbiome to maximize the profits attained. Further, it has been documented that microorganisms thriving under adverse environmental conditions adapt according to persisting conditions and develop tolerant traits. Thus, focusing future research in deciphering potential and mechanisms adopted by microbes with adaptive traits could help to engineer plant microbiome with a more extravagant ability to ameliorate stress and support plant growth under a constantly changing environment.

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References

Ahmad P, Hashem A, Abd-Allah EF, Alqarawi AA, John R, Egamberdieva D, Gucel S (2015) Role of *Trichoderma harzianum* in mitigating NaCl stress in Indian mustard (*Brassica juncea* L) through antioxidative defense system. Front Plant Sci 6:868. https://doi.org/10.3389/fpls.2015.00868

Akhtar SS, Mekureyaw MF, Pandey C, Roitsch T (2020) Role of cytokinins for interactions of plants with microbial pathogens and pest insects. Front Plant Sci 10:1777

Alami Y, Achouak W, Marol C, Heulin T (2000) Rhizosphere soil aggregation and plant growth promotion of sunflowers by an exopolysaccharide-producing *Rhizobium* sp. strain isolated from sunflower roots. Appl Environ Microbiol 66(8):3393–3398

Ali M, Baek KH (2020) Jasmonic acid signaling pathway in response to abiotic stresses in plants. Int J Mol Sci 21(2):621

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

Bal HB, Nayak L, Das S, Adhya TK (2013) Isolation of ACC deaminase producing PGPR from rice rhizosphere and evaluating their plant growth promoting activity under salt stress. Plant and Soil 366(1):93–105

Baltruschat H, Fodor J, Harrach BD, Niemczyk E, Barna B, Gullner G et al (2008) Salt tolerance of barley induced by the root endophyte *Piriformospora indica* is associated with a strong increase in antioxidants. New Phytol 180(2):501–510

Braun H, Woitsch L, Hetzer B, Geisen R, Zange B, Schmidt-Heydt M (2018) *Trichoderma harzianum*: inhibition of mycotoxin producing fungi and toxin biosynthesis. Int J Food Microbiol 280:10–16

Bulgarelli D, Schlaeppi K, Spaepen S, Van Themaat EVL, Schulze-Lefert P (2013) Structure and functions of the bacterial microbiota of plants. Annu Rev Plant Biol 64:807–838

Bulgari R, Franzoni G, Ferrante A (2019) Biostimulants application in horticultural crops under abiotic stress conditions. Agronomy 9(6):306

Claydon N, Allan M, Hanson JR, Avent AG (1987) Antifungal alkyl pyrones of *Trichoderma harzianum*. Trans British Mycol Soc 88:503

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

Copeland JK, Yuan L, Layeghifard M, Wang PW, Guttman DS (2015) Seasonal community succession of the phyllosphere microbiome. Mol Plant Microbe Interact 28(3):274–285

del Carmen Orozco-Mosqueda M, del Carmen Rocha-Granados M, Glick BR, Santoyo G (2018) Microbiome engineering to improve biocontrol and plant growth-promoting mechanisms. Microbiol Res 208:25–31

Donn S, Kirkegaard JA, Perera G, Richardson AE, Watt M (2015) Evolution of bacterial communities in the wheat crop rhizosphere. Environ Microbiol 17(3):610–621

Doty SL (2017) Functional importance of the plant endophytic microbiome: implications for agriculture, forestry, and bioenergy. In: Functional importance of the plant microbiome. Springer, Cham, pp 1–5

Egamberdieva D, Wirth SJ, Alqarawi AA, Abd Allah EF, Hashem A (2017) Phytohormones and beneficial microbes: essential components for plants to balance stress and fitness. Front Microbiol 8:2104

Gaiero JR, McCall CA, Thompson KA, Day NJ, Best AS, Dunfield KE (2013) Inside the root microbiome: bacterial root endophytes and plant growth promotion. Am J Bot 100(9): 1738–1750

Ghiasian M (2020) Endophytic microbiomes: biodiversity, current status, and potential agricultural applications. In: Advances in plant microbiome and sustainable agriculture. Springer, Singapore, pp 61–82

Ghorbanpour M, Omidvari M, Abbaszadeh-Dahaji P, Omidvar R, Kariman K (2018) Mechanisms underlying the protective effects of beneficial fungi against plant diseases. Biol Contr 117:147–157

Großkinsky DK, Tafner R, Moreno MV, Stenglein SA, De Salamone IEG, Nelson LM, Novak O, Strnad M, van der Graaff E, Roitsch T (2016) Cytokinin production by *Pseudomonas fluorescens* G20-18 determines biocontrol activity against *Pseudomonas syringae* in *Arabidopsis*. Sci Rep 6(1):1–11

Gupta S, Pandey S (2019) ACC deaminase producing bacteria with multifarious plant growth promoting traits alleviates salinity stress in French bean (*Phaseolus vulgaris*) plants. Front Microbiol 10:1506

Halverson LJ (2009) Role of alginate in bacterial biofilms. In: Rehm BHA (ed) Alginates, biology and applications. Springer, Berlin, Heidelberg, pp 135–151

Hassan S, Mathesius U (2012) The role of flavonoids in root–rhizosphere signalling: opportunities and challenges for improving plant–microbe interactions. J Exp Bot 63(9):3429–3444

He A, Sun J, Wang X, Zou L, Fu B, Chen J (2019) Reprogrammed endophytic microbial community in maize stalk induced by *Trichoderma asperellum* biocontrol agent against fusarium diseases and mycotoxin accumulation. Fungal Biol 123(6):448–455

Hussain SS, Mehnaz S, Siddique KH (2018) Harnessing the plant microbiome for improved abiotic stress tolerance. In: Plant microbiome: stress response. Springer, Singapore, pp 21–43

Iqbal Z, Iqbal MS, Hashem A, Abd Allah EF, Ansari MI (2021) Plant defense responses to biotic stress and its interplay with fluctuating dark/light conditions. Front Plant Sci 12:297

Jabnoun-Khiareddine H, Daami-Remadi M, Ayed F, El Mahjoub M (2009) Biological control of tomato Verticillium wilt by using indigenous *Trichoderma* spp. African J Plant Sci Biotechnol 3(1):26–36

Jalil SU, Ansari MI (2018) Plant microbiome and its functional mechanism in response to environmental stress. Int J Green Pharm 12(01):81–92

Kaushal M, Wani SP (2016) Plant-growth-promoting rhizobacteria: drought stress alleviators to ameliorate crop production in drylands. Ann Microbiol 66(1):35–42

Kerchev P, van der Meer T, Sujeeth N, Verlee A, Stevens CV, Van Breusegem F, Gechev T (2020) Molecular priming as an approach to induce tolerance against abiotic and oxidative stresses in crop plants. Biotechnol Adv 40:107503

Khan WU, Ahmad SR, Yasin NA, Ali A, Ahmad A, Akram W (2017) Application of *Bacillus megaterium* MCR-8 improved phytoextraction and stress alleviation of nickel in *Vinca rosea*. Int J Phytoremediation 19(9):813–824

Kim YC, Anderson AJ (2018) Rhizosphere pseudomonads as probiotics improving plant health. Mol Plant Pathol 19(10):2349–2359

Kohl J, Kolnaar R, Ravensberg WJ (2019) Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. Front Plant Sci 10:845

Kohler J, Hernández JA, Caravaca F, Roldán A (2008) Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plants. Funct Plant Biol 35(2):141–151

Kour D, Rana KL, Yadav AN, Sheikh I, Kumar V, Dhaliwal HS, Saxena AK (2020) Amelioration of drought stress in foxtail millet (*Setaria italica* L.) by P-solubilizing drought-tolerant microbes with multifarious plant growth promoting attributes. Environ Sustain 3(1):23–34

Kravchenko LV, Azarova TS, Leonova-Erko EI, Shaposhnikov AI, Makarova NM, Tikhonovich IA (2003) Root exudates of tomato plants and their effect on the growth and antifungal activity of *Pseudomonas* strains. Microbiology 72(1):37–41

Kumar A, Verma JP (2018) Does plant—microbe interaction confer stress tolerance in plants: a review? Microbiol Res 207:41–52

Lata R, Chowdhury S, Gond SK, White JF Jr (2018) Induction of abiotic stress tolerance in plants by endophytic microbes. Lett Appl Microbiol 66(4):268–276

Latha P, Karthikeyan M, Rajeswari E (2019) Endophytic bacteria: prospects and applications for the plant disease management. In: Plant health under biotic stress. Springer, Singapore, pp 1–50

Li Y, Wu X, Chen T, Wang W, Liu G, Zhang W, Li S, Wang M, Zhao C, Zhou H, Zhang G (2018) Plant phenotypic traits eventually shape its microbiota: a common garden test. Front Microbiol 9:2479

Liu H, Brettell LE (2019) Plant defense by VOC-induced microbial priming. Trends Plant Sci 24(3):187–189

Liu H, Brettell LE, Qiu Z, Singh BK (2020) Microbiome-mediated stress resistance in plants. Trends Plant Sci

Lopes MJDS, Dias-Filho MB, Gurgel ESC (2021) Successful plant growth-promoting microbes: inoculation methods and abiotic factors. Front Sustain Food Syst 5:48

Lurthy T, Cantat C, Jeudy C, Declerck P, Gallardo K, Barraud C, Leroy F, Ourry A, Lemanceau P, Salon C, Mazurier S (2020) Impact of bacterial siderophores on iron status and ionome in pea. Front Plant Sci 11:730

Marulanda A, Barea JM, Azcón R (2009) Stimulation of plant growth and drought tolerance by native microorganisms (AM fungi and bacteria) from dry environments: mechanisms related to bacterial effectiveness. J Plant Growth Regul 28(2):115–124

Massalha H, Korenblum E, Malitsky S, Shapiro OH, Aharoni A (2017) Live imaging of root–bacteria interactions in a microfluidics setup. Proc Natl Acad Sci 114(17):4549–4554

Mayak S, Tirosh T, Glick BR (2004) Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. Plant Sci 166(2):525–530

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37(5):634–663

Mohapatra S, Mittra B (2017) Alleviation of *Fusarium oxysporum* induced oxidative stress in wheat by *Trichoderma viride*. Arch Phytopathol Plant Protect 50(1–2):84–96

Mukhtar T, Smith D, Sultan T, Seleiman MF, Alsadon AA, Ali S, Chaudhary HJ, Solieman THI, Ibrahim AA, Saad MA (2020) Mitigation of heat stress in *Solanum lycopersicum* L. by ACC-deaminase and exopolysaccharide producing *Bacillus cereus*: effects on biochemical profiling. Sustainability 12(6):2159

Naseem H, Bano A (2014) Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. J Plant Interact 9(1):689–701

Naveed M, Hussain MB, Zahir ZA, Mitter B, Sessitsch A (2014) Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. Plant Growth Regul 73(2):121–131

Palyzova A, Svobodová K, Sokolová L, Novák J, Novotný Č (2019) Metabolic profiling of *Fusarium oxysporum* f. sp. *conglutinans* race 2 in dual cultures with biocontrol agents *Bacillus amyloliquefaciens, Pseudomonas aeruginosa*, and *Trichoderma harzianum*. Folia Microbiol 64(6):779–787. https://doi.org/10.1007/s12223-019-00690-7

Park YG, Mun BG, Kang SM, Hussain A, Shahzad R, Seo CW, Kim AY, Lee SU, Oh KY, Lee DY, Lee IJ, Yun BW (2017) *Bacillus aryabhattai* SRB02 tolerates oxidative and nitrosative stress and promotes the growth of soybean by modulating the production of phytohormones. PLoS One 12(3):e0173203

Pascale A, Proietti S, Pantelides IS, Stringlis IA (2020) Modulation of the root microbiome by plant molecules: the basis for targeted disease suppression and plant growth promotion. Front Plant Sci 10:1741

Pascale A, Vinale F, Manganiello G, Nigro M, Lanzuise S, Ruocco M, Marra R, Lombardi N, Woo SL, Lorito M (2017) Trichoderma and its secondary metabolites improve yield and quality of grapes. Crop Prot 92:176–181

Qu Q, Zhang Z, Peijnenburg WJGM, Liu W, Lu T, Hu B, Chen J, Chen J, Lin Z, Qian H (2020) Rhizosphere microbiome assembly and its impact on plant growth. J Agric Food Chem 68(18): 5024–5038

Rai S, Solanki MK, Solanki AC, Surapathrudu K (2019) Biocontrol potential of *Trichoderma* spp.: current understandings and future outlooks on molecular techniques. In: Plant health under biotic stress. Springer, Singapore, pp 129–160

Sachdev S, Ansari SA, Ansari MI, Fujita M, Hasanuzzaman M (2021) Abiotic stress and reactive oxygen species: generation, signaling, and defense mechanisms. Antioxidants 10(2):277

Sachdev S, Singh RP (2016a) Current challenges, constraints and future strategies for development of successful market for biopesticides. Clim Change Environ Sustain 4(2):129–136

Sachdev S, Singh RP (2016b) Studies on trends in use of pesticides and fertilizers for tomato cultivation in the vicinity of Lucknow, India. Int J Sci Technol Soc 2(1–2):49–54

Sachdev S, Singh RP (2018a) Root colonization: imperative mechanism for efficient plant protection and growth. MOJ Ecol Environ Sci 3:240–242

Sachdev S, Singh RP (2018b) Isolation, characterisation and screening of native microbial isolates for biocontrol of fungal pathogens of tomato. Clim Change Environ Sustain 6(1):46–58

Sachdev S, Singh RP (2020) *Trichoderma*: a multifaceted fungus for sustainable agriculture. In: Ecological and practical applications for sustainable agriculture. Springer, Singapore, pp 261–304

Sah SK, Reddy KR, Li J (2016) Abscisic acid and abiotic stress tolerance in crop plants. Front Plant Sci 7:571

Salomon MV, Bottini R, de Souza Filho GA, Cohen AC, Moreno D, Gil M, Piccoli P (2014) Bacteria isolated from roots and rhizosphere of *Vitis vinifera* retard water losses, induce abscisic acid accumulation and synthesis of defense-related terpenes in in vitro cultured grapevine. Physiol Plant 151(4):359–374. https://doi.org/10.1111/ppl.12117

Sandhya VSKZ, Ali SZ, Grover M, Reddy G, Venkateswarlu B (2010) Effect of plant growth promoting *Pseudomonas* spp. on compatible solutes, antioxidant status and plant growth of maize under drought stress. Plant Growth Regul 62(1):21–30

Sandhya VZAS, Grover M, Reddy G, Venkateswarlu B (2009) Alleviation of drought stress effects in sunflower seedlings by the exopolysaccharides producing *Pseudomonas putida* strain GAP-P45. Biol Fertil Soils 46(1):17–26

Sapre S, Gontia-Mishra I, Tiwari S (2019) ACC deaminase-producing bacteria: a key player in alleviating abiotic stresses in plants. In: Plant growth promoting Rhizobacteria for agricultural sustainability. Springer, Singapore, pp 267–291

Saravanakumar D, Kavino M, Raguchander T, Subbian P, Samiyappan R (2011) Plant growth promoting bacteria enhance water stress resistance in green gram plants. Acta Physiol Plant 33: 203–209. https://doi.org/10.1007/s11738-010-0539-1

Schlaeppi K, Bulgarelli D (2015) The plant microbiome at work. Mol Plant Microbe Interact 28(3): 212–217

Schulz-Bohm K, Gerards S, Hundscheid M, Melenhorst J, de Boer W, Garbeva P (2018) Calling from distance: attraction of soil bacteria by plant root volatiles. ISME J 12(5):1252–1262

Segarra G, Van der Ent S, Trillas I, Pieterse CMJ (2009) MYB72 a node of convergence in induced systemic resistance triggered by a fungal and a bacterial beneficial microbe. Plant Biol 5:1190–1196. https://doi.org/10.1111/j.1438-8677.2008.00162.x

Shubha J, Srinivas C (2017) Diversity and extracellular enzymes of endophytic fungi associated with *Cymbidium aloifolium* L. Afr J Biotechnol 16(48):2248–2258

Stone BW, Weingarten EA, Jackson CR (2018) The role of the phyllosphere microbiome in plant health and function. Annual Plant Rev 2018:533–556

Subiramani S, Ramalingam S, Muthu T, Nile SH, Venkidasamy B (2020) Development of abiotic stress tolerance in crops by plant growth-promoting rhizobacteria (PGPR). In: Phyto-microbiome in stress regulation. Springer, Singapore, pp 125–145

Turner TR, James EK, Poole PS (2013) The plant microbiome. Genome Biol 14(6):1–10

Vinale F, Flematti G, Sivasithamparam K, Lorito M, Marra R, Skelton BW, Ghisalberti EL (2009) Harzianic acid, an antifungal and plant growth promoting metabolite from *Trichoderma harzianum*. J Nat Prod 72(11):2032–2035

Vinale F, Manganiello G, Nigro M, Mazzei P, Piccolo A, Pascale A, Ruocco M, Marra R, Lombardi N, Lanzuise S, Varlese R, Cavallo P, Lorito M, Woo SL (2014b) A novel fungal metabolite with beneficial properties for agricultural applications. Molecules 19(7):9760–9772. https://doi.org/10.3390/molecules19079760

Vinale F, Marra R, Scala F, Ghisalberti EL, Lorito M, Sivasithamparam K (2006) Major secondary metabolites produced by two commercial *Trichoderma* strains active against different phytopathogens. Lett Appl Microbiol 43(2):143–148

Vinale F, Sivasithamparam K, Ghisalberti EL, Woo SL, Nigro M, Marra R, Lombardi N, Pascale A, Ruocco M, Lanzuise S, Manganiello G, Lorito M (2014a) *Trichoderma* secondary metabolites active on plants and fungal pathogens. Open Mycol J 8(1):127–139

Vurukonda SSKP, Vardharajula S, Shrivastava M, SkZ A (2016) Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. Microbiol Res 184:13–24

Walker TS, Bais HP, Grotewold E, Vivanco JM (2003) Root exudation and rhizosphere biology. Plant Physiol 132(1):44–51

Youssef SA, Tartoura KA, Abdelraouf GA (2016) Evaluation of *Trichoderma harzianum* and *Serratia proteamaculans* effect on disease suppression, stimulation of ROS-scavenging enzymes and improving tomato growth infected by *Rhizoctonia solani*. Biol Contr 100:79–86

14 Role of Effective Management of Harvested Crop to Increase Productivity Under Stress Environment

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

Abstract

Post-harvest losses of fruits, vegetables, and crops are an important and concerned problem of food industries. It is a measure of quantity and quality of food loss that is initiated from harvesting of the crop till its intake or usage of its end product. Post-harvest quality has been considered as a global issue, and lowering the losses after harvest has been an essential phase of food production. Improper harvesting, delay in transportation, and storage of products are some of the causes of post-harvest losses of agricultural crops, fruits, and vegetables. Many factors are governing the post-harvest life of fruits, crops and vegetables like water status in harvested crops, respiration rate, microbial invasion and growth, weather conditions, ethylene production, etc. Frequent occurrence and recurrence of abiotic stresses in the climate change era cause strong negative effects on perishable commodities after harvest which is the reason behind the poor quality of products. It is well known that exposure of freshly harvested crops to multiple stresses is a common process as the post-harvest process is a long chain system involving handling, storing, and marketing. Changes in cellular activities under stress environment after harvest of crops are another cause of post-harvest losses which are in conjugation with mishandling damages and microbial deterioration. Management of post-harvest losses under abiotic stress is vital for quality-rich agricultural products. Adoption of careful handling, timely harvest, and transportation, proper storage and packaging of products are some of the post-harvest management measures for improving the shelf life of food commodities. Application of chemicals both at pre- or post-harvest stage helps in extension of shelf life of the products as it helps in protecting it from microbes and abiotic stress damage. Exogenous application of salicylic acid, nitric oxide,

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and hydrogen sulphide in certain harvested fruits and vegetables help in enhancing the shelf life of the product. The chapter highlights the post-harvest losses in crops and their management under stress conditions.

Keywords

Abiotic stress · Crop · Losses · Management · Post-harvest · Storage

14.1 Introduction

Post-harvest losses in any crop are of utmost importance as the product obtained in the market is solely dependent on these losses. The post-production operations are crucial for giving stability to food chain. Post-harvest losses in food commodities can be defined as losses occurring in food items after harvest which can be measured on basis of losses in quantity and quality of the food commodity all along the supply chain (beginning from harvest till consumption or production of its end product) (De Lucia and Assennato 1994; Hodges et al. 2010). The losses occurring after harvest in food crops are mainly during harvesting, drying, transporting, threshing, storing, marketing, and mill processing (Grover and Singh 2013). At field and during storage, damage and injury of storage products are mainly responsible due to insects, microbes (bacteria, yeasts, and fungi), birds, rodents, and other pests (Tournas 2004). During storage, qualitative and quantitative losses are mostly seen. Many factors are involved in quantitative losses like an infestation of insects, birds, pests, temperature, relative humidity, etc. Qualitative losses are responsible for the reduction in nutritive value, and a number of factors govern these losses (Prusky 2011). The environmental condition and insect pest damage are the important factors responsible for storage losses of products. Post-harvest losses differ from commodity to commodity, an area covered under production, and season of cultivation.

In India, post-harvest losses are 7–10% of the total produce (loss from farm to market) and 4–5% loss (from market to distribution stage) (World Bank Study 2011). Considering the total production of fruits, vegetables, and crop product as 240 million tonnes, losses after harvest has been estimated to be about 15–25 million tonnes. This amount increased to 926 billion or US$ 14.33 billion in India as per the Associated Chambers of Commerce of India (2016) report. In undeveloped countries, post-harvest losses are accountable for 2550% (Spurgeon 1976). In India, loss after harvest of crops ranges from 25% to 40%. Basavaraja et al. (2007) had revealed that losses occurring after harvest at the field in the case of rice are about 3.82 kg/ q while for wheat 3.28 kg/q. Gautam et al. (2017) had illustrated that the highest losses may be seen in mango with a loss of 1542.3q/y, followed by papaya (1470.5q/year) and banana (1422q/year); however, during storage of these fruits, the losses contribute to 43.4% in banana, 39.75% in papaya and 38.3% in mango. Contrastingly, Kasso and Bekele (2018) had shown that post-harvest losses are relatively much more in tomatoes than in mango and coffee (45.32, 43.53, and 15.75%, respectively). Post-harvest losses in different crops range from as low as

2.8% to as high as 18.1% on the basis of the process during harvesting or after harvesting (like handling and storage) (Jha et al. 2016). Mintel et al. (2020) had reported that post-harvest losses were maximum in perishable commodities ranging between 2.6% and 11.8% trailing behind cereals and processed foods (with a range of 0.5–2.0% and 0.1–0.5%, respectively) at the retail level. The percentage loss is dependent on the pre- and post-harvest practices adopted as well as the type of crop produced (whether it is fast deteriorating crop or a less deteriorating crop). Many factors contribute to post-harvest losses like careless handling, short of knowledge and ability, and inappropriate methods during harvesting, transporting, storability, and marketing (Osman et al. 2009; Kasso and Bekele 2018).

This problem of losses after harvest becomes more crucial and further devastating when the crops are affected by the frequent abiotic stresses which are mostly seen in prevailing conditions as a result of climate change. Abiotic stresses have a strong negative impact on crop growth, production, productivity, and quality of the product. During the past decade, the problem of climate change and accentuation of abiotic stresses has risen up. Predictions on the upcoming frequent occurrence of drought, water logging, flooding, high temperatures, etc., due to increasing carbon dioxide concentration, heat waves, and other climatic events are frequent. There is a need for developing and promoting strategizes for minimizing and coping with the occurrence and recurrence of abiotic stresses for agricultural sustenance. Ansari and Tuteja (2013) had revealed that impacts of several abiotic stresses were seen on perishable commodities starting from its production to its final utilization, emphasizing the loss in quality of the product. Alteration at cellular levels after harvest of crops causes a regular change with further acceleration under natural stresses, damages during mishandling, and microbial deterioration (Pedreschi and Lurie 2015). Several studies had revealed that under abiotic stress, post-harvest losses occurring in the product cause a reduction in shelf life thus affecting its quality which is detrimental in market lookout (Matas et al. 2009; Singh et al. 2013). Post-harvest proper practices and advanced technologies may help in lowering the losses occurring after harvest and prior to intake of the product (Kitinoja and Kader 2002) that may improve the shelf life of harvested vegetables, fruits, and crops (Arah et al. 2016). The chapter highlights the post-harvest losses in crops and their management under stress conditions.

14.2 Post-Harvest Management

Post-harvest management is a system wherein cleaning and washing of the plant products, selection and grading as well as storing and packaging of the product, etc. is involved. The post-harvest management is mainly a practice for improving the quality and appearance of the product with the removal of elements that are detrimental (Kumar and Prasad 2020). For any product available in the market, appearance and palatability are important factors. Studies had reported that certain invasion of pathogens after harvest or alteration in weather aberrations are a risk to the quality and quantity of the products (Atanda et al. 2011; Romina and Lurie 2015;

Fallick 2004). Further, post-harvest strategies adopted in harvested crops help in maintaining the standards of freshness. Food Association Organization (2009) had illustrated that there are many controlling variables involved in the management of post-harvest losses. These are fungicide treatment, variation in temperature and relative humidity, etc. Basically, post-harvest management is adding up to value addition. Kader (1992) had projected that about 5–25% of fruits and vegetables after harvest have deteriorated. There is a need to understand the role of various factors associated with abiotic stress in post-harvest losses. A combination of several factors, like microbial attack, physical damage, senescence, etc., further accentuates the post-harvest losses under abiotic stress conditions (Kader 1992). Imahori (2012) had revealed the importance of protection and enhancement of technologies adopted for managing these post-harvest losses.

Management after the harvest of food commodities involves all sorts of treatments. To increase shelf life and minimize the losses occurring after harvest, freshly harvested food commodities need to go through various management strategies (Misra et al. 2020c). Better production practices, careful harvesting, proper packaging, storage, and transport contribute to good-quality produce (Bachmann and Earles 2000). Because of the high moisture content, fruits and vegetables are inherently more prone to deteriorating. Even after the harvest, they are biologically active and carry out transpiration, respiration, ripening, and other biochemical activities, which deteriorate the quality of the produce (Kasso and Bekele 2018). As per a study report, about 25–30% of the fruits and vegetables produced are lost due to quality deterioration or low-value demand (Kasso and Bekele 2018). Abera et al. (2020) revealed that losses after harvest vary from one processing to another, viz., 20.5%, 7.3%, 2.9%, and 8.6% at the grower, hotel, retailer, and wholesaler level and on an overall basis, the range of total losses vary from 17.2 to 33.3; however, Maiti et al. (2018) had shown that post-harvest losses in India occur at a range of 15–20% at growers place with the same amount at the packaging level, but during transportation and marketing, the losses increased to 30–40%. World Bank et al. (2011) revealed that post-harvest loss in the eastern and southern region of Africa account for 20–40% which values to approximately US $1.6 billion per year. Every year the wastage cost amounts to approximately Rs. 675,000 million. Even if a small amount is saved as small as 1%, then also there will be a saving of Rs. 6750 million per year. Also, the amount required in minimizing the losses occurring after harvest of crops is far much lesser than producing the same amount of crop with high quality in a fresh manner. This makes the management of post-harvest losses of utmost importance and need of the hour (Kumar et al. 2012).

14.3 Causes of Post-Harvest Losses in Crops

Post-harvest losses begin after harvesting of crops from fields to transportation to packaging centres to storage to retail markets (Solomon 2009). Abera et al. (2020) had illustrated that these losses mainly occur at grower’s place, transportation, and markets. Adverse losses after harvest are initiated due to improper pre- and post-harvest management. Biological causes of deterioration of food commodities involve metabolic changes, physical disorders, pathogen attacks, and mechanical damages (Misra et al. 2016c). Respiration, ethylene production and compositional changes are incorporated with the changes in the metabolic condition of the product obtained after harvest (Hansen 1966). Many environmental conditions plays role in enhancing or decreasing the rate of biological losses such as temperature, relative humidity, oxygen, and CO_2 concentration as well as ethylene (Misra et al. 2020a). Physiological deterioration is another cause on which rate of loss is dependent when deterioration occurs by natural means such as physical damage, high or low temperatures, etc. (Guru and Mishra 2017). Texture and moisture content of the harvested crop are other components for physiological deterioration as it helps in physical damage. Improper packaging methods and carelessness during handling and transportation may lead to bruises, injuries, wounds, rots, etc. (Kihurani and Kaushal 2016).

14.4 Physiology of Post-Harvest Losses

Quality production of harvested crops is dependent on the growth condition of the crop and the physiological and biochemical alterations. The cells of the harvested crop remain alive, and so they undergo physiological activities leading to a loss in the main constituent. Maturity plays an important role in the physiology of post-harvest losses in crops (Arah et al. 2015). Harvesting at proper time of maturity causes the good quality of crops. Poor shelf life of the crops is a result of uneven ripening (either due to early harvesting or late harvesting of the crop). It is known that when a crop is harvested, the rate of respiration is increased which causes an increase in losses after harvest (Misra et al. 2020c). Respiration produces sugars, fats, and proteins by the deterioration of the valued end product leading to recurring its value, flavour, and weight on which it is sold. The respiration rate of a commodity is a determinant of how the food commodity is transported and its shelf life after harvest. Temperature is among the factors controlling the rate of respiration after harvest. In certain plants, the respiration rate is dependent on maturity status (Lopez et al. 2014).

14.5 Components of Post-Harvest Management

14.5.1 Harvesting Time and Method

The time of harvest of the crop is the most important criterion for the quality harvest of the crop (Selvakumar 2014). Generally, fruits and vegetables are harvested when they are physically seen to be in a condition of maturity and in the right condition to be consumed. This is often termed harvest maturity. In several vegetables and fruits, the optimum maturity status is achieved at a very small age like green peas, cucumber, etc., and delay in their harvesting may often lead to more fibre production. The right maturity status is the best time for attaining quality fruits, while unripened fruits on harvesting not only give poor quality but also of lesser value to the consumers (Barman et al. 2015). Size, taste, softness, quality, and colour are dependent on the time of harvest of the crop (Selvakumar 2014). Mechanical harvesting of fruits and vegetables is now more commercially being done for convenience; however, it causes more mechanical injuries to fruits and vegetables. The cumulative effect of injuries due to mechanical harvesting has been reported (Miller 2003). Mechanical damage during harvesting of crops leads to moisture loss which may go as high as 400% by even a small bruise. Damages that are either equivalent or more than the yield causes complete damage to affected cells. This is followed by undesirable metabolic activities like rise in respiration rate and ethylene production. On totality reduction in the shelf life of the product and quality is the result of mechanical damages in harvested crops (Sargent et al. 1992).

Harvesting of crops should be done when temperatures are low, i.e. in the early morning. Harvested crops should be kept in the shade so as to prevent further losses occurring after harvest. Time of harvesting and the method by which harvesting is being performed both are equally important for a quality product. Improper harvesting and handling issues of the food commodity cause a direct impact on the quality of the product thus lowering its market value (Kasso and Bekele 2018). Products that need to be stored for a longer time should be handled with care and free from skin breaks, injuries, bruises, rots, etc., as this may help in the invasion of microbes and their proliferation which leads to heavy deterioration of the product. Peel injury or bruises in harvested vegetables and fruits will act as an entry point for microbes which results in rotting (Barth et al. 2009). This is one of the reasons behind the harvesting of banana bunches 30 cm with stalks (Barman et al. 2015).

14.5.2 Transportation

Losses in harvested crops are majorly seen during transportation (Fig. 14.1). Harvested crops are generally transported via rail or truck from one place to another. Exporting harvested crops are transported via ships or aeroplanes. The main requirement in the transportation of crops and food commodities is the proper management of temperature, humidity, and proper ventilation. For far-off places, ventilated trucks, refrigerated containers, and trailers are a good option as it helps in dissipating the heat, and minimizing the respiration losses leading to avoidance of high temperature losses (Kader 2013). Refrigerated trucks are an effective and convenient way for maintaining the quality of the product, but it is an expensive measure (Ju-Chia and Mu-Chen 2010). Substantial cost saving can also be done without deteriorating the quality of the product by the sage of only insulated trucks for a short distance. Utmost care is taken while transportation of products as vibration may cause adverse brushing and damages on the harvested products. Proper cushioning, stacking of food products and packaging are other ways by which movement and vibration of products could be minimized during transportation (Jung et al. 2018).

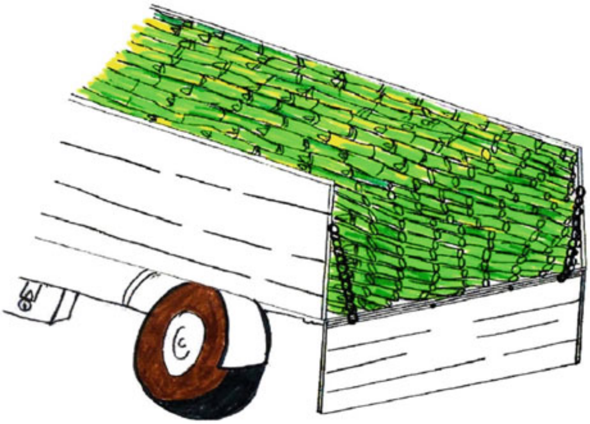

Fig. 14.1 Proper transportation method: transporting of harvested canes with proper ventilation and removal of extra trash and mud in sugarcane to avoid post-harvest deterioration

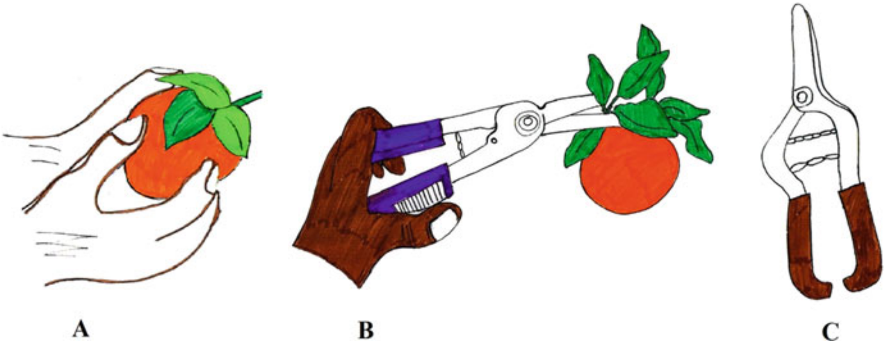

Fig. 14.2 Handling method of fruits by avoiding mechanical damage A. Proper hand picking B. Clipper for harvesting citrus fruits C. Use of thin curved blade equipment for grapes

14.5.3 Handling

Physical handling should be precisely done as it causes a strong impact on the post-harvest quality of the product (Fig. 14.2). Carefree handling prior to harvesting and after harvesting of the crops leads to mechanical injures, bruises, and damages which accentuate the post-harvest losses of the product thus lowering the quality of the product (Arah et al. 2015). Highly perishable fruits, vegetables, and crop products, bulkiness, softness, and wet condition of food commodities are at higher risk to injuries and damages during handling which causes loss in appearance and freshness of the desired product (Murthy et al. 2009; Atanda et al. 2011). Insufficient handling of harvested products and not using the right technologies can cause a reduction of 50–70% during handling of harvested crops (Olayemi et al. 2012). To prevent the losses caused by this component, care should be taken while handling such products especially during packaging and transporting.

14.5.4 Storage

Storage is the foremost crucial component of handling products after harvest. A considerable amount of agricultural crops, horticultural crops, fruits, and vegetables are being lost due to improper storage conditions (Kiaya 2014). The main aim of the storage of products is to regulate the transpiration and respiration losses as well as maintain the ripening condition, besides undesirable biochemical changes or pathogen infestation. Improper storage leads to fruit and vegetable deterioration (Singh et al. 2014) which is a resultant of many factors:

1. Loss in moisture content and wilting of food products.
2. Undesirable growth in vegetables like sprouting in onion, potato, etc.
3. Food spoilage due to the growth of microbes like bacteria, yeasts, moulds, etc., and insect pests.
4. Ripening condition.
5. Loss in texture and colour.
6. Detrimental changes in metabolism and respiration process of products.

The storability condition of every crop varies after harvest depending on whether the food commodity is durable or perishable (Haard 1984). Durable and perishable commodities vary in their characteristics (Table 14.1). For efficient and long storability and reducing the losses after harvest of crops, hygiene and proper monitoring of stored product are important (Olsen and Kleinkopf 2020). In closed storing centres, temperature and humidity regulation is equally important as monitoring of insects pests, and rodent attacks (El-Aziz 2011). Pre-cooling methods are another strategy for reducing the losses after harvest.

14.5.5 Packaging of Products

Packaging of fruits, vegetables, pulses, etc. could be a preventive measure from damage (either during storage or during transportation), and dehydration. It helps in easy handling, marketing and quality maintenance. Proper labelling on packets with complete details of the product handling and storage condition further helps in the quality keeping of the product (Hailu 2015). Packaging material and styling vary from product to product, quantity to quantity, and distance of the place to be reached. During packaging of harvested products, the packager needs to take care that it should be inexpensive, is easy to handle, gives proper protection from damaging either physical or through insects, is easily degradable, and has proper ventilated (Thompson 2003). For high-value products, stylish modified containers made of fibre wood, plastic crates are mostly used, while for lesser value products, bamboo baskets or nylon net sacs are used (Vigeault et al. 2009; Twede et al. 2015). Pre-packaging of the products is a good way and provides added value to the product. Non-biodegradable plastic trays and wrapping materials should be avoided

Table 14.1 Comparison of characteristics of perishable and durable commodities

Characteristics	Perishable commodities	Durable/non-perishable commodities
Moisture content (range %)	High (50–95)	Low (10–15)
Respiration rate after harvest	High	Low
Heat production	High	Low
Texture of the commodity	Soft and higher risk towards physical injury	Hard texture so lesser risk for physical injury
Phase of ontogeny	Senescent	Dormant
Storability	Short duration	Long duration
Size of fruits	5 g to 5 kg	<1 g
Losses during storage	Partial endogenous (transpiration, respiration etc.) and exogenous factors	Exogenous factors (insects, moisture and rodents, etc.)
Examples of crops	Sugarcane, sugar beet, cabbage, sweet corn, broccoli, mushrooms, green onions peas, etc.	Nuts, sweet potato, grapes, apples, etc.

Source: Modified from Haard (1984).

as it causes an increase in waste material which is hard to be degraded and act as a pollutant for the environment (Cwiertka 2020).

14.6 Post-Harvest Crop Losses Under Stress Environment

Water stress is the major abiotic stress that had a strong negative impact on the production and quality of fruits after harvest (Ripoll et al. 2014). The post-harvest quality of apples, sugarcane, and many other crops are susceptible to water stress (El-Soda et al. 2014; Misra et al. 2016b, 2020c). The water scarcity in apples, pears, and sugarcane has demonstrated huge losses in yield and quality particularly during storage (Veličković 1994; Misra et al. 2020c; Lopez et al. 2011). Shibairo et al. (1998) had demonstrated that higher membrane leakage at pre-harvest and weight loss after harvest was seen in carrots during water stress conditions. In Kensington mango, chilling injury causes susceptibility towards this stress if, at pre-harvest phase, water stress conditions were imposed on mango plant (Léchaudel and Joas 2007). Water stress on tuber crops causes several diseases such as black spot disorder and potato wart diseases in potatoes (Stevens and Davelaar 1997; Obidiegwu et al. 2014) as well as decompartmentation (generally seen as an effect of mechanical damage) (Hamouz et al. 2006). Salt stress is another stress condition that greatly hampers the crop quality after harvest. In tomatoes, salt stress had a strong influence on the size and brix depicting susceptibility towards this stress as a result of water loss after harvest (Mizrahi et al. 1988; Feleafel and Mirdad 2014).

Though sugar beet crop has tolerance capability towards salt stress, salt stress causes a negative impact on the harvested sugar beet during storage (Misra et al. 2020b). Nunes et al. (2009) had revealed that temperature intensity and magnitude also influences the post-harvest quality of the product by losses in flavour, change in texture, softening of product, internal browning, and surface pitting. A rise in temperatures during the late season may further accelerate the losses in apples such as superficial scald, while low temperatures cause a reduction in susceptibility of pre-harvest pears (Whitaker 2013). Toivonen and Mark-Hodges (2011) have illustrated that harvested apples and their storage had the least impact of temperature variation when the fruit has been stored at the post-climacteric stage of maturity. East et al. (2008) showed that during the storage of apples, high temperature increases the rate of ripening and softening of the fruit. Low light and less optimal conditions for photosynthesis had been known to have a short life span of cut lettuce (Witkowska and Woltering 2010). Gruda (2005) had shown similar results in tomato plants during the onset of spring season with smaller sizes along with an increased surface area to volume ratio that imparted susceptibleness to post-harvest deterioration (Toivonen and Mark-Hodges 2011). Studies had reported that even lower light incidence causes a reduction in the amount of ascorbate in green house fruits and vegetables, thus inclining these food commodities towards susceptibility to post-harvest deterioration and stresses (Noctor and Foyer 1998; Stevens et al. 2008). Lauxmann et al. (2014) had revealed that damages during storage, decay, and product deterioration in many fruits and vegetables are the result of low temperatures. The main cause of bruising in fruits during mechanical damage is abrasion, cuts, punctures, etc. (Fenyvesi et al. 2014). Association of the impact of abiotic stress on product quality after harvest with alteration at the cellular level is reported. These changes include changes in organic acids, lipids, antioxidants, mitogen-activated protein kinase, ethylene, etc. (Ansari and Tuteja 2015).

14.7 Post-Harvest Crop Management Strategies for Stress Environment

Management of post-harvest losses under abiotic stress is important for maintaining the high quality of the agricultural product. It is a way to fulfill the demands of high-quality products by the consumers (Ansari and Tuteja 2015). Besides following normal management strategies for minimizing the post-harvest losses, some particular strategies may also be followed for stress conditions. For high temperatures, the application of cloth for shading purposes so that heat and radiation could be reduced. The sprinkling of water over-harvested crops is the most effective method of reducing high temperature impact (Laxman et al. 2020). For low temperatures, spray of parachlorophenoxy acetic acid (30 ppm) enhances fruit production, while a spray of ethrel (200 ppm) for 2–3 days prior to transplanting helps to improve rooting system in tomato plants. A gradual cooling temperature of 2 °C lowers the susceptibility of tomato to freezing stress as exposure of fruit to consistent cooling temperature helps in developing stress resistance system to chilling temperatures

(Gálvez et al. 2010). Wang (1993) had shown that utilization of either hot or warm water helps in mitigating the effect of chilling stress on fruits after harvest. Baldwin (2003) had revealed the use of another strategy where a modified controlled atmosphere (MCA) was used for managing the post-harvest losses in fruits. Also, the exogenous use of nitric oxide (at 10–40 μL L^{-1}) on mangoes helps in reducing the post-harvest losses under chilling stress, while application of hydrogen sulphide on harvested strawberries causes a rise in reducing sugars, free amino acids, and soluble proteins with increased in its shelf life (Hu et al. 2012). Application of growth regulators was also reported to further accelerate the mitigation of the impact of stress on the post-harvest quality of the agricultural product (Singh et al. 2013). Moreover, treatments of oxalic acid, methyl jasmonate, 2,4-D polyamines, and salicylic acid on mango fruit help in lowering the quality losses after harvest due to chilling injuries (Singh et al. 2013). In pineapple fruit, aspartic acid protease application gave positive results in imparting stress resistance towards chilling temperatures (Raimbault et al. 2013). For drought, the use of anti-transpirants and growth regulators, seed priming, and inducing drought hardiness are some ways by which harvested crops could be managed from strong impact of the stress after harvest. Mulching of crops that were exposed to drought conditions gave positive results. Li et al. (2001) had shown that water content in soil is managed by the use of black plastic mulch. Li and Zhao (1997) had shown that water use efficiency is enhanced by the usage of these plastic mulches. In sugarcane, benzalkonium chloride and sodium metasilicate (BKC + SMS) spray on to harvested canes help in reducing the sucrose losses after harvest (Misra et al. 2016a, 2020c). Furthermore, this treatment was also effective in increasing the shelf life of harvested canes under water logging conditions (Misra et al. 2016b). Urea spray on the crops also increases the drought tolerance level by reducing the osmotic potential. External application of calcium treatment has also been reported to improve the adaptation towards drought.

14.8 Conclusion

Post-harvest management involves cleaning and washing of the plant products, selection and grading as well as storing and packaging of the product, etc. The post-harvest management is mainly practice for improving the quality and appearance of the product with the removal of elements that are detrimental to crop products. The significance of post-harvest management lies in its potential to satisfy the need for food by the people which could be fulfilled by eliminating the losses incurred by post-harvest mismanagement. Post-harvest management has the power of making rural industries in agricultural-dependent countries like India. This could be achieved by adopting suitable technologies. The involvement of technologies for the management of post-harvest losses is essential for lowering food insecurity. Post-harvest losses are considered as an element of the integrated approach to fulfil the needs and demands of food.

Abiotic stresses are the ones that are responsible for harmful changes at the cellular level in the post-harvest scenario. Though many measures have been initiated in minimizing the accelerating losses after the harvest of agricultural products, mitigation of the impact of abiotic stresses on post-harvest quality has still not been resolved much. A network complex of several pathways at the cellular level had stimulated as a response to abiotic stress in harvested fruits. Furthermore, to save the quality losses occurring in harvested products, elicitation of synthesis of ethylene is an utmost challenging task. Management strategies under abiotic stress as per conventional method have been able to minimize the quality losses occurring after harvest of product to a certain extent. The use of mass spectrometers, nanotechnology and bioinformatics tools is an advancement in proteomic research on the post-harvest quality of agricultural products. Besides, metabolomics research on this aspect will be of great use in the development of a parallel network system in association with biological implication, while its exhaustive information on this aspect particularly its physiology will pave new directions to improve the quality of harvested agricultural products under stress environment.

References

Abera G, Ibrahim AM, Forsido SF, Kuyu CG (2020) Assessment on post-harvest losses of tomato (*Lycopersicon esculentem* Mill.) in selected districts of East Shewa Zone of Ethopia using a commodity system analysis methodology. Heliyon 6:e03749

Ansari MW, Tuteja N (2013) Stress-induced ethylene in postharvest losses of perishable products. Stewart Postharvest Rev 9:1–5

Ansari MW, Tuteja N (2015) Post-harvest quality risks by stress/ethylene: management to mitigate. Phytoplasma 252:21–32

Arah IK, Ahorbo GK, Anku EK, Kumah EK, Amaglo H (2016) Postharvest handling practices and treatment methods for tomato handlers in developing countries: a mini review. Adv Agric 2016: 6436945. https://doi.org/10.1155/2016/6436945

Arah IK, Amaglo H, Kumah EK, Ofori H (2015) Pre-harvest and post-harvest factors affecting the quality and shelf life of harvested tomatoes: a mini review. Int J Agron 2018:478041. https://doi.org/10.1155/2015/478041

Associated Chambers of Commerce of India (2016) Steps taken to reduce post harvest food losses, PIB, Feb 2016

Atanda SA, Pessu PO, Agoda S, Isong IU, Ikotun (2011) The concepts and problems of post harvest food losses in perishable crops. African J Food Sci 5(11):603–613

Bachmann J, Earles R (2000) Post harvest handling of fruits and vegetables. In: Appropriate technology transfer for rural areas. CRC Press, New York, pp 1–19

Baldwin EA (2003) Coating and other supplemental treatments to maintain vegetable quality. In: Bartz JA, Brecht JK (eds) Postharvest physiology and pathology of vegetables. Marcel Dekker, New York, pp 413–456

Barman K, Ahmad MS, Siddiqui MW (2015) Factors affecting the quality of fruits and vegetables: recent understandings. In: Siddiqui ME (ed) Post harvest biology and technology of horticultural crops. Principles and practices for quality maintenance. CRC Press, New York

Barth M, Hankinson TR, Zhuang H, Breidt F (2009) Microbiological spoilage of fruits and vegetables compendium of the microbiological spoilage of foods and beverages. Springer, New York, pp 135–183

Basavaraja H, Mahajanashwtti SB, Udagaati NC (2007) Economic analysis of post harvest loss in food grains in India: a case study of Karnataka. Agric Econ Res Rev 20(1):117–126

Cwiertka KJ (2020) Packagaing of food and drink in Japan. In: Meiselman H (ed) Handbook of eating and drinking. Springer, Cham, pp 509–524

De Lucia M, Assennato D (1994) Agricultural Engineering in development: post harvest operations and management of food grains. Food and Agriculture organizations of the United Nations, Rome, p 160

East AR, Tanner DJ, Maguire KM, Mawson AJ (2008) The influence of breaks in storage temperature on 'Cripps pink' (pink lady™) apple physiology and quality. Hort Sci 43:818–824

El-Aziz SEA (2011) Control strategies of stored product pests. Aust J Entomol 8(2):101–122

El-Soda M, Boer MP, Bagheri H, Hanhart CJ, Koornneef M, Aarts MGM (2014) Genotype–environment interactions affecting preflowering physiological and morphological traits of *Brassica rapa* grown in two watering regimes. J Exp Bot 65:697–708

Fallick E (2004) Pre storage hot water treatments immersion, rinsing, brushing. Post Harvest Biol Technol 32:125–134

Feleafel MN, Mirdad ZM (2014) Ameliorating tomato productivity and water use efficiency under water salinity. J Animal Plant Sci 24:302–309

Fenyvesi L, Fenyvesi D, Csatár A (2014) Stress analysis in fruits. Adv Mech Eng. https://doi.org/10.1155/2013/874673

Food Association Organization (FAO) (2009) Course on agribusiness management for producers' associations. Module 4–Post-harvest and marketing. In: Santacoloma P, Roettger A, Tartanac F (eds) Training materials for agricultural management, marketing and finance. Food and Agriculture Organization of the United Nations, Rome

Gálvez AB, García MV, Corrales JC, López AC, Valenzuela JAL (2010) Effect of gradual cooling storage on chilling injury and phenylalanine ammonia-lyase activity in tomato fruit. J Food Biochem 34:295–307

Gautam AN, Sahu RM, Asathi BK (2017) Extent of post harvest losses at different stages of fruits in Madhya Pradesh. In: Compendium of abstracts of the 3rd international conference on bio-resource and stress management. Jaipur, India, 8th Nov 2017

Grover DK, Singh JM (2013) Post–harvest losses in wheat crop in Punjab: past and present. Agric Econ Res Rev 26(2):293–297

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

Guru GK, Mishra S (2017) Physiological factors leading to post-harvest crop losses. In: Vishunavat K, Singh Y, Sharma G (eds) Proceeding of technological advances to minimize pre and post harvest losses in agricultural and horticultural crops to enhance farmers income. GB Pant University of Agriculture and Technology, Pantnagar, pp 68–76

Haard NF (1984) Post harvest physiology and biochemistry of fruits and vegetables. J Chem Educ 61(4):277–283

Hailu G (2015) Extent, causes and reduction strategies of post harvest losses of fresh fruits and vegetables: a review. J Biol Agric Health Care 5(5):49–64

Hamouz K, Bečka D, Morava J (2006) Susceptibility to mechanical damage of potatoes cultivated in different environmental conditions. Int Agrophysics 20:47–53

Hansen E (1966) Post harvest physiology of fruits. Annu Rev Plant Physiol 17:459–480

Hodges RJ, Bernard M, Knipschild H, Rembold F (2010) African post harvest losses information system- a network for the estimation of cereal weight losses. In: Carvalho MO (ed) Proceedings of the 10th international working conference on stored products protection. IICT, Lisbon, pp 958–964

Hu LY, Hu SL, Wu J, Li YH, Zheng JL, Wei ZJ, Liu J, Wang HL, Liu YS, Zhang H (2012) Hydrogen sulfide prolongs postharvest shelf life of strawberry and plays an antioxidative role in fruits. J Agric Food Chem 60:8684–8693

Imahori Y (2012) Post harvest stress treatments in fruits and vegetables. In: Ahmad P, Prasad MNV (eds) Abiotic responses in plants: metabolism, productivity, sustainability. Springer, New York

Jha S, Vishwakarma R, Ahmad T, Rai A (2016) Assessment of quantitative harvest and post-harvest losses of major crops/commodities in India

Ju-Chia K, Mu-Chen C (2010) Developing an advanced multi temperature joint distribution system for food cold chain. Food Contr 21(4):559–566

Jung HM, Lee S, Lee W-H, Cho B-K, Lee SH (2018) Effect of vibration stress on quality of packaged grapes during transportation. Eng Agric Environ Food 11(2):79–83

Kader AA (1992) Post harvest biology and technology: an overview. In: Kader A (ed) Post harvest technology of horticultural crops. Division of Agriculture and Natural Resources, University of California, Oakland, pp 15–20

Kader AA (2013) Postharvest technology of horticultural crops—an overview from farm to fork. Ethiopian J Appl Sci Technol 1:1–8

Kasso M, Bekele A (2018) Post harvest loss and quality deterioration of horticultural crops in Dire Dawa region Ethopia. J Saudi Soc Agric Sci 17(1):88–96

Kiaya V (2014) Post harvest losses and strategies to reduce them. Technical paper. Scientific & Technical Department, pp 1–25

Kihurani AW, Kaushal P (2016) Storage techniques and commercialization. In: Sharma HK, Njintang NY, Singhal RS, Kaushal P (eds) Tropical roots and tubers: production, processing and technology. Wiley, pp 253–280

Kitinoja L, Kader AA (2002) Small-scale postharvest handling practices: a manual for horticultural crops. University of California, Davis

Kumar A, Bantilan C, Kumar P, Kumar S (2012) Food security in India: trends, patterns, and determinants. Indian J Agric Econ 67(3):445–463

Kumar U, Prasad K (2020) Role of production and post-harvest management practices in enhancing quality and shelf life of vegetables. In: Singh HK, Solankey SS, Roy MK (eds) Farmers prosperity through improved agricultural technologies. Jaya Publishing House, New Delhi, pp 141–153

Lauxmann MA, Borsani J, Osorio S, Lombardo VA, Budde CO, Bustamante CA, Monti LL, Andreo CS, Fernie AR, Drincovich MF, Lara MV (2014) Deciphering the metabolic pathways influencing heat and cold responses during post-harvest physiology of peach fruit. Plant Cell Environ 37:601–616

Laxman RH, Upreti KK, Shivashankara KS, Sadashiva AT, Reddy KM, Aghora TS, Mishra S (2020) Management strategies for alleviating abiotic stress in vegetable crops. In: Rakshit A, Singh HB, Singh AK, Singh US, Fraceto L (eds) New frontiers in stress management for durable agriculture. Springer, New York, pp 523–542

Léchaudel M, Joas J (2007) An overview of preharvest factors influencing mango fruit growth, quality and postharvest behaviour. Braz J Plant Physiol 19:287–298

Li FM, Zhao SL (1997) New approaches in researches of water use efficiency in semiarid area of Loess Plateau. Chin J Appl Ecol 8:104–109. (in Chinese with English abstract)

Li FM, Yan X, Jun W, Shi-qing L, Tong-chao W (2001) The mechanism of yield decrease of spring wheat resulted from plastic film mulching. Sci Agric Sin 34:330–333

Lopez AP, Chavez-Franco SH, Villasenor-Perea CA, Espinosa-Solares T, Hernandez-Gomez LH, Lobato-Calleros C (2014) Respiration rate and mechanical properties of peach fruit during storage at three maturity stages. J Food Eng 142:111–117

Lopez G, Larrigaudière C, Girona J, Behboudian MH, Marsal J (2011) Fruit thinning in 'conference' pear grown under deficit irrigation: implications for fruit quality at harvest and after cold storage. Scientia Hort 129:64–70

Maiti R, Thakur AK, Gupta A, Mandal D (2018) Post harvest management for agricultural produce. In: Research trends in bioresource management and technology. American Academic Press, Washington, DC, pp 137–166

Matas AJ, Gapper NE, Chung MY, Giovannoni JJ, Rose JKC (2009) Biology and genetic engineering of fruit maturation for enhanced quality and shelf-life. Curr Opin Biotechnol 20: 197–203

Miller RA (2003) Harvest and handling injury: physiology biochemistry and detection. In: Bartz JA, Brecht JK (eds) Postharvest physiology and pathology of vegetables. Marcel Dekker, New York, pp 177–208

Mintel B, Tamru S, Reardon T (2020) Post-harvest losses in rural-urban value chains: evidence from Ethiopia. Food Policy 98:10860. https://doi.org/10.1016/j.foodpol.2020.101860

Misra V, Solomon S, Ansari MI (2016a) Impact of drought on post-harvest quality of sugarcane crop. Adv Life Sci 20(5):9496–9505

Misra V, Solomon S, Singh P, Prajapati CP, Ansari MI (2016b) Effect of water logging on post-harvest sugarcane deterioration. Agri 5(2):119

Misra V, Solomon S, Shrivastava AK, Shukla SP, Ansari MI (2016c) Post-harvest sugarcane deterioration: *Leuconostoc* and its effect. J Funct Environ Biol 6(1):1–7

Misra V, Solomon S, Mall AK, Prajapati CP, Ansari MI (2020a) Impact of chemical treatments on *Leuconostoc* bacteria from harvested stored/stale cane. Biotechnol Rep 27:e00501

Misra V, Mall AK, Pathak AD (2020b) Sugarbeet: a sustainable crop for salt stress conditions. In: Hasaanzuman M (ed) Agronomic crops. Springer, Singapore, pp 40–62. https://doi.org/10.1007/978-981-15-0025-1_10

Misra V, Solomon S, Hassan A, Allah EFE, Al-Arjani AF, Mall AK, Prajapati CP, Ansari MI (2020c) Minimization of postharvest sucrose losses in drought affected sugarcanes using chemical formulation. Saudi J Biol Sci 27(1):309–317

Mizrahi Y, Taleisnik E, Kagan-Zur V, Zohar Y, Offenbach R, Matan E, Golan R (1988) A saline irrigation regime for improving tomato fruit quality without reducing yield. J Am Soc Hort Sci 113:202–205

Murthy DS, Gajanana TM, Sudha M, Dakshinamoorthy V (2009) Marketing and post harvest losses in fruits: its implications on availability and economy. Indian J Agric Econ 64(2):259–275

Noctor G, Foyer CH (1998) Ascorbate and glutathione: keeping active oxygen under control. Annu Rev Plant Physiol Plant Mol Biol 49:249–279

Nunes MCN, Emond JP, Rauth M, Dea S, Chau KV (2009) Environmental conditions encountered during typical retail display affect fruit and vegetable quality and amount of waste. Postharvest Biol Technol 51:232–241

Obidiegwu JE, Flath K, Gebhardt C (2014) Managing potato wart: a review of present research status and future perspective. Theor Appl Genet 127:763–780

Olayemi FF, Adegbola JA, Bamishaiye EI, Awagu EF (2012) Assessment of postharvest losses of some selected crops in eight local government areas of rivers state, Nigeria. Asian J Rural Develop 2(1):13–23

Olsen N, Kleinkopf (2020) Storage management. In: Potato production systems. Springer, New York, pp 523–545

Osman A, Saari N, Saleh R, Bakar J, Zainal ND, Yacob M (2009) Post harvest handling practices on selected local fruits and vegetables at different levels of the distribution chain. J Agribusiness Market 2:39–53

Pedreschi R, Lurie S (2015) Advances and current challenges in understanding post harvest abiotic stresses in perishables. Postharvest Biol Technol 107:77–89

Prusky D (2011) Reduction of the incidence of post harvest quality losses and future prospects. Food Sec 3:463–474

Raimbault AK, Zuily-Fodil Y, Soler A, Cruz de Carvalho MH (2013) A novel aspartic acid protease gene from pineapple fruit (*Ananas comosus*): cloning, characterization and relation to postharvest chilling stress resistance. J Plant Physiol 170:1536–1540

Ripoll J, Urban L, Staudt M, Lopez-Lauri F, Bidel LPR, Bertin N (2014) Water shortage and quality of fleshy fruits-making the most of the unavoidable. J Exp Bot 65:407. https://doi.org/10.1093/jxb/eru197

Romina P, Lurie S (2015) Advances and current challenges in understanding post harvest abiotic stresses in perishables. Post Harvest Biol Technol 107:77–89

Sargent SA, Brecht JK, Zoellner JJ (1992) Sensitivity of tomatoes at mature-green and breaker ripeness stages to internal bruising. J Am Soc Hortic Sci 117:119–123

Selvakumar R (2014) A textbook of Glaustas olericulture. New Vishal, New Delhi, pp 961–967

Shibairo SI, Upadhyaya MK, Toivonen PMA (1998) Influence of preharvest water stress on postharvest moisture loss of carrots (*Daucus carota* L.). J Hort Sci Biotechnol 73:347–352

Singh V, Hedayetullah M, Zaman P, Meher J (2014) Postharvest technology of fruits and vegetables: an overview. J Postharvest Technol 2(2):124–135

Singh Z, Rajesh K, Singh V, Sane A, Nath P (2013) Mango-postharvest biology and biotechnology. Crit Rev Plant Sci 3:217–236

Solomon S (2009) Post harvest deterioration of sugarcane. Sugar Tech 11:109–123

Spurgeon D (1976) Hidden harvest-a systems approach to postharvest technology. International Development Research Centre, Ottawa, p 7

Stevens LH, Davelaar E (1997) Biochemical potential of potato tubers to synthesize blackspot pigments in relation to their actual blackspot susceptibility. J Agric Food Chem 45:4221–4226

Stevens R, Page D, Gouble B, Garchery C, Zamir D, Causse M (2008) Tomato fruit ascorbic acid content is linked with monodehydroascorbate reductase activity and tolerance to chilling stress. Plant Cell Environ 31:1086–1096

Thompson AK (2003) Fruit and vegetables: harvesting, handling and storage. Blackwell, New York

Toivonen PMA, Mark-Hodges D (2011) Abiotic stress in harvested fruits and vegetables. In: Abiotic stress in plants-mechanisms and adaptations. InTech, Rijeka, pp 39–56

Tournas VH (2004) Spoilage of vegetable crops by bacteria and fungi and related health hazards. Crit Rev Microbiol 31(1):33–44

Twede D, Kamdem D-P, Shires D (2015) Cartons, crates and corrugated board. DEStech Publications, Lancaster, p 561

Veličković M (1994) The influence of irrigation of fruit weight change of some major cultivars during refrigerated storage. Rev Res Work Facul Agric Belgrade 39:139–143

Vigeault C, Thompson J, Wu S (2009) Designing container for handling fresh horticultural produce. In: Benkebia N (ed) Post-harvest technologies for horticultural crops, vol 2. Asian Productivity Organization, Tokyo, pp 25–247

Wang CY (1993) Approaches to reducing chilling injury of fruits and vegetables. Hortic Rev 15: 63–95

Whitaker BD (2013) Genetic and biochemical bases of superficial scald storage disorder in apple. Acta Hortic 989(201305):47–60

Witkowska I, Woltering EJ (2010) Pre-harvest light intensity affects shelf-life of fresh-cut lettuce. Acta Hortic 877:223–227

World Bank (2011) Missing food: the case of post-harvest grain losses in Sub-Saharan Africa economic sector work report No. 60371-AFR. World Bank, Washington, DC

Bioactive Compost for Managing Plant Growth Under Stress Environment

15

Swati Sachdev, Shamim Akhtar Ansari, and Mohammad Israil Ansari

Abstract

With the progression of global human population, degradation of environment, and climate change, agricultural productivity is declining, threatening the world food security. To safeguard the need of present as well as future generation to access adequate amount and quality of food, focusing toward agricultural practices that ensure food security while maintaining harmony with environment is imperative. Application of organic compost and beneficial microorganisms has gained worldwide attention for improving plant growth and productivity under normal and stressed environment. Organic compost is regarded as natural soil conditioner and fertilizers due to their ability to improve soil structure and chemical properties such as soil pH, water holding capacity, organic carbon content, nutrient level, etc. Similarly, the beneficial microorganisms promote development and yield of associated plants even under stress conditions by stimulating root elongation through production of phytohormones; facilitating absorption of essential and limited nutrients; reducing growth of pathogens; fortifying plant defense mechanism; improving antioxidant, osmolyte, and other enzymes activity in plants; etc. Thus, actively applying compost rich in beneficial microorganisms, i.e., bioactive compost, or manipulating microbial population of poor compost through microbial enrichment can help plants to combat and sustain growth under influence of biotic and abiotic stresses.

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Keywords

Beneficial microorganisms · Water holding capacity · Phytohormones · Antioxidants · Pathogens · Plant growth promotion

15.1 Introduction

Zero hunger is the utmost important goal for every development program dedicated to human and environment sustainability. As human population is exceeding at greater pace, need to enhance crop productivity dramatically is the only key criterion to establish food security. However, production of food at high rates is quite a challenging task for the mankind. This challenge is presented by number of biotic and abiotic factors that not just restrict the existing ability to yield agricultural output but even abridge the future production potential and quality. It is likely that by the year 2050, world's population will rise by 33%, reaching to 9.7 billion (Berners-Lee et al. 2018) and the demand for agricultural crops will hike by 60% (Arif et al. 2020). As the global demand for food inflate in the future, the coverage of fertile land for agriculture will shrink with more human settlements, urbanization, and industrialization (Peerzado et al. 2019). Besides, change in share of agricultural land, degradation of environment, and increasing intensity and longevity of environmental stresses (biotic and abiotic) may breach the global food security and threaten human survival.

Incidence of both biotic and abiotic stresses, in particular, pathogenic diseases, pest attack, drought, water-logging, heat waves, chilling and freezing, nutrient deficiency, etc., is not an unusual phenomenon in natural environment (Jalil and Ansari 2018; Bulgari et al. 2019; Iqbal et al. 2021). Plants often encountered these stresses but manage to cope up due to their inherent tolerance and defense mechanisms. However, occurrence of these stresses for longer duration and/or at extreme intensity overshadows plant's defense expertise and results in reduced yield or sometimes even causes crop failure (Raza et al. 2019; Saijo and Loo 2020). The major reason for extended frequency, life span, and strengthened power of biotic and abiotic stress is anthropogenic. Modern agricultural practices adopted by humans including use of agrochemicals, extraction of water for irrigation, tillage and monoculture practices, expansion of agricultural land, and agriculture intensification have earned enormous benefits in terms of improved agricultural output, reduced plant diseases incidence rate, and monetary profits. In 20 years from 1985 to 2005, global crop production has increased by 28% (Arif et al. 2020). However, these gains have been received at the cost of environmental sustainability (Majeed et al. 2018; Khan et al. 2021). Unprecedented application of chemical fertilizers and pesticides, overexploitation of resources, clearing of forest for agriculture activities, and others have increased soil erosion, resulted in loss of fertile land and loss of biodiversity, depleted natural resources, increased pest resilience, increased chances of disease resurgence, and most importantly affected climatic conditions (Berners-Lee et al. 2018; Khan et al. 2021). Due to alteration in environmental services and climate change, plants are subjected to chronic environmental stresses that encroach their health and productivity, threatening global food security (Dresselhaus and Hückelhoven 2018). Studies have shown that yield of major cereal crops like wheat, rice, and maize, constituting nearly 57% of global agricultural calorific requirement, is declining or stagnating (Arif et al. 2020).

The necessity for enhancing crop productivity is the need of present hour. Nonetheless, adoption of approaches that are environmentally sound and sustainable is equally important. Some scientific data have revealed that 48% of the agricultural farms have experienced problem of nutrient deficiency. This problem cannot be mitigated simply by adding chemical-based fertilizers as such soil is often found to be deficient in soil organic carbon (SOC) and have low microbial biodiversity (Arif et al. 2020). To enhance crop productivity under unfavorable environment, promoting soil health and physicochemical characteristics in a sustainable and eco-friendly manner is crucial. In context to this, the present chapter attempts to address the role of bioactive compost in managing plant growth under stress conditions and present avenues provided by application of bioactive compost to foster soil quality and health by manifesting environmental sustainability.

15.2 Stress Mutilating Plant Growth and Development

Exposure of plants to biotic and abiotic stresses, occurring individually, in conjugation, and/or in sequence, alters growth and developmental process (Mertens et al. 2021) (Fig. 15.1). When intensity and duration of such stresses prolonged, concluding results are usually abridged productivity and intensified burden of economic debt (Raza et al. 2019). Biotic stress corresponds to biological threat to plants induced by pests and pathogens spanning from unicellular bacteria to multicellular arthropods. Pathogenic microbes, such as bacteria (*Ralstonia solanacearum*, *Erwinia* spp., *Xanthomonas* spp.), fungi (*Fusarium* spp., *Botrytis cinerea*), viruses (mosaic virus, yellow dwarf virus), nematodes (*Meloidogyne* spp.), and oomycetes (*Phytophthora* spp.), and herbivores (beetles, aphids) (Chen et al. 2018; Miles et al. 2019; Scott et al. 2019; Mohd Taha et al. 2019; Bolívar-Anillo et al. 2020; Ghareeb et al. 2020; Kleczewski et al. 2020; Timilsina et al. 2020; Xue et al. 2020; Mertens et al. 2021) attack plants during different stages of ontogenesis and stagnate or reduce plant growth (Mertens et al. 2021). Annually, biotic stress has been reported to claim almost 20–40% of agricultural crop yield worldwide (Khan et al. 2021). Among various pathogens, fungi and viruses are considered as severe threat for plants (Saddique et al. 2018). Till now around 8100 phytopathogenic species of fungi have been reported globally (Saddique et al. 2018). The phytopathogens and herbivores attack at different sites and cause either localized or systematic infection (Gimenez et al. 2018). The infection may result in vascular wilt, canker, root rot, root knot, spots on leaf, nutrition deprivation, overproduction of reactive oxygen species (ROS), and/or even cell death (Rossi et al. 2017; Gimenez et al. 2018; Saddique et al. 2018; Petrasch et al. 2019).

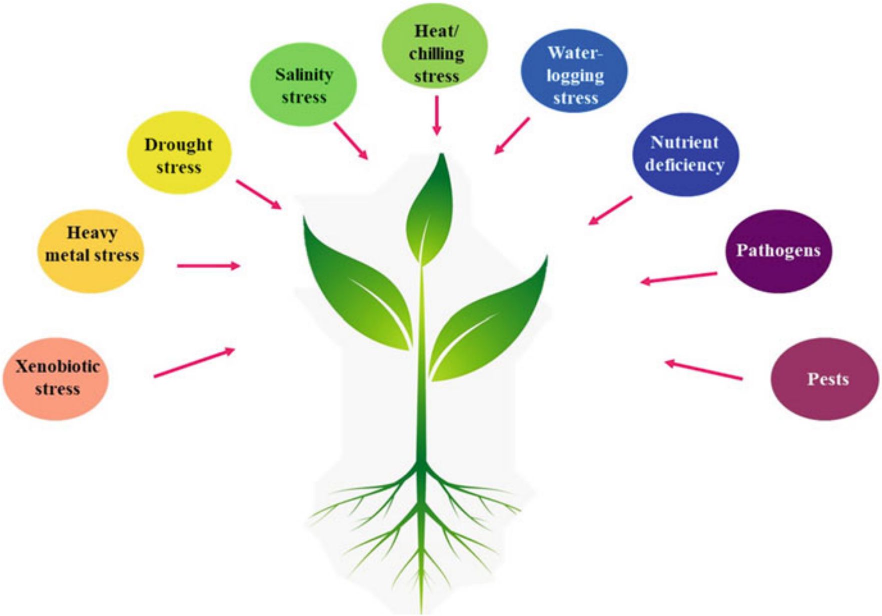

Fig. 15.1 Biotic and abiotic stresses that affect plant growth and development

Abiotic factors, such as temperature, water, salt, nutrients, xenobiotic compounds, toxic gases, heavy metals, and others, present at level above or below optimum induce negative effect on plant growth causing toxicity and reduced productivity (Jalil and Ansari 2018; Ali and Baek 2020). Plants subjected to abiotic stress often suffer from loss of photosynthetic activity, lessen stomatal conductance, poor development of root, reduced seed germination and seedling vigor, leaf senescence, functional loss of protein and enzymes, nutrient deficiency, stunted growth, abridged plant biomass and productivity, overproduction of ROS, and even death under severe conditions (Ansari and Lin 2010; Lopes et al. 2021; Iqbal et al. 2021; Sachdev et al. 2021). Overproduction of ROS may trigger oxidative stress which disturbs the nutritional status and the antioxidant activity in plants (Apel and Hirt 2004).

15.3 Bioactive Compost

Plants growing in natural environment are often associated with a number of microorganisms. Some of these associated microorganisms, known as plant probiotic microorganisms, show beneficial relationship with plants (de Souza Vandenberghe et al. 2017). The probiotics act as biofertilizers or biostimulator and bioprotectants that aids in plant growth promotion under normal as well as adverse environmental conditions (de Souza Vandenberghe et al. 2017). Plant probiotic microorganisms allied with plant roots facilitate nutrient availability, reduce toxicity of soil contaminants, manage biotic stress, and alleviate effects of environmental stresses such as drought, salinity, water-logging, etc. (de Souza Vandenberghe et al. 2017). Thus, maintaining good health of soil and retaining viable population of beneficial microorganisms in vicinity zone of plant roots, termed as rhizosphere, may be effective in promoting plant growth under influence of both biotic and abiotic stress. The bioactive compost rich in beneficial microorganisms is an effective approach for augmenting biological population in rhizosphere and stimulating soil physicochemical properties including improved soil structure and elevated organic carbon content (Chaudhary et al. 2020; De Corato 2020). Therefore, bioaugmentation of soil with bioactive compost manipulates the structure and activity of rhizospheric microbial diversity that can facilitate reduction or suppression of pathogens and disease (De Corato 2020). In addition to favorable development of wild microbiome, biocontrol microorganism present in bioactive compost can also directly participate in suppression of plant pathogens and diseases, and plant growth promotion (De Corato 2020).

Compost is the decomposed organic matter which is used as organic fertilizer and soil conditioner (Ramadass and Palaniyandi 2007). Compost is prepared through a regulated aerobic biological decomposition process known as composting, where complex organic materials are broken down into simpler materials such as water, carbon dioxide, and humus-like product (Chaudhary et al. 2020). Composting facilitates conversion of municipal solid organic waste into useful product which is rich in carbon, nutrients, and stabilized organic matter, is free from several phytopathogens, and offers eco-friendly option to manage environment pollution (Ramadass and Palaniyandi 2007; Chaudhary et al. 2020). The compost which is rich in beneficial microbes is known as bioactive compost. The compost prepared from municipal solid waste is generally low in nutrients such as nitrogen and phosphorus and does not generate significant benefits (Kavitha and Subramanian 2007; Saha et al. 2020). Therefore, normal composts are converted into bioactive composts through microbial enrichment like N-fixing bacteria, potash mobilizing bacteria, microbial biocontrol agent, etc. (Kavitha and Subramanian 2007; Saha et al. 2020). Such microbes improve nutritional status and the performance of the compost, i.e., ability to promote plant growth as well as management of biotic stress (Kavitha and Subramanian 2007; Saha et al. 2020). For instance, inoculation of N-fixing and phosphate solubilizing microorganisms like *Azotobacter*, *Phosphobacteria*, and *Pseudomonas* in compost enhanced its nutritive value (Kavitha and Subramanian 2007). Similarly, the addition of biodecomposer to pea plant compost reduced time required for composting; elevated N, P, and K content; and also increased wheat and rice grain by 9.4% and 6.9%, respectively (Eusuf Zai et al. 2009).

15.4 Potential of Bioactive Compost in Plant Growth Promotion Under Biotic Stress

Application of pathogen suppressing composts has shown tremendous potential in controlling diseases in multiple crops caused by pathogens *Fusarium oxysporum*, *Pythium* spp., *Phytophthora capsici*, *Verticillium dahlia*, *Rhizoctonia solani,* and many others along with stimulation of plant growth (González-Hernández et al. 2021) (Table 15.1). In addition to bioactive agents, the presence of nutrients and other organic compounds, such as humic acid, phenols, etc., has been reported to impart resistance against pathogens (González-Hernández et al. 2021). In particular, application of K has been mentioned to improve resistance against fungal and bacterial pathogens and insect pest in many cases (Amtmann et al. 2008). Application of K fertilizers had been reported to link with reduction of fungal and bacterial diseases in 70% and 69% of the reported studies, respectively, and infection caused by insects and mites were observed to be reduced in 63% of the studies (Amtmann et al. 2008). Gonzalez-Hernandez and his coworkers (2021) studied the biocontrol potential of compost teas on pathogens *P. capsici* and *R. solani* that are responsible for root rot, stem, foliar and fruit blight, damping-off, and seed decay in pepper plant. The compost rich in humic acid, nitrate, potassium oxide, and beneficial microorganisms like nitrogen fixing bacteria, actinomycetes, and other aerobic bacteria was reported to suppress the growth of *P. capsici* and *R. solani* by 31.7% and 38.0%, respectively, under in vitro condition. The compost also promoted the plant growth parameters, advanced crop cycle, and improved soil characteristics. The compost that is biologically inactive or poor has been reported to provide tolerance against phytopathogens after fortification with biocontrol agents such as *Trichoderma* spp., *Pseudomonas fluorescence*, and others (Saha et al. 2020). Application of compost enriched with biocontrol *Trichoderma harzianum* T-22 suppressed the growth of phytopathogen *R. solani* (Pugliese et al. 2011). Compost derived from various organic sources improved suppressiveness of peat against fungal pathogens *Pythium ultimum*, *R. solani*, and *Sclerotinia minor* responsible for causing damping off (Pane et al. 2011, 2013).

The biocontrol agents present in bioactive compost eliminate or suppress pathogens by exploiting several mechanisms such as microbiostasis and fungistasis, competition for infection sites and nutrition, production of lytic enzymes and antibiotic, induced systemic resistance, and improved nutritional status of plant (Mehta et al. 2014; Sachdev and Singh 2018a; De Corato 2020) (Fig. 15.2). The first three mechanisms act directly on pathogens by inhibiting their survival in soil and preventing invasion into the host plant whereas as the other two mechanisms indirectly affect pathogens by suppressing their development, colonization, and progression within host plant (De Corato 2020). Microbiostasis and fungistasis refer to inhibition of pathogen growth, development, reproduction, and sporulation without killing them, due to scarcity of nutrients in soil resulting from increased microbial biomass in soil (De Corato 2020). Competition for infection site and nutrition depends upon ability of biocontrol agents to efficiently colonize infection sites by producing biofilm and availability and acquisition of nutrients from soil.

Table 15.1 Bioactive compost amendment alleviated biotic and abiotic stress in multiple crops

Stress (pathogen/disease/stress)	Crop	Compost and beneficial microbes	Reference
Biotic stress			
Pathogens of tomato (*Fusarium oxysporum* f. sp. *radicis-lycopersici*, *Pyrenochaeta lycopersici*, *Rhizoctonia solani*, *Pythium ultimum*)	Tomato	On amendment of compost significant reduction of diseases reported that was may be due to increase of siderophore producing microbes within root zone of the plant	De Brito et al. (1995)
Fusarium wilt	Flax	Municipal solid waste compost	Serra-wittling et al. (1996)
Oomycetes- *P. ultimum* and *Phytophthora fragariae*	Cucumber	Chitin waste-based compost containing gram-positive bacteria showed antagonistic effect on pathogen	Labrie et al. (2001)
Aspergillus niger	Onion seed	Sunflower and alfalfa compost was used. Fluorescent pseudomonads and *Pantoea agglomerans* present in compost produced antifungal compounds that inhibited the growth of pathogens mycelia	Ozer and Koycu (2006)
Sclerotium rolfsii	Bean plant	The mycoparasite present in biosolid compost including sewage sludge and yard waste attacked sclerotia and suppressed their germination	Danon et al. (2007)
Fusarium wilt	Cucumber	Sludge compost containing *Fusarium oxysporum* was used that reduced diseases incidence	Huang et al. (2012)
Fusarium solani f. sp. *melongenae*	Brinjal	Vermicompost and neem cake added along with *Trichoderma harzianum* reduced wilt incidence, improved fruit yield, and increased growth attributes	Bhadauria et al. (2012)
Verticillium dahliae	Olive	Olive mill waste OMW-MI containing *Bacillus amyloliquefaciens* and *Burkholderia* reduced the density of pathogen microsclerotia in rhizosphere as well as plant mortality and increased root and shoot extension	Vitullo et al. (2013)

(continued)

Table 15.1 (continued)

Stress (pathogen/disease/stress)	Crop	Compost and beneficial microbes	Reference
Fusarium oxysporum f. sp. *cubense*	Banana	Compost from pig manure and canola cake in addition with *B. amyloliquefaciens* W19 reduces the incidence of banana wilt. The microorganisms produced antimicrobial lipopeptides and volatile antifungal compounds showing antagonistic activity against pathogen	Wang et al. (2013)
Abiotic stress			
Water-deficit stress	Cucumber seed	*Pseudomonas fluorescens* with compost and biochar was used that mitigated effect of stress and significantly improved growth parameters, chlorophyll, and relative water content and also alleviated leaf electrolyte leakage	Nadeem et al. (2017)
Lead	Radish	Compost + *Bacillus* sp. CIK-512 significantly increased growth parameters, photosynthetic rate, and stomatal conductance, regulated homeostasis of antioxidant activities, and reduced malondialdehyde content as well as lead accumulation	Ahmad et al. (2018)
Soil degradation and low soil fertility	Date palm	Compost + arbuscular mycorrhizal fungi (*Rhizoglomus irregulare*) stimulated root length; leaf area; root dry weight; N, P, and K content; stomatal conductance; and chlorophyll fluorescence, raised number of sclerenchyma fibers and vascular bundles, increased root diameter and lignification of endodermis of date palm seedling	Anli et al. (2020)
Salinity stress	Tomato, sunflower, quinoa, and maize	Halotolerant plant growth-promoting rhizobacteria (PGPR) used with compost increased crop growth, biomass, and resilience toward stress	Castiglione et al. (2021)

(continued)

Table 15.1 (continued)

Stress (pathogen/disease/stress)	Crop	Compost and beneficial microbes	Reference
Lead stress	Mint plant	Rhizobacteria (*Alcaligenes faecalis* and *B. amyloliquefaciens*) used with compost and biochar significantly improved soil organic matter and N, P, and K content. Plant growth attributes, chlorophyll, and nutrient content was increased whereas lead uptake was reduced	Zafar-ul-Hye et al. (2021)

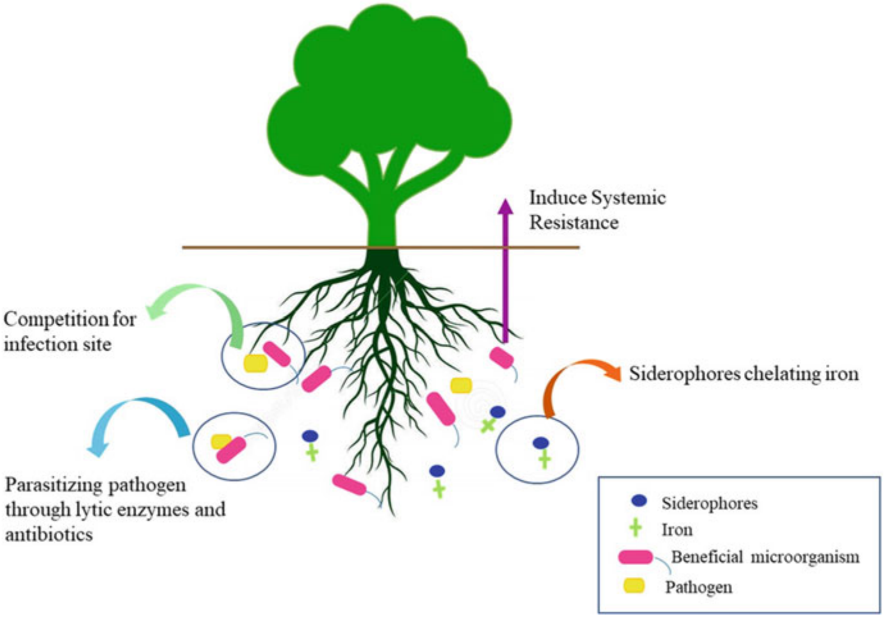

Fig. 15.2 Various mechanisms deployed by beneficial microorganisms to reduce biotic stress on plants

Several beneficial microorganisms produce iron-chelating siderophores that reduce availability to iron to pathogens, resulting in starvation and elimination of latter (Sachdev and Singh 2020). For instance, competition for nutrients has been demonstrated as effective mechanism for suppressing growth of fungal pathogen *Botrytis cinerea*, which is sensitive to low nutrient level (Benítez et al. 2004). Macías-Rodríguez et al. (2018) reported that in the presence of carbohydrate, growth of *Trichoderma atroviride* was enhanced which restricted growth of the fungal pathogen *Phytophthora cinnamomi* on interaction due to competition for both space and nutrition. Many beneficial microbiota such as *Trichoderma harzianum*, *Bacillus subtilis*, and *Pseudomonas fluorescence* produce antibiotics (harzianic acid, zwittermicin A, fengycin, phenazine) and lytic enzymes (chitinase, glucanase) (Mehta et al. 2014; Wang et al. 2021) that inhibit mycelial growth, and conidia germination (De Corato 2020). Biocontrol microorganisms either attack and parasitize pathogens resulting in cell lysis and death of pathogen and/or kill them by phagocytosis (De Corato 2020). Inhibition of growth of plant pathogens like *Fusarium* spp., *Pythium* spp., *R. solani*, *Sclerotinia sclerotiorum*, *Sclerotium rolfsii*, and root knot nematodes through parasitism displayed by *Trichoderma* spp. has been well documented (Howell 2003; Affokpon et al. 2011; Contreras-Cornejo et al. 2016; Mathews et al. 2019). Studies have also reported that cell wall degrading enzymes can act synergistically with antifungal compounds and inhibit pathogen spore germination (De Corato 2020). The bioactive compost contains several plant growth-promoting microorganisms that improve nutritional status of plants and enhance plant tolerance toward biotic stress (Mehta et al. 2014; De Corato 2020). Additionally, a large number of microorganisms colonizing host root elicit systemic resistance that assist in suppression of diseases (De Corato 2020; Sachdev and Singh 2020). *T. atroviride* has been reported to induce systemic resistance in tomato against root knot causing nematode (Rubio et al. 2019).

15.5 Bioactive Compost Stimulating Plant Growth Under Abiotic Stress

Plants growing in natural environment frequently encounter with number of abiotic stresses such as salinity, water deficiency, water-logging, temperature fluctuation (heat/chilling stress), nutrition deficiency, low/high light intensity, toxic levels of heavy metals, and others that trigger oxidative stress, early senescence, impaired seed germination, plant dehydration, membrane dysfunction, photosynthesis inhibition, and reduced plant productivity to half (Wang et al. 2003; Agarwal and Grover 2006; Meena et al. 2017; Sachdev et al. 2021). Amendment of bioactive compost in soil improves soil health and promotes productivity of plants growing therein (Sharma et al. 2017). Several studies have confirmed upgraded soil and crop attributes on application of compost rich in plant growth-promoting microbial population. The tomato plant treated with bioactive compost along with half of the recommended dose of chemical fertilizer reported to display increment in yield by 31.83%, lycopene content by 35.52%, and antioxidants increase by 24–63%, and defense-related enzymes content was elevated by 11–54% as compared to recommended dose of chemical fertilizers (Verma et al. 2015). Similarly, use of microbial amended compost for growth of calendula and marigold, increased carotenoid content of flowers, and improved enzymes, humus, available nitrogen, and organic carbon content in soil (Sharma et al. 2017). Bioactive compost comprising beneficial microorganisms also aid in soil fertility, stimulate rhizospheric

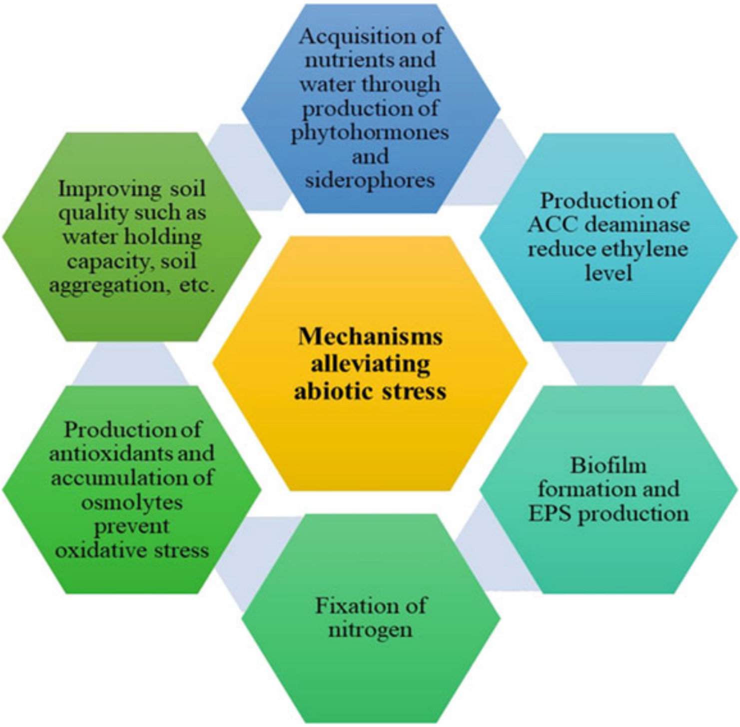

Fig. 15.3 Mechanisms employed by beneficial microorganisms for alleviating abiotic stress in plants

microbiome, and promote plant growth under abiotic stress condition (Table 15.1). The growth of plants such as *Acer platanoides*, *Cornus alba, Fraxinus excelsior*, *Robinia pseudoacacia*, and *Spiraea vanhouttei* was found to be improved under saline stress when treated with green waste compost containing arbuscular mycorrhiza (Marosz 2012). The nano-sized compost along with microbial isolates (*Bacillus cereus*, *Lysinibacillus* sp. and *Rhodotorula glutinis*) from compost improved growth parameters, chlorophyll content, and antioxidant enzymes and reduced malondialdehyde (MDA) content in turf grass under drought condition (Duo et al. 2018).

The mechanisms involved by biological counterpart of bioactive compost for plant growth under abiotic stress include increased mobilization of insoluble nutrients, enhanced availability of limited nutrients through production of siderophores, fixation of nitrogen, increased accumulation of osmolytes, up- and downregulation of stress-responsive genes, synthesis of phytohormones and enzymes like Indole-3-acetic acid (IAA) and 1-aminocyclopropane-1-carboxylate (ACC) deaminase, improved soil properties such as pH alteration, water holding capacity and soil aggregation via production of exopolysaccharides (EPS), and recovering of degraded soil (Verma et al. 2015; Nadeem et al. 2017; Sachdev et al. 2018; Ullah et al. 2021) (Fig. 15.3). Capacity of beneficial microorganisms to colonize plant roots efficiently is the most important trait that facilitates plant growth promotion (PGP) and alleviation of abiotic stress (Sachdev and Singh 2018b). Successful colonization of plant roots facilitate water and nutrients uptake and acidify ambient environment via synthesis of organic acids that enhance solubilization of minerals and micronutrients for biofertilization (Harman 2011; Kaya et al. 2009; Akladious and Abbas 2014; Contreras-Cornejo et al. 2016). *Pseudomonas azotoformans* FAP5 with the ability to produce EPS, form biofilm, colonize root effectively, synthesize IAA, and solubilize tricalcium phosphate and ACC deaminase activity improved growth parameters, photosynthetic pigment efficiency, and other physiological attributes of wheat plants grown under drought stress (Ansari et al. 2021). Production of phytohormones, enzymes, and accumulation of osmolytes in plants under influence of microorganisms also impart tolerance against abiotic stress by improving root growth, reducing concentration of ethylene, and alleviating oxidative stress in plant (Sachdev et al. 2018; Zerrouk et al. 2019). The phytohormones like auxin and gibberellins produced by beneficial microorganisms promote lateral root formation and water uptake efficiency of plant (Doni et al. 2014). Plant growth-promoting rhizobacteria *Pseudomonas plecoglossicida* strain Pp20, with ability to produce PGP hormone-IAA and enzyme ACC deaminase which degrade ethylene, reduced salt and aluminium-induced damage in *Zea mays* and improved growth attributes including chlorophyll and carbohydrate content (Zerrouk et al. 2019). Treatment of *Arabidopsis* seedlings with *T. virens* or *T. atroviride* reported to increase lateral roots and root hair growth, conferring tolerance against salt stress (Contreras-Cornejo et al. 2014). *T. harzianum* Th-14-inoculated wheat seed showed higher osmolyte concentration that maintained cellular macromolecule structure and function and lowered MDA content under salt stress condition (Rawat et al. 2011). The overexpression of genes encoding for membrane proteins aquaglyceroporins in *T. harzianum* which participates in regulation of water and solute movement via bio-membranes induced biocontrol against *Fusarium oxysporum* and tolerance against drought stress in bean plant by increasing leaf area, root growth, and dry weight (Vieira et al. 2018a, b). Similarly, Adams et al. (2007) reported *T. harzianum* T-22-induced phytostabilization of metal-contaminated sites and plant growth promotion.

15.6 Conclusion and Future Prospects

Bioactive compost enriched with beneficial microorganism possessing a number of mechanisms to promote plant growth under abiotic and biotic stress has demonstrated tremendous potential. Tapping this potential efficiently can safeguard the problem of food unavailability for growing population. In addition to plant growth, the use of bioactive compost can reduce the input of agrochemicals in agricultural fields and minimize the size of solid waste generated through agricultural and municipal activities, thereby reducing the negative impacts on environment. Therefore, the use of bioactive compost should be encouraged at farm levels to incur maximum gains. However, before commercializing application of bioactive compost at large scale, the detailed studies on microbial population or communities inhabiting compost and their probable mechanisms used for alleviating environmental stress is needed. For instance, quantifying the species abundance, species richness, species evenness, and their function should be elucidated through in-depth studies. Identifying the structure of microbial communities and their function facilitate in optimization of doses for particular crop(s), in accordance with soil and prevailing environmental conditions.

Conflict of Interest There is no conflict of interest.

References

Adams P, De-Leij FA, Lynch JM (2007) *Trichoderma harzianum* Rifai 1295–22 mediates growth promotion of crack willow (*Salix fragilis*) saplings in both clean and metal-contaminated soil. Microb Ecol 54(2):306–313

Affokpon A, Coyne DL, Htay CC, Agbèdè RD, Lawouin L, Coosemans J (2011) Biocontrol potential of native *Trichoderma* isolates against root-knot nematodes in West African vegetable production systems. Soil Biol Biochem 43(3):600–608

Agarwal S, Grover A (2006) Molecular biology, biotechnology and genomics of flooding-associated low O_2 stress response in plants. Crit Rev Plant Sci 25(1):1–21

Ahmad I, Akhtar MJ, Mehmood S, Akhter K, Tahir M, Saeed MF, Hussain MB, Hussain S (2018) Combined application of compost and *Bacillus* sp. CIK-512 ameliorated the lead toxicity in radish by regulating the homeostasis of antioxidants and lead. Ecotoxicol Environ Saf 148:805–812

Akladious SA, Abbas SM (2014) Application of *Trichoderma harzianum* T22 as a biofertilizer potential in maize growth. J Plant Nutr 37(1):30–49

Ali M, Baek KH (2020) Jasmonic acid signaling pathway in response to abiotic stresses in plants. Int J Mol Sci 21(2):621

Amtmann A, Troufflard S, Armengaud P (2008) The effect of potassium nutrition on pest and disease resistance in plants. Physiol Plant 133(4):682–691

Anli M, Symanczik S, El Abbassi A, Ait-El-Mokhtar M, Boutasknit A, Ben-Laouane R, Toubali S, Baslam M, Mader P, Hafidi M, Meddich A (2020) Use of arbuscular mycorrhizal fungus *Rhizoglomus irregulare* and compost to improve growth and physiological responses of *Phoenix dactylifera* 'Boufgouss'. Plant Biosyst 5:1–9

Ansari FA, Jabeen M, Ahmad I (2021) *Pseudomonas azotoformans* FAP5, a novel biofilm-forming PGPR strain, alleviates drought stress in wheat plant. Int J Environ Sci Technol 5:1–16

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

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

Arif I, Batool M, Schenk PM (2020) Plant microbiome engineering: expected benefits for improved crop growth and resilience. Trends Biotechnol 38:1385

Benítez T, Rincón AM, Limón MC, Codon AC (2004) Biocontrol mechanisms of *Trichoderma* strains. Int Microbiol 7(4):249–260

Berners-Lee M, Kennelly C, Watson R, Hewitt CN, Kapuscinski AR, Locke KA, Peters CJ (2018) Current global food production is sufficient to meet human nutritional needs in 2050 provided there is radical societal adaptation. Elem: Sci Anth 2018:6

Bhadauria BP, Singh Y, Puri S, Singh PK (2012) Ecofriendly management of Fusarium wilt of brinjal. Ecol Environ Conserv 18:1049–1052

Bolívar-Anillo HJ, Garrido C, Collado IG (2020) Endophytic microorganisms for biocontrol of the phytopathogenic fungus *Botrytis cinerea*. Phytochem Rev 19(3):721–740

Bulgari R, Franzoni G, Ferrante A (2019) Biostimulants application in horticultural crops under abiotic stress conditions. Agronomy 9(6):306

Castiglione S, Oliva G, Vigliotta G, Novello G, Gamalero E, Lingua G, Cicatelli A, Guarino F (2021) Effects of compost amendment on glycophyte and halophyte crops grown on saline soils: isolation and characterization of rhizobacteria with plant growth promoting features and high salt resistance. Appl Sci 11(5):2125

Chaudhary S, Vaish B, Singh RP, Prasad V (2020) Bioactive compost: an approach for managing plant growth in environmentally stressed soils. In: New frontiers in stress management for durable agriculture. Springer, Singapore, pp 257–267

Chen Y, Wang J, Yang N, Wen Z, Sun X, Chai Y, Ma Z (2018) Wheat microbiome bacteria can reduce virulence of a plant pathogenic fungus by altering histone acetylation. Nat Commun 9(1): 1–14

Contreras-Cornejo HA, Macías-Rodríguez L, Del-Val EK, Larsen J (2016) Ecological functions of *Trichoderma* spp. and their secondary metabolites in the rhizosphere: interactions with plants. FEMS Microbiol Ecol 92(4):fiw036

Contreras-Cornejo HA, Macías-Rodríguez L, Alfaro-Cuevas R, López-Bucio J (2014) *Trichoderma* spp. improve growth of *Arabidopsis* seedlings under salt stress through enhanced root development, osmolite production, and Na+ elimination through root exudates. Mol Plant Microbe Interact 27(6):503–514

Danon M, Zmora-Nahum S, Chen Y, Hadar Y (2007) Prolonged compost curing reduces suppression of *Sclerotium rolfsii*. Soil Biol Biochem 39(8):1936–1946

De Brito AM, Gagne S, Antoun H (1995) Effect of compost on rhizosphere microflora of the tomato and on the incidence of plant growth-promoting rhizobacteria. Appl Environ Microbiol 61(1): 194–199

De Corato U (2020) Disease-suppressive compost enhances natural soil suppressiveness against soil-borne plant pathogens: a critical review. Rhizosphere 13(100):192

de Souza Vandenberghe LP, Garcia LMB, Rodrigues C, Camara MC, de Melo Pereira GV, de Oliveira J, Soccol CR (2017) Potential applications of plant probiotic microorganisms in agriculture and forestry. AIMS Microbiol 3(3):629

Doni F, Isahak A, Zain CRCM, Yusoff WMW (2014) Physiological and growth response of rice plants (*Oryza sativa* L.) to *Trichoderma* spp. inoculants. Amb Express 4(1):1–7

Dresselhaus T, Hückelhoven R (2018) Biotic and abiotic stress responses in crop plants. Agronomy 8(11):267

Duo LA, Liu CX, Zhao SL (2018) Alleviation of drought stress in turfgrass by the combined application of nano-compost and microbes from compost. Russ J Plant Physiol 65(3):419–426

Eusuf Zai AK, Horiuchi T, Matsui T (2009) Bio-active compost from pea plant enriched with chicken manure and oilseed rape cake and its effect on yields and nutrient recovery efficiencies of wheat and rice. Archiv Agron Soil Sci 55(4):345–357

Ghareeb RY, Alfy H, Fahmy AA, Ali HM, Abdelsalam NR (2020) Utilization of *Cladophora glomerata* extract nanoparticles as eco-nematicide and enhancing the defense responses of tomato plants infected by *Meloidogyne javanica*. Sci Rep 10(1):1–15

Gimenez E, Salinas M, Manzano-Agugliaro F (2018) Worldwide research on plant defense against biotic stresses as improvement for sustainable agriculture. Sustainability 10(2):391

González-Hernández AI, Suárez-Fernández MB, Pérez-Sánchez R, Gómez-Sánchez MÁ, Morales-Corts MR (2021) Compost tea induces growth and resistance against *Rhizoctonia solani* and *Phytophthora capsici* in pepper. Agronomy 11(4):781

Harman GE (2011) *Trichoderma*—not just for biocontrol anymore. Phytoparasitica 39(2):103–108

Howell CR (2003) Mechanisms employed by *Trichoderma* species in the biological control of plant diseases: the history and evolution of current concepts. Plant Dis 87(1):4–10

Huang X, Shi D, Sun F, Lu H, Liu J, Wu W (2012) Efficacy of sludge and manure compost amendments against Fusarium wilt of cucumber. Environ Sci Pollut Res 19(9):3895–3905

Iqbal Z, Iqbal MS, Hashem A, Abd Allah EF, Ansari MI (2021) Plant defense responses to biotic stress and its interplay with fluctuating dark/light conditions. Front Plant Sci 12:297

Jalil SU, Ansari MI (2018) Plant microbiome and its functional mechanism in response to environmental stress. Int J Green Pharm 12(01):81–92

Kavitha R, Subramanian P (2007) Bioactive compost—a value added compost with microbial inoculants and organic additives. J Appl Sci 7(17):2514–2518

Kaya C, Ashraf M, Sonmez O, Aydemir S, Tuna AL, Cullu MA (2009) The influence of arbuscular mycorrhizal colonisation on key growth parameters and fruit yield of pepper plants grown at high salinity. Sci Hortic 121(1):1–6

Khan M, Khan AU, Hasan MA, Yadav KK, Pinto M, Malik N, Yadav VK, Khan AH, Islam S, Sharma GK (2021) Agro-nanotechnology as an emerging field: a novel sustainable approach for improving plant growth by reducing biotic stress. Appl Sci 11(5):2282

Kleczewski N, Chapara V, Bradley CA (2020) Occurrence of viruses and *Clavibacter michiganensis* in winter wheat in Illinois, 2009 to 2011 and 2019 to 2020. Plant Health Prog 21(4):317–320

Labrie C, Leclerc P, Côté N, Roy S, Brzezinski R, Hogue R, Beaulieu C (2001) Effect of chitin waste-based composts produced by two-phase composting on two oomycete plant pathogens. Plant and Soil 235(1):27–34

Lopes MJDS, Dias-Filho MB, Gurgel ESC (2021) Successful plant growth-promoting microbes: inoculation methods and abiotic factors. Front Sustain Food Syst 5:48

Macías-Rodríguez L, Guzmán-Gómez A, García-Juárez P, Contreras-Cornejo HA (2018) *Trichoderma atroviride* promotes tomato development and alters the root exudation of carbohydrates, which stimulates fungal growth and the biocontrol of the phytopathogen *Phytophthora cinnamomi* in a tripartite interaction system. FEMS Microbiol Ecol 94(9):fiy137

Majeed A, Muhammad Z, Ahmad H (2018) Plant growth promoting bacteria: role in soil improvement, abiotic and biotic stress management of crops. Plant Cell Rep 37(12):1599–1609

Marosz A (2012) Effect of green waste compost and mycorrhizal fungi on calcium, potassium, and sodium uptake of woody plants grown under salt stress. Water Air Soil Pollut 223(2):787–800

Mathews JR, Sivparsad BJ, Laing MD (2019) Greenhouse evaluation of *Trichoderma harzianum* for the control of Sclerotinia wilt (*Sclerotinia sclerotiorum*) of sunflower. South Afr J Plant Soil 36(1):69–72

Meena KK, Sorty AM, Bitla UM, Choudhary K, Gupta P, Pareek A, Singh DP, Prabha R, Sahu PK, Gupta VK, Singh HB, Krishanani KK, Minhas PS (2017) Abiotic stress responses and microbe-mediated mitigation in plants: the omics strategies. Front Plant Sci 8:172

Mehta CM, Palni U, Franke-Whittle IH, Sharma AK (2014) Compost: its role, mechanism and impact on reducing soil-borne plant diseases. Waste Manag 34(3):607–622

Mertens D, Boege K, Kessler A, Koricheva J, Thaler JS, Whiteman NK, Poelman EH (2021) Predictability of biotic stress structures plant defence evolution. Trends Ecol Evol 36(5): 444–456

Miles LS, Breitbart ST, Wagner HH, Johnson MT (2019) Urbanization shapes the ecology and evolution of plant-arthropod herbivore interactions. Front Ecol Evol 7:310

Mohd Taha MD, Mohd Jaini MF, Saidi NB, Abdul Rahim R, Md Shah UK, Mohd Hashim A (2019) Biological control of *Erwinia mallotivora*, the causal agent of papaya dieback disease by indigenous seed-borne endophytic lactic acid bacteria consortium. PLoS One 14(12):e0224431

Nadeem SM, Imran M, Naveed M, Khan MY, Ahmad M, Zahir ZA, Crowley DE (2017) Synergistic use of biochar, compost and plant growth-promoting rhizobacteria for enhancing cucumber growth under water deficit conditions. J Sci Food Agric 97(15):5139–5145

Ozer N, Koycu ND (2006) The ability of plant compost leachates to control black mold (*Aspergillus niger*) and to induce the accumulation of antifungal compounds in onion following seed treatment. BioControl 51(2):229–243

Pane C, Piccolo A, Spaccini R, Celano G, Villecco D, Zaccardelli M (2013) Agricultural waste-based composts exhibiting suppressivity to diseases caused by the phytopathogenic soil-borne fungi *Rhizoctonia solani* and *Sclerotinia minor*. Appl Soil Ecol 65:43–51

Pane C, Spaccini R, Piccolo A, Scala F, Bonanomi G (2011) Compost amendments enhance peat suppressiveness to *Pythium ultimum*, *Rhizoctonia solani* and *Sclerotinia minor*. Biol Contr 56(2):115–124

Peerzado MB, Magsi H, Sheikh MJ (2019) Land use conflicts and urban sprawl: Conversion of agriculture lands into urbanization in Hyderabad, Pakistan. J Saudi Soc Agric Sci 18(4): 423–428

Petrasch S, Knapp SJ, Van Kan JA, Blanco-Ulate B (2019) Grey mould of strawberry, a devastating disease caused by the ubiquitous necrotrophic fungal pathogen *Botrytis cinerea*. Mol Plant Pathol 20(6):877–892

Pugliese M, Liu B, Gullino ML, Garibaldi A (2011) Microbial enrichment of compost with biological control agents to enhance suppressiveness to four soil-borne diseases in greenhouse. J Plant Dis Protect 118(2):45–50

Ramadass K, Palaniyandi S (2007) Effect of enriched municipal solid waste compost application on soil available macronutrients in the rice field. Archiv Agron Soil Sci 53(5):497–506

Rawat L, Singh Y, Shukla N, Kumar J (2011) Alleviation of the adverse effects of salinity stress in wheat (*Triticum aestivum* L.) by seed biopriming with salinity tolerant isolates of *Trichoderma harzianum*. Plant and Soil 347(1):387–400

Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, Xu J (2019) Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. Plan Theory 8(2):34

Rossi FR, Krapp AR, Bisaro F, Maiale SJ, Pieckenstain FL, Carrillo N (2017) Reactive oxygen species generated in chloroplasts contribute to tobacco leaf infection by the necrotrophic fungus *Botrytis cinerea*. Plant J 92(5):761–773

Rubio MB, de Medeiros HA, Morán-Diez ME, Castillo P, Hermosa R, Monte E (2019) A split-root method to study systemic and heritable traits induced by *Trichoderma* in tomato plants. In: Methods in rhizosphere biology research. Springer, Singapore, pp 151–166

Sachdev S, Ansari SA, Ansari MI, Fujita M, Hasanuzzaman M (2021) Abiotic stress and reactive oxygen species: generation, signaling, and defense mechanisms. Antioxidants 10(2):277

Sachdev S, Singh A, Singh RP (2018) Optimization of culture conditions for mass production and bio-formulation of *Trichoderma* using response surface methodology. 3 Biotech 8(8):1–8

Sachdev S, Singh RP (2018a) Isolation, characterisation and screening of native microbial isolates for biocontrol of fungal pathogens of tomato. Clim Change Environ Sustain 6(1):46–58

Sachdev S, Singh RP (2018b) Root colonization: imperative mechanism for efficient plant protection and growth. MOJ Ecol Environ Sci 3:240–242

Sachdev S, Singh RP (2020) *Trichoderma*: a multifaceted fungus for sustainable agriculture. In: Ecological and practical applications for sustainable agriculture. Springer, Singapore, pp 261–304

Saddique M, Kamran M, Shahbaz M (2018) Differential responses of plants to biotic stress and the role of metabolites. In: Plant metabolites and regulation under environmental stress. Academic Press, Amsterdam, pp 69–87

Saha N, Biswas S, Mondal S, Dey D, Dasgupta S (2020) Value addition in compost. In: Recent trends in composting technology. IK International, New Delhi

Saijo Y, Loo EPI (2020) Plant immunity in signal integration between biotic and abiotic stress responses. New Phytol 225(1):87–104

Scott P, Bader MKF, Burgess T, Hardy G, Williams N (2019) Global biogeography and invasion risk of the plant pathogen genus *Phytophthora*. Environ Sci Policy 101:175–182

Serra-Wittling C, Houot S, Alabouvette C (1996) Increased soil suppressiveness to Fusarium wilt of flax after addition of municipal solid waste compost. Soil Biol Biochem 28(9):1207–1214

Sharma A, Saha TN, Arora A, Shah R, Nain L (2017) Efficient microorganism compost benefits plant growth and improves soil health in calendula and marigold. Hortic Plant J 3(2):67–72

Timilsina S, Potnis N, Newberry EA, Liyanapathiranage P, Iruegas-Bocardo F, White FF, Goss EM, Jones JB (2020) Xanthomonas diversity, virulence and plant–pathogen interactions. Nat Rev Microbiol 18(8):415–427

Ullah N, Ditta A, Imtiaz M, Li X, Jan AU, Mehmood S, Rizwan MS, Rizwan M (2021) Appraisal for organic amendments and plant growth-promoting rhizobacteria to enhance crop productivity under drought stress: a review. J Agron Crop Sci 207:783

Verma S, Sharma A, Kumar R, Kaur C, Arora A, Shah R, Nain L (2015) Improvement of antioxidant and defense properties of tomato (var. Pusa Rohini) by application of bioaugmented compost. Saudi J Biol Sci 22(3):256–264

Vieira PM, Zeilinger S, Brandao RS, Vianna GR, Georg RC, Gruber S, Aragao FJL, Ulhoa CJ (2018a) Overexpression of an aquaglyceroporin gene in the fungal biocontrol agent *Trichoderma harzianum* affects stress tolerance, pathogen antagonism and *Phaseolus vulgaris* development. Biol Contr 126:185–191. https://doi.org/10.1016/j.biocontrol.2018.08.012

Vieira PM, Zeilinger S, Brandao RS, Vianna GR, Georg RC, Gruber S, Aragao FJL, Ulhoa CJ (2018b) Overexpression of an aquaglyceroporin gene in the fungal biocontrol agent *Trichoderma harzianum* affects stress tolerance, pathogen antagonism and *Phaseolus vulgaris* development. Biol Contr 126:185–191

Vitullo D, Altieri R, Esposito A, Nigro F, Ferrara M, Alfano G, Ranalli G, Cicco VD, Lima G (2013) Suppressive biomasses and antagonist bacteria for an eco-compatible control of *Verticillium dahliae* on nursery-grown olive plants. Int J Environ Sci Technol 10(2):209–220

Wang B, Yuan J, Zhang J, Shen Z, Zhang M, Li R, Ruan Y, Shen Q (2013) Effects of novel bioorganic fertilizer produced by *Bacillus amyloliquefaciens* W19 on antagonism of Fusarium wilt of banana. Biol Fertil Soils 49(4):435–446

Wang SY, Shi XC, Chen X, Laborda P, Zhao YY, Liu FQ, Laborda P (2021) Biocontrol ability of phenazine-producing strains for the management of fungal plant pathogens: a review. Biol Contr 104:548

Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218(1):1–14

Xue H, Lozano-Durán R, Macho AP (2020) Insights into the root invasion by the plant pathogenic bacterium *Ralstonia solanacearum*. Plan Theory 9(4):516

Zafar-ul-Hye M, Tahzeeb-ul-Hassan M, Wahid A, Danish S, Khan MJ, Fahad S, Brtnicky N, Hussain GS, Battaglia ML, Datta R (2021) Compost mixed fruits and vegetable waste biochar with ACC deaminase rhizobacteria can minimize lead stress in mint plants. Sci Rep 11(1):1–20

Zerrouk IZ, Rahmoune B, Khelifi L, Mounir K, Baluska F, Ludwig-Müller J (2019) Algerian Sahara PGPR confers maize root tolerance to salt and aluminum toxicity via ACC deaminase and IAA. Acta Physiologiae Plant 41(6):91

16

Salicylic Acid: Metabolism, Regulation, and Functions in Crop Abiotic Stress Tolerance

Shalini Tiwari, Charu Lata, and Puneet Singh Chauhan

Abstract

Salicylic acid (SA), a plant phenolic derivative, is distributed in a wide range of species. It is a product of shikimic acid and phenylpropanoid metabolism of plants. SA synthesize in plants through different regulatory pathways depending on the requirement of the plant cell via these pathways. It has direct involvement in various plant phenomenon including growth, flower initiation, and ions uptake. In physiological processes, it has role in stomatal movement, ethylene biosynthesis, and leaf abscission. SA also enhances chlorophyll and carotenoid pigments level and photosynthetic rate and alters some important enzyme activities. Earlier, it was considered that SA plays a key role during biotic stress in plants; however, now it is well recognized that SA is also associated with various abiotic stress responses. Moreover, recently SA is also known to mediate interaction between plant and beneficial microbes. Therefore, the present chapter gives coverage to all the abovementioned aspects.

Keywords

Abiotic stress · Beneficial microbes · Chlorophyll · Metabolism · Regulation · Salicylic acid

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16.1 Introduction

Salicylates are group of members that are phenolic in nature and are derived from salicylic acid (SA). Basic structure of salicylates consists of aromatic ring with a hydroxyl group (-OH) as side chain. Even before chemical identification, humans used salicylates in the form of plant extract as pain killers (analgesics) from thousands of years (Klessig et al. 2018), which is evident from the poplar bark discovered from dental plaque of Neanderthals (*Homo neanderthalensis*) fossils from El Sidron cave (Weyrich et al. 2017). Ancient culture script of several countries across the globe mentioned the use of plants that contain salicylates as medicinal herb (Vlot et al. 2009). SA was firstly isolated by John A. Buchner (1828) from white willow bark (Salix) and named it as salicyl alcohol glucoside (salicine). Later, Raffaele Piria (1838) named it as salicylic acid (SA). Chemical structure of SA showed it is a mono-hydroxybenzoic acid, i.e., benzoic acid ($C_6H_5COO^-$ aromatic ring) with a hydroxy group (-OH) at the ortho position (hydroxy side chain) (Fig. 16.1). Physical state of salicylic acid exists in odorless, white crystalline powder with melting range of 157–160 °C and with poor solubility in water but high solubility in organic solvents.

It is also classified as a major plant hormone that regulates plant growth and development (Tiwari et al. 2017a, b) and is universally found across the entire plant kingdom (Maruri-López et al. 2019). SA is also known to have diverse regulatory roles in plant metabolism. In plants, SA is mainly considered to play a crucial role in defense against biotrophic pathogens, i.e., biotic stress. Even after methylation, SA (methyl-SA) becomes volatile in nature and transports to relay signals to neighboring plants about pathogen attack (Heil and Ton 2008). Additionally, apart from its role in plant defense, several investigations reported involvement of SA in response to abiotic stress as well, mainly salinity, drought, extreme temperatures, and heavy metals (Tiwari et al. 2017a, b). Furthermore, exogenously applied SA, travel and transport to various plant tissues to generate defense response. Interestingly, due to its medicinal properties, it also gains attention to researchers and therefore been used as an analgesic drug for, e.g., as a precursor of the well-known painkiller aspirin.

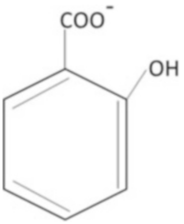

Fig. 16.1 Structural formula of salicylic acid

16.2 Biosynthesis of Salicylic Acid

SA is a naturally occurring compound and is biosynthesized from isochorismate or cinnamic acid that are intermediate of the shikimate pathway and phenylpropanoid pathway, respectively (Dempsey et al. 2011). These pathways are known for synthesis of aromatic amino acids and various phenolic compounds. Earlier, isochorismate was identified as a plastidial precursor, and after conversion to SA, it is known to be transported to the cytosol with the help of enhanced disease susceptibility 5 (EDS5) carrier. A recent study by Murphy et al. (2020) discarded the earlier theory and proved that EDS5 is an isochorismate transporter and not of SA. Isochorismate transportation from plastid to cytosol suggests that the conversion of isochorismate into SA is completed in the cytosol and not in the plastid. Another pathway that uses cinnamic acid as precursor is also cytosolic and comprises reactions of non-oxidative pathways in both coenzyme A (CoA)-dependent and CoA-independent manner by converting benzoic acid (benzoate) into SA after hydroxylation at C-2 position. The CoA-dependent β-oxidative pathway of peroxisome also produces benzoic acid that convert into SA in cytosol (Murphy et al. 2020). These abovementioned possible routes, i.e., conversion of isochorismate in SA, decarboxylation of cinnamic acid side chain to generate benzoate and further to SA, and hydroxylation of cinnamic acid followed by decarboxylation reaction to form salicylic acid, have been illustrated in the Fig. 16.2.

16.3 Metabolism of Salicylic Acid

Due to diverse role in plant metabolism, SA modifies into diverse bioactive derivatives and hence has unique molecular properties. The formation of bioactive derivatives occurs via different chemical reactions within plant cell including methylation, glycosylation, amino acid conjugation, sulfonation, and hydroxylation (Fig. 16.3). These modifications are for different purposes that means either for its activation or inactivation for regulatory roles or for its storage.

16.3.1 Glycosylation

The attachment of carbohydrate moiety, i.e., glycosyl donor, is called glycosylation. Salicylate glucose ester (SGE) and SA 2-O-β-D-glucoside (SAG) are the derivatives of SA via glycosylation. Both the derivatives are the inactive form of SA and reside in vacuoles. Therefore, before any cellular functioning, both the derivatives have to go through hydrolysis for their conversion into active SA form (Husen et al. 2019). For example, two uridine diphosphate glucosyltransferases (UGTs), UGT74F1 and UGT74F2, are known for the glycosylation of SA in *Arabidopsis thaliana* (Dean and Delaney 2008).

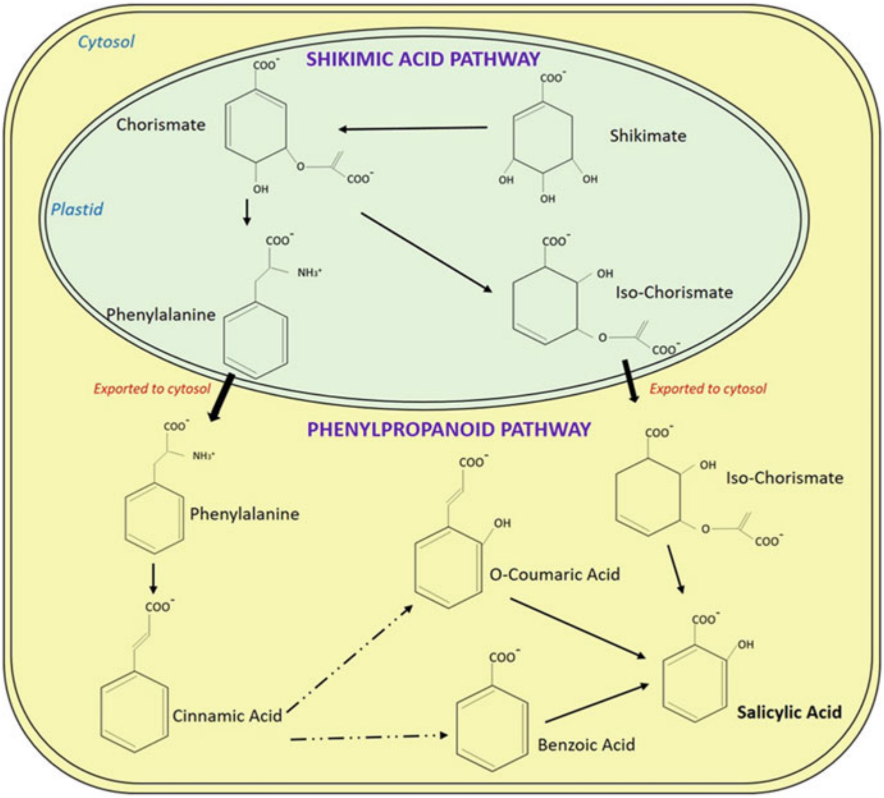

Fig. 16.2 Pathways for the synthesis of salicylic acid

16.3.2 Methylation

In plants, methylation can occur at carboxyl group (-COOH) of SA in presence of S-adenosyl-L-methionine methyl-transferases (SAM-MTs). Methylation inactivates SA into methyl-SA (methyl salicylate, MeSA) and converts to active form of SA by the enzyme methylesterases (MESs) (Park et al. 2007a, b). MeSA also regulates SA synthesis. Due to volatile nature of methyl salicylate (MeSA), it is important for taste and fragrance of many fruits and flowers (Tieman et al. 2010).

16.3.3 Sulfonation

Generally, the sulfonation of organic substrates is catalyzed by the enzyme sulfotransferases. In *Arabidopsis*, sulfotransferases gene family exhibit 21 members (Günal et al. 2019). Sulfonated salicylic acid derivatives also play positive roles in signaling. The sulfotransferase (SOT12) from *Arabidopsis* add sulfonate group to the second -OH group of SA (Husen et al. 2019). Baek et al. (2010) showed that

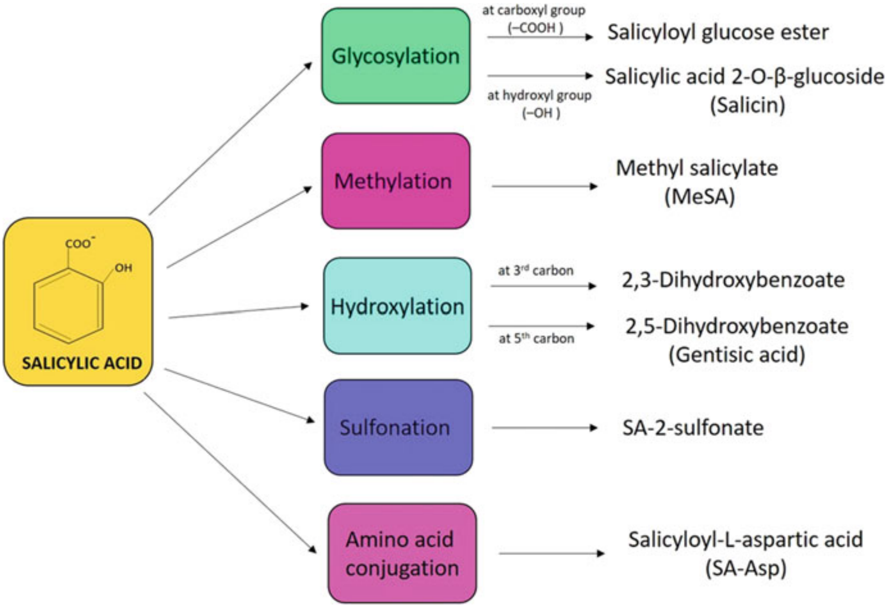

Fig. 16.3 Various chemical processing for salicylic acid metabolism

mutation in SOT12 gene induce inhibition of SA-mediated primary root growth and compromised pathogen-induced SA accumulation and resistance.

16.3.4 Amino Acid Conjugation

All glycoside hydrolase family 3 (GH3) enzymes play crucial roles in conjugation of specific amino acid onto different phytohormones. In plants, dominant form of conjugated SA is salicyloyl-L-aspartate (SA-Asp), which is an inactive form (Husen et al. 2019). In *Arabidopsis*, gh3.5 mutants did not report to alter the pathogen-induced SA-Asp level but still affects the resistance (Park et al. 2007a, b; Zhang et al. 2007). Further, it was also investigated that in mutant plant an unknown GH3 enzyme conjugate aspartate onto SA (Westfall et al. 2016).

16.3.5 Hydroxylation

In a reversible reaction, free hydroxyl (•OH) radicals were scavenged by SA to form two products dihydroxybenzoic acid (DHBA): 2,3-DHBA and 2,5-DHBA (gentisic acid) in the absence of any enzyme (Husen et al. 2019). In *Arabidopsis*, downy mildew resistant 6 (DMR6) gene encode SA-5 hydrolase (S5H) that has ability for conversion of SA into 2,5-DHBA (Zhang et al. 2017). In *Arabidopsis*, two genes also encode DMR6 homolog named DMR6-like oxygenase 1 (DLO1) and DLO2 that encode S3H and contribute to enhanced production of 2,3-DHBA (Husen et al. 2019). These DHBAs further modified by UGT89A2 to their inactive forms via the glycosylation (Chen and Li 2017).

16.4 Role of Salicylic Acid Under Abiotic Stress

SA is an essential hormone in plant innate immunity that helps in providing resistance to both local and systemic tissue under stress including pathogen attacks, hypersensitive responses, and cell death via inducing biosynthesis of several secondary metabolites in plants (Mishra et al. 2017). It is also well documented that SA and its derivatives impart influence on various physiological and biochemical reactions of the plants including growth and development, ion uptake, membrane permeability, photosynthesis, enzyme activities, and flowering of plants (Husen et al. 2019). Being an essential regulator of plant-pathogen interactions, SA is also known to mediate signaling between plant-beneficial microbe interaction (Tiwari et al. 2016; Tiwari et al. 2017a, b). Apart from these functions, SA has been also shown to regulate various aspects of plants during different abiotic stresses (Fig. 16.4; Table 16.1).

16.4.1 Salinity

Among abiotic stress, salinity is the major constraint imposed on plants that limits the crop growth globally and causes severe damage in plants throughout their life cycle (Tiwari et al. 2020a; Chauhan et al. 2019; Hirayama and Shinozaki 2010). It has been estimated that soil salinity damages more than 77 million hectares of irrigated land of 1.5 billion hectares of the world's total cultivated land (Kamran et al. 2020), and a considerable area of land affected by salinity is increasing day by day worldwide (Munns and Tester 2008). In fact, the loss of plant productivity under salinity is due to cellular ionic and osmotic imbalances. In many crops such as *Vicia faba*, *Brassica juncea*, *Brassica carinata, Medicago sativa*, and *V. radiata*, the role of SA in strengthening salinity stress tolerance mechanisms has been extensively demonstrated (Husen et al. 2018, 2019; Azooz 2009; Nazar et al. 2015; Palma et al. 2013; Khan and Khan 2014). SA-mediated membrane potential restoration and salt-induced K^+ ion loss prevention through the GORK channel and eventually improved salinity tolerance were shown in *A. thaliana* (Jayakannan et al. 2013). In another instance, due to an enhanced transcript level of antioxidant genes, exogenously sourced SA has been reported to boost salt tolerance in *Triticum aestivum* (Li et al. 2013). Similarly, exogenous application of SA in both presence and absence of beneficial microbe also enhances salinity tolerance in rice (*Oryza sativa*) and suggested its important role in cross-talk between plant and microbe under stress condition (Tiwari et al. 2017a).

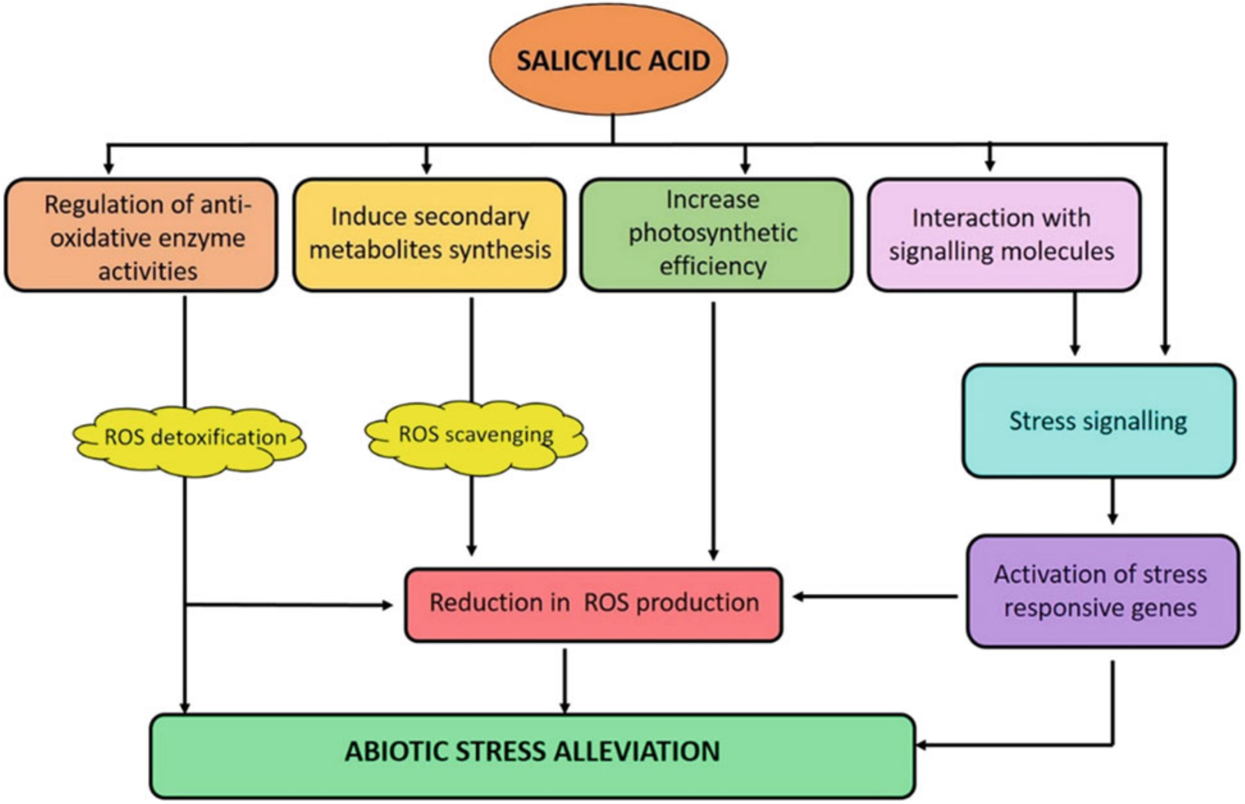

Fig. 16.4 Different roles of salicylic acid for abiotic stress amelioration

Table 16.1 Studies showing the exogenous application of salicylic acid in various plants under different abiotic stresses

Plant	Stress	SA application	References
Capsicum annuum L. (sweet pepper)	Salinity	0.5 mM foliar spray	Kaya et al. (2020)
Amaranthus tricolor L. (Joseph's coat)	Salinity	0.005 mM foliar spray, cotreatment	Hoang et al. (2020)
Vigna radiata L. (mung bean)	Salinity	1 and 1.5 mM seed priming	Lotfi et al. (2020)
Mentha pulegium L. (squaw mint)	Salinity	0.5, 1 and 1.5 mM foliar spray	Farhadi and Ghassemi-Golezani (2020)
Crocus sativus L. (saffron)	Salinity	1 mM corm soaking	Babaei et al. (2020)
Oryza sativa L. (rice)	Salinity	2 mM priming	Sheteiwy et al. (2019)
Solanum lycopersicum mill. (tomato)	Salinity	100 mg L^{-1} pretreatment	Souri and Tohidloo (2019)
Brassica napus L. (rapeseed)	Salinity	1 mM foliar spray	Farhangi-Abriz et al. (2019)
Zea mays L. (maize)	Salinity	1 mM spray	El-Katony et al. (2019)
Oryza sativa L. (rice)	Salinity	0.5 and 1.0 mM inoculated in nutrient solution	Kim et al. (2018)
Nitraria tangutorum Bobr. (nitre bush)	Salinity	0.5, 1.0 and 1.5 mM inoculated to nutrient solution	Yan et al. (2018)
Carthamus tinctorius L. (safflower)	Salinity	1 mM inoculated to nutrient solution	Shaki et al. (2018)
Pisum sativum L. (pea)	Salinity		Yadu et al. (2017)
Rosmarinus officinalis L. (rosemary)	Salinity	100, 200, and 300 ppm spray	El-Esawi et al. (2017)
Cucurbita pepo L. (squash)	Salinity	1 mM foliar spray	Abd El-Mageed et al. (2016)
Allium cepa L. (onion)	Salinity	1 mM and 2 mM irrigation and foliar spray	Semida et al. (2017)
Brassica juncea L. (brown mustard)	Salinity	0.5 mM spray	Nazar et al. (2015)
Solanum lycopersicum Mill. (tomato)	Salinity	0.01 μM and 100 μM pretreatment	Horváth et al. (2015)
Solanum lycopersicum Mill. (tomato)	Salinity	100 μM pretreatment	Tari et al. (2015)
Hordeum vulgare L. (barley)	Salinity	50 μM	Fayez and Bazaid (2014)
Arabidopsis thaliana L. (mouse-ear-cress)	Salinity	50 μM pretreatment	Jayakannan et al. (2013)
Medicago sativa L. (alfalfa)	Salinity	0.1 and 0.5 mM pretreatment	Palma et al. (2013)

(continued)

Table 16.1 (continued)

Plant	Stress	SA application	References
Triticum aestivum L. (wheat)	Salinity	0.5 mM	Li et al. (2013)
Vigna radiata L. (mung bean)	Salinity	0.5 mM spray	Nazar et al. (2011)
Gerbera jamesonii L. (gerbera daisy)	Salinity	0.5 mM pretreatment	Kumara et al. (2010)
Oryza sativa L. (rice)	Drought	0.5 or 1 mmol/L inoculated in nutrient solution	Sohag et al. (2020)
Hordeum vulgare L. (barley)	Drought	0.5 mM	Abdelaal et al. (2020)
Zea mays L. (maize)	Drought	2 mM foliar application	Tayyab et al. (2020)
Rosmarinus officinalis L. (rosemary)	Drought	1, 2 and 3 mM spray	Abbaszadeh et al. (2020)
Brassica rapa L. (field mustard)	Drought	1.5 mM spray	Lee et al. (2019)
Ocimum basilicum L. (sweet basil)	Drought	200 ppm foliar spray	Damalas (2019)
Olea europaea L. (olive tree)	Drought	10, 100 and 1000 μM spray	Brito et al. (2018)
Triticum aestivum L. (wheat)	Drought	10 mM seed priming	Ilyas et al. (2017)
Triticum aestivum L. (wheat)	Drought	0.5 mM foliar spray	Sharma et al. (2017)
Fragaria × ananassa (strawberry)	Drought	0.1 mM irrigation	Ghaderi et al. (2015)
Nigella sativa L. (black cumin)	Drought	5, and 10 μM pretreatment	Kabiri et al. (2014)
Brassica juncea L. (brown mustard)	Drought	50 μM foliar spray	Alam et al. (2013)
Triticum aestivum L. (wheat)	Drought	0.5 mM	Kang et al. (2012)
Zea mays L. (maize)	Drought	100, 150, 200 ppm foliar spray	Rao et al. (2012)
Hordeum vulgare L. (barley)	Drought	500 μM SA	Habibi (2012)
Oryza sativa L. (rice)	Drought	100 mg L^{-1}	Farooq et al. (2010a, b)
Triticum aestivum L. (wheat)	Drought	Seed soaking with 0.5 mM SA	El Tayeb and Ahmed (2010)
Triticum aestivum L. (wheat)	Temperature	100 μM foliar spray	Wang et al. (2020)
Musa acuminata Colla. (banana)	Temperature	1 mM dipping fruit in SA solution	Chen et al. (2020)
Festuca arundinacea Schreb. (tall fescue)	Temperature	1 mM foliar spray	Pirnajmedin et al. (2020)

(continued)

Table 16.1 (continued)

Plant	Stress	SA application	References
Trifolium alexandrinum L. (Egyptian *clover*)	Temperature	50 to 100 μg/mL pretreatment	Kaur and Goyal (2019)
Zea mays L. (maize)	Temperature	10–800 μM, foliar spraying	Khanna et al. 2016
Solanum lycopersicum mill. (tomato)	Temperature	0.25, 0.5, and 0.75 mM, seed priming	Singh and Singh (2016)
Triticum aestivum L. (wheat)	Temperature	100 mM, foliar spraying	Kumar et al. (2015)
Oryza sativa L. (rice)	Temperature	1 mM, foliar Spraying	Mohammed and Tarpley (2011)
Vitis vinifera L. (grape vine)	Temperature	100 μM pretreatment	Wang et al. (2010)
Brassica juncea L. (brown mustard)	Heavy metal (cd)	0.01 mM foliar spraying	Faraz et al. (2020)
Artemisia annua L. (sweet wormwood)	Heavy metal (as)	10^{-5} and 10^{-6} μM applied to soil	Naeem et al. (2020)
Solanum tuberosum L. (potato)	Heavy metal (cd)	600 μM foliar spraying	Li et al. (2019)
Triticum aestivum L. (wheat)	Heavy metal (cd)	50 μM, pretreatment	Shakirova et al. (2016)
Zea mays L. (maize)	Heavy metal (Cr)	100 μM L^{-1}, foliar spraying	Islam et al. (2016)
Glycine max L. (soybean)	Heavy metal (Al)	10 μM, cotreatment	Lan et al. (2016)
Oryza sativa L. (rice)	Heavy metal (as)	100 μM pretreatment	Singh et al. (2015)
Brassica oleracea L. (wild cabbage)	Heavy metal (co, Ni, cd, Cr, Pb)	50 and 100 mM, cotreatment	Sinha et al. (2015)
Hordeum vulgare L. (barley)	Heavy metal (cd)	0.25 and 0.5 mM pretreatment	Tamás et al. (2015)
Phaseolus vulgaris L. (common bean)	Heavy metal (cd)	1 mM, foliar spraying	Wael et al. (2015)
Brassica juncea L. (brown mustard)	Heavy metal (Mn)	10 μM, foliar spraying	Parashar et al. (2014)
Triticum aestivum L. (wheat)	Heavy metal (cd)	500 μM, seed soaking	Agami and Mohamed (2013)
Oryza sativa L. (rice)	Heavy metal (cu)	100 μM SA, pretreatment	Mostofa and Fujita (2013)
Phaseolus aureus L. (mung bean)	Heavy metal (cd)	100 μM SA, seed soaking	Zhang et al. (2011)

16.4.2 Drought

Drought has been known to be one of the most severe abiotic stresses impacting agriculture. It can significantly decrease photosynthesis, stomatal conductance, leaf area, chlorophyll content, root elongation, decline in RWC, and reactive oxygen species (ROS) generation and eventually reduce plant growth (Tiwari et al. 2016; Khan et al. 2015). Several reports stated the role of SA in positive regulation of plant responses against drought stress. SA-induced stomatal closure was observed as the most possible mechanism for maintaining water content in plant leaves (Tiwari et al. 2017b). The role of SA in drought stress has also been explained by the SA-related *Arabidopsis* mutant (He et al. 2014). Gene expression profiling studies have reported that several TFs, such as AP2/ERFs, bHLH, Zn fingers, etc., respond to SA under drought stress suggesting the essential role of SA in stress response (Gao et al. 2015; Tiwari et al. 2017b). Exogenous application of SA in tomato and bean plants also seemed to be helpful in enhancing drought resistance (Singh and Gautam 2013). Likewise, interplay of SA was also reported in plants under drought stress upon exogenous application of SA in rice crop in the presence of beneficial microbe (Tiwari et al. 2017a).

16.4.3 Heavy Metal Stress

In different terrestrial ecosystems, heavy metal stress has become a major concern to sustainable agriculture and environmental system worldwide. Agricultural soils mainly receive metal pollutants from rapidly growing industrialization (Tiwari and Lata 2018). Various reports stated the SA significance in the minimization of adverse effect of metal stress on plants. Exogenously applied SA was reported to improve growth and photosynthetic traits in several crop plants including lead (Pb)-exposed *Oryza sativa*, cadmium (Cd)-exposed *Zea mays*, and copper (Cu)-exposed *Phaseolus vulgaris* (Jing et al. 2007; Krantev et al. 2008; Zengin 2014). Recent evidence has also indicated that under metal stress, SA is a major regulator of photosynthesis, photosystem II (PSII), photosynthetic pigments, and enzyme activity including Rubisco and carbonic anhydrase (Khan et al. 2015). Recently, SA-mediated control of H_2O_2 accumulation in Linum usitatissimum under Cd stress also attribute to increased metal tolerance due to SA signaling (Belkadhi et al. 2015). SA also reported to significantly inhibit chlorosis caused due to iron (Fe) deficiency in plants (Khan et al. 2015).

16.5 SA, an Essential Regulator of Plant-Microbe Interactions Under Abiotic Stress Condition

Plants constantly interact with plethora of microorganisms that includes bacteria, yeast, fungi, and viruses (Tiwari et al. 2019). As regards this, an interactive relationship establishes among plants and microbes. This interconnection alters various growth and developmental parameters in both plants and microbes. Now the concern is these microbes might belong to pathogenic or beneficial category for plants. In case of pathogenic microbe-plant interaction, the first line of defense for plants is its innate immunity, i.e., immunity through pathogen-associated molecular pattern-triggered immunity (PTI) or effector-triggered immunity (ETI). Both ETI and PTI have the ability to block the infection caused by pathogens in plants, both at infected or nearby uninfected tissues (Henry et al. 2013). After this, secondary defense response triggered in plants is associated with hormone-induced defense signaling pathways. Mainly, the hormones that involved in these responses are SA, jasmonic acid (JA), and ethylene (Henry et al. 2013). In tobacco and cucumber plants, the role of SA during plant-microbe interactions was recorded for the first time in 1990. After that, several studies have been published that showed the effect of SA in regulation of plant-pathogen interactions. Interestingly, from past few decades, there are studies that showed the role of SA during beneficial microbes-plants interaction, mainly under the abiotic stress condition (Tiwari et al. 2020a, b; Chauhan et al. 2019; Bisht et al. 2019). Hence, the present chapter also includes the studies related to the role of SA under abiotic stress condition in plants under the influence of beneficial microbes. Here, some of the most relevant findings have been described. In a study, the role of plant growth-promoting rhizobacteria (PGPR) *Bacillus amyloliquefaciens* in rice (*Oryza sativa* L.) under various abiotic stresses such as salinity, drought, desiccation, and temperature (heat, cold, and freeze) was investigated (Tiwari et al. 2017a). This study showed that exogenous application of SA in rice alters different physiological, biochemical, and molecular parameters including osmolyte concentration and membrane integrity. That indicates the role of *B. amyloliquefaciens* in SA-induced abiotic stress tolerance. Recently, a study also reported that *B. amyloliquefaciens* inoculated SA treated *Arabidopsis* plants modulate the transcript level of some members of GRAM-domain containing gene family under abiotic stress (Tiwari et al. 2021). Interestingly, PR1 gene which is a pathogenesis-related gene and also a key component of SA signaling showed that basal level expression in drought-stressed chickpea plants under *Pseudomonas putida* inoculation indicates that beneficial microbes ameliorate abiotic stress condition without any induction of pathogenicity in treated plants (Tiwari et al. 2016). In another study, SA level was found to be enhanced in maize by a PGPR named *Ochrobactrum* sp. under water deficit condition (Mishra et al. 2020). This study showed that it is possible due to the volatile organic compounds (VOCs) released by PGPR that activates induced systemic response (ISR) regulated by plant growth regulators including SA. Under drought stress, this SA-induced regulation results in increased stomatal closure and hence less water loss. Overall, it can be said that SA might play the significant role during PGPR-induced abiotic stress amelioration.

16.6 Conclusion

In order to cope with the adverse effects of abiotic stress, many physiological and molecular processes are stimulated by plants. Research has shown SA to be an effective and potential weapon for minimizing or alleviating the adverse effects of plant abiotic stress. The application of SA has been shown to be effective in ideal or stressful conditions for plants. In order to protect plants under abiotic stress conditions, SA may control multiple plant metabolic processes and modulate the development of varied osmolytes and secondary metabolites and also preserve plant-nutrient status. Interestingly, recent studies also showed the existence of crosstalk between SA and beneficial microbe-mediated abiotic stress tolerance in plants. Overall, the literature evaluated here verified the focus of SA-related studies in abiotic stressed plants, primarily on the disclosure of different physiological/biochemical processes.

References

Abbaszadeh B, Layeghhaghighi M, Azimi R, Hadi N (2020) Improving water use efficiency through drought stress and using salicylic acid for proper production of *Rosmarinus officinalis* L. Ind Crop Prod 144:111893

Abd El-Mageed TA, Semida WM, Mohamed GF, Rady MM (2016) Combined effect of foliar-applied salicylic acid and deficit irrigation on physiological–anatomical responses, and yield of squash plants under saline soil. S Afr J Bot 106:8–16

Abdelaal KA, Attia KA, Alamery SF, El-Afry MM, Ghazy AI, Tantawy DS, Al-Doss AA, El-Shawy ES, Abu-Elsaoud A, Hafez YM (2020) Exogenous application of proline and salicylic acid can mitigate the injurious impacts of drought stress on barley plants associated with physiological and histological characters. Sustainability 12(5):1736

Agami RA, Mohamed GF (2013) Exogenous treatment with indole-3-acetic acid and salicylic acid alleviates cadmium toxicity in wheat seedlings. Ecotoxicol Environ Saf 94:164–171

Alam MM, Hasanuzzaman M, Nahar K, Fujita M (2013) Exogenous salicylic acid ameliorates short-term drought stress in mustard (*Brassica juncea* L.) seedlings by upregulating the antioxidant defense and glyoxalase system. Aus J Crop Sci 7:1053–1063

Azooz MM (2009) Salt stress mitigation by seed priming with salicylic acid in two faba bean genotypes differing in salt tolerance. Int J Agric Biol 11(4):343–350

Babaei S, Niknam V, Behmanesh M (2020) Comparative effects of nitric oxide and salicylic acid on salinity tolerance in saffron (*Crocus sativus*). Plant Biosystems 3:1–10

Baek D, Pathange P, Chung JS, Jiang J, Gao L, Oikawa A, Hirai MY, Saito K, Pare PW, Shi H (2010) A stress-inducible sulphotransferase sulphonates salicylic acid and confers pathogen resistance in *Arabidopsis*. Plant Cell Environ 33(8):1383–1392

Belkadhi A, De Haro A, Obregon S, Chaïbi W, Djebali W (2015) Positive effects of salicylic acid pretreatment on the composition of flax plastidial membrane lipids under cadmium stress. Environ Sci Pollut Res 22(2):1457–1467

Bisht N, Tiwari S, Singh PC, Niranjan A, Chauhan PS (2019) A multifaceted rhizobacterium *Paenibacillus lentimorbus* alleviates nutrient deficiency-induced stress in *Cicer arietinum* L. Microbiol Res 223:110–119

Brito C, Dinis LT, Meijón M, Ferreira H, Pinto G, Moutinho-Pereira J, Correia C (2018) Salicylic acid modulates olive tree physiological and growth responses to drought and rewatering events in a dose dependent manner. J Plant Physiol 230:21–32

Buchner A (1828) Ueber das Rigatellische Fiebermittel und über eine in der Weidenrinde entdeckte alcaloidische Substanz. Repertorium für die Pharmacie 29:405–420

Chauhan PS, Lata C, Tiwari S et al (2019) Transcriptional alterations reveal *Bacillus amyloliquefaciens*- rice cooperation under salt stress. Sci Rep 9:11912

Chen HY, Li X (2017) Identification of a residue responsible for UDP-sugar donor selectivity of a dihydroxybenzoic acid glycosyltransferase from *Arabidopsis* natural accessions. Plant J 89(2): 195–203

Chen L, Zhao X, Wu JE, He Y, Yang H (2020) Metabolic analysis of salicylic acid-induced chilling tolerance of banana using NMR. Food Res Int 128:108796

Damalas CA (2019) Improving drought tolerance in sweet basil (*Ocimum basilicum*) with salicylic acid. Sci Hortic 246:360–365

Dean JV, Delaney SP (2008) Metabolism of salicylic acid in wild-type, ugt74f1 and ugt74f2 glucosyltransferase mutants of *Arabidopsis thaliana*. Physiol Plant 132:417–425

Dempsey DM, Vlot AC, Wildermuth MC, Klessig DF (2011) Salicylic acid biosynthesis and metabolism. Arabidopsis Book 2011:9

El Tayeb MA, Ahmed NL (2010) Response of wheat cultivars to drought and salicylic acid. Amer Eur J Agronom 3:1–7

El-Esawi MA, Elansary HO, El-Shanhorey NA, Abdel-Hamid AM, Ali HM, Elshikh MS (2017) Salicylic acid-regulated antioxidant mechanisms and gene expression enhance rosemary performance under saline conditions. Front Physiol 8:716

El-Katony TM, El-Bastawisy ZM, El-Ghareeb SS (2019) Timing of salicylic acid application affects the response of maize (*Zea mays* L.) hybrids to salinity stress. Heliyon 5(4):e01547

Faraz A, Faizan M, Sami F, Siddiqui H, Hayat S (2020) Supplementation of salicylic acid and citric acid for alleviation of cadmium toxicity to *Brassica juncea*. J Plant Growth Regul 39(2): 641–655

Farhadi N, Ghassemi-Golezani K (2020) Physiological changes of *Mentha pulegium* in response to exogenous salicylic acid under salinity. Sci Hortic 267:109325

Farhangi-Abriz S, Alaee T, Tavasolee A (2019) Salicylic acid but not jasmonic acid improved canola root response to salinity stress. Rhizosphere 9:69–71

Farooq M, Wahid A, Lee DJ, Cheema SA, Aziz T (2010a) Drought stress: comparative time course action of the foliar applied glycinebetaine, salicylic acid, nitrous oxide, brassinosteroids and spermine in improving drought resistance of rice. J Agronom Crop Sci 196(5):336–345

Farooq M, Wahid A, Lee D-J, Cheema SA, Aziz T (2010b) DROUGHT STRESS: comparative time course action of the foliar applied glycinebetaine, salicylic acid, nitrous oxide, brassinosteroids and spermine in improving drought resistance of rice. J Agron Crop Sci 196: 336–345

Fayez KA, Bazaid SA (2014) Improving drought and salinity tolerance in barley by application of salicylic acid and potassium nitrate. J Saudi Soc Agric Sci 23:45–55

Gao Y, Gao S, Xiong C, Yu G, Chang J, Ye Z, Yang C (2015) Comprehensive analysis and expression profile of the homeodomain leucine zipper IV transcription factor family in tomato. Plant Physiol Biochem 96:141–153

Ghaderi N, Normohammadi S, Javadi T (2015) Morpho-physiological responses of strawberry (*Fragaria× ananassa*) to exogenous salicylic acid application under drought stress. J Agric Sci Technol 17:167–178

Günal S, Hardman R, Kopriva S, Mueller JW (2019) Sulfation pathways from red to green. J Biol Chem 294(33):12293–12312

Habibi G (2012) Exogenous salicylic acid alleviates oxidative damage of barley plants under drought stress. Acta Biologica Szegediensis 56:57–63

He Q, Zhao S, Ma Q, Zhang Y, Huang L, Li G, Hao L (2014) Endogenous salicylic acid levels and signaling positively regulate *Arabidopsis* response to polyethylene glycol-simulated drought stress. J Plant Growth Regul 33(4):871–880

Heil M, Ton J (2008) Long-distance signalling in plant defence. Trends Plant Sci 13(6):264–272

Henry E, Yadeta KA, Coaker G (2013) Recognition of bacterial plant pathogens: local, systemic and transgenerational immunity. New Phytol 199(4):908–915

Hirayama T, Shinozaki K (2010) Research on plant abiotic stress responses in the post-genome era: past, present and future. Plant J 61(6):1041–1052

Hoang HL, de Guzman CC, Cadiz NM, Hoang TT, Tran DH, Rehman H (2020) Salicylic acid and calcium signaling induce physiological and phytochemical changes to improve salinity tolerance in red amaranth (*Amaranthus tricolor* L.). J Soil Sci Plant Nutr 22:1–1

Horváth E, Csiszár J, Gallé Á, Poór P, Szepesi Á, Tari I (2015) Hardening with salicylic acid induces concentration-dependent changes in abscisic acid biosynthesis of tomato under salt stress. J Plant Physiol 83:54–63

Husen A, Iqbal M, Khanum N, Aref IM, Sohrab SS, Meshresa G (2019) Modulation of salt-stress tolerance of niger (Guizotia abyssinica), an oilseed plant, by application of salicylic acid. J Environ Biol 40:94–104. https://doi.org/10.22438/jeb/40/1/MRN-808

Husen A, Iqbal M, Sohrab SS, Ansari MKA (2018) Salicylic acid alleviates salinity-caused damage to foliar functions, plant growth and antioxidant system in Ethiopian mustard (*Brassica carinata* A. Br.). Agric Food Sec 7:44. https://doi.org/10.1186/s40066-018-0194-0

Ilyas N, Gull R, Mazhar R, Saeed M, Kanwal S, Shabir S, Bibi F (2017) Influence of salicylic acid and jasmonic acid on wheat under drought stress. Commun Soil Sci Plant Anal 48(22): 2715–2723

Islam F, Yasmeen T, Arif MS, Riaz M, Shahzad SM, Imran Q, Ali I (2016) Combined ability of chromium (Cr) tolerant plant growth promoting bacteria (PGPB) and salicylic acid (SA) in attenuation of chromium stress in maize plants. Plant Physiol Biochem 108:456–467

Jayakannan M, Bose J, Babourina O, Rengel Z, Shabala S (2013) Salicylic acid improves salinity tolerance in *Arabidopsis* by restoring membrane potential and preventing salt-induced K+ loss via a GORK channel. J Exp Bot 64:2255–2268

Jing C, Cheng ZH, Li LP, Sun ZY, Pan XB (2007) Effects of exogenous salicylic acid on growth and H_2O_2-metabolizing enzymes in rice seedlings under lead stress. J Environ Sci 19(1):44–49

Kabiri R, Nasibi F, Farahbakhsh H (2014) Effect of exogenous salicylic acid on some physiological parameters and alleviation of drought stress in *Nigella sativa* plant under hydroponic culture. Plant Protec Sci 50(1):43–51

Kamran M, Parveen A, Ahmar S et al (2020) An overview of hazardous impacts of soil salinity in crops, tolerance mechanisms, and amelioration through selenium supplementation. Int J Mol Sci 21(1):148

Kang G, Li G, Xu W, Peng X, Han Q, Zhu Y (2012) Proteomics reveals the effects of salicylic acid on growth and tolerance to subsequent drought stress in wheat. J Proteome Res 11:6066–6079

Kaur H, Goyal M (2019) Salicylic acid priming enhances low temperature stress tolerance in Egyptian clover (*Trifolium alexandrinum* L.) by influencing antioxidant system. Indian J Exp Biol 57:507–515

Kaya C, Ashraf M, Alyemeni MN, Ahmad P (2020) The role of endogenous nitric oxide in salicylic acid-induced up-regulation of ascorbate-glutathione cycle involved in salinity tolerance of pepper (*Capsicum annuum* L.) plants. Plant Physiol Biochem 147:10–20

Khan MIR, Fatma M, Per TS, Anjum NA, Khan NA (2015) Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. Front Plant Sci 6:462

Khan MIR, Khan NA (2014) Ethylene reverses photosynthetic inhibition by nickel and zinc in mustard through changes in PS II activity, photosynthetic nitrogen use efficiency, and antioxidant metabolism. Protoplasma 251(5):1007–1019

Khanna P, Kaur K, Gupta AK (2016) Salicylic acid induces differential antioxidant response in spring maize under high temperature stress. Indian J Exp Biol 54:386–393

Kim Y, Mun BG, Khan AL, Waqas M, Kim HH, Shahzad R, Imran M, Yun BW, Lee IJ (2018) Regulation of reactive oxygen and nitrogen species by salicylic acid in rice plants under salinity stress conditions. PLoS One 13(3):e0192650

Klessig DF, Choi HW, Dempsey DM (2018) Systemic acquired resistance and salicylic acid: past, present, and future. Mol Plant-Microbe Interac 31(9):871–888

Krantev A, Yordanova R, Janda T, Szalai G, Popova L (2008) Treatment with salicylic acid decreases the effect of cadmium on photosynthesis in maize plants. J Plant Physiol 165(9): 920–931

Kumar RR, Sharma SK, Goswami S, Verma P, Singh K, Dixit N, Pathak H, Viswanathan C, Rai RD (2015) Salicylic acid alleviates the heat stress-induced oxidative damage of starch biosynthesis pathway by modulating the expression of heat-stable genes and proteins in wheat (*Triticum aestivum*). Acta Physiol Plant 37:1–12

Kumara GDK, Xia Y, Zhu Z, Basnayake BMVS, Beneragama CK (2010) Effects of exogenous salicylic acid on antioxidative enzyme activities and physiological characteristics in gerbera (*Gerbera jamesonii* L.) grown under NaCl stress. Agri Life Sci 36:591–601

Lan T, You JF, Kong L, Yu M, Liu M, Yang Z (2016) The interaction of salicylic acid and Ca2+ alleviates aluminum toxicity in soybean (*Glycine max* L.). Plant Physiol Biochem 98:146–154

Lee BR, Zhang Q, Park SH, Islam MT, Kim TH (2019) Salicylic acid improves drought-stress tolerance by regulating the redox status and proline metabolism in *Brassica rapa*. Hort Environ Biotechnol 60(1):31–40

Li G, Peng X, Wei L, Kang G (2013) Salicylic acid increases the contents of glutathione and ascorbate and temporally regulates the related gene expression in salt-stressed wheat seedlings. Gene 529:321–325

Li Q, Wang G, Wang Y, Yang D, Guan C, Ji J (2019) Foliar application of salicylic acid alleviate the cadmium toxicity by modulation the reactive oxygen species in potato. Ecotoxicol Environ Saf 172:317–325

Lotfi R, Ghassemi-Golezani K, Pessarakli M (2020) Salicylic acid regulates photosynthetic electron transfer and stomatal conductance of mung bean (*Vigna radiata* L.) under salinity stress. Biocatal Agric Biotechnol 26:101635

Maruri-López I, Aviles-Baltazar NY, Buchala A, Serrano M (2019) Intra and extracellular journey of the phytohormone salicylic acid. Front Plant Sci 10:423

Mishra MK, Srivastava M, Singh G, Tiwari S, Niranjan A, Kumari N, Misra P (2017) Overexpression of *Withania somnifera* SGTL1 gene resists the interaction of fungus *Alternaria brassicicola* in *Arabidopsis thaliana*. Physiol Mol Plant Pathol 97:11–19

Mishra SK, Khan MH, Misra S, Dixit VK, Gupta S, Tiwari S, Gupta SC, Chauhan PS (2020) Drought tolerant *Ochrobactrum* sp. inoculation performs multiple roles in maintaining the homeostasis in *Zea mays* L. subjected to deficit water stress. Plant Physiol Biochem 150:1–4

Mohammed AR, Tarpley L (2011) Effects of night temperature, spikelet position and salicylic acid on yield and yield-related parameters of rice (*Oryza sativa* L.) plants. J Agronom Crop Sci 197: 40–49

Mostofa MG, Fujita M (2013) Salicylic acid alleviates copper toxicity in rice (*Oryza sativa* L.) seedlings by up-regulating antioxidative and glyoxalase systems. Ecotoxicology 22:959–973

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

Murphy AM, Zhou T, Carr JP (2020) An update on salicylic acid biosynthesis, its induction and potential exploitation by plant viruses. Curr Opin Virol 42:8–17

Naeem M, Sadiq Y, Jahan A, Nabi A, Aftab T, Khan MM (2020) Salicylic acid restrains arsenic induced oxidative burst in two varieties of *Artemisia annua* L. by modulating antioxidant defence system and artemisinin production. Ecotoxicol Environ Saf 202:110851

Nazar R, Iqbal N, Sayeed S, Khan NA (2011) Salicylic acid alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in two mung bean cultivars. J Plant Physiol 168:807–815

Nazar R, Umar S, Khan NA (2015) Exogenous salicylic acid improves photosynthesis and growth through increase in ascorbate glutathione metabolism and S assimilation in mustard under salt stress. Plant Signal Behav 10(3):e1003751

Palma F, López-Gómez M, Tejera NA, Lluch C (2013) Salicylic acid improves the salinity tolerance of *Medicago sativa* in symbiosis with *Sinorhizobium meliloti* by preventing nitrogen fixation inhibition. Plant Sci 208:75–82

Parashar A, Yusuf M, Fariduddin Q, Ahmad A (2014) Salicylic acid enhances antioxidant system in *Brassica juncea* grown under different levels of manganese. Int J Biol Macromol 70:551–558

Park JE, Park JY, Kim YS, Staswick PE, Jeon J, Yun J, Kim SY, Kim J, Lee YH, Park CM (2007a) GH3-mediated auxin homeostasis links growth regulation with stress adaptation response in *Arabidopsis*. J Biol Chem 282(13):10036–10046

Park SW, Kaimoyo E, Kumar D, Mosher S, Klessig DF (2007b) Methyl salicylate is a critical mobile signal for plant systemic acquired resistance. Science 318(5847):113–116

Piria R (1838) Sur la composition de la salicine et quelques-unes de ses réactions. Comptes Rendus de l'Académie des Sciences, Paris 6:338

Pirnajmedin F, Majidi MM, Taleb H, Maibody SA, Saeidi G (2020) Amelioration of high temperature stress by exogenously applied salicylic acid: genotype-specific response of physiological traits. Agron J 112:1573–1579

Rao SR, Qayyum A, Razzaq A, Ahmad M, Mahmood I, Sher A (2012) Role of foliar application of salicylic acid and L-tryptophan in drought tolerance of maize. J Animal Plant Sci 22:768–772

Semida WM, Abd El-Mageed TA, Mohamed SE, El-Sawah NA (2017) Combined effect of deficit irrigation and foliar-applied salicylic acid on physiological responses, yield, and water-use efficiency of onion plants in saline calcareous soil. Archiv Agron Soil Sci 63(9):1227–1239

Shaki F, Maboud HE, Niknam V (2018) Growth enhancement and salt tolerance of safflower (*Carthamus tinctorius* L.), by salicylic acid. Curr Plant Biol 13:16–22

Shakirova FM, Allagulova CR, Maslennikova DR, Klyuchnikova EO, Avalbaev AM, Bezrukova MV (2016) Salicylic acid-induced protection against cadmium toxicity in wheat plants. Environ Exp Bot 122:19–28

Sharma M, Gupta SK, Majumder B, Maurya VK, Deeba F, Alam A, Pandey V (2017) Salicylic acid mediated growth, physiological and proteomic responses in two wheat varieties under drought stress. J Proteomics 163:28–51

Sheteiwy MS, An J, Yin M, Jia X, Guan Y, He F, Hu J (2019) Cold plasma treatment and exogenous salicylic acid priming enhances salinity tolerance of *Oryza sativa* seedlings. Protoplasma 256(1):79–99

Singh AP, Dixit G, Mishra S, Dwivedi S, Tiwari M, Mallick S, Pandey V, Trivedi PK, Chakrabarty D, Tripathi RD (2015) Salicylic acid modulates arsenic toxicity by reducing its root to shoot translocation in rice (*Oryza sativa* L.). Front. Plant Sci 6:340

Singh PK, Gautam S (2013) Role of salicylic acid on physiological and biochemical mechanism of salinity stress tolerance in plants. Acta Physiol Plant 35(8):2345–2353

Singh SK, Singh PK (2016) Effect of seed priming of tomato with salicylic acid on growth, flowering, yield and fruit quality under high temperature stress conditions. Int J Adv Res 4: 723–727

Sinha P, Shukla AK, Sharma YK (2015) Amelioration of heavy-metal toxicity in cauliflower by application of salicylic acid. Commun Soil Sci Plant Anal 46:1309–1319

Sohag AA, Tahjib-Ul-Arif M, Brestic M, Afrin S, Sakil MA, Hossain MT, Hossain MA, Hossain MA (2020) Exogenous salicylic acid and hydrogen peroxide attenuate drought stress in rice. Plant Soil Environ 66(1):7–13

Souri MK, Tohidloo G (2019) Effectiveness of different methods of salicylic acid application on growth characteristics of tomato seedlings under salinity. Chem Biolog Technol Agri 6(1):26

Tamás L, Mistrík I, Alemayehu A, Zelinová V, Boˇcová B, Huttová J (2015) Salicylic acid alleviates cadmium-induced stress responses through the inhibition of cd-induced auxin-mediated reactive oxygen species production in barley root tips. J Plant Physiol 173:1–8

Tari I, Csiszár J, Horváth E, Poór P, Takács Z, Szepesi A (2015) The alleviation of the adverse effects of salt stress in the tomato plant by salicylic acid shows a time and organ-specific antioxidant response. Acta Biol Cracov Bot 57:21–30

Tayyab N, Naz R, Yasmin H, Nosheen A, Keyani R, Sajjad M, Hassan MN, Roberts TH (2020) Combined seed and foliar pre-treatments with exogenous methyl jasmonate and salicylic acid mitigate drought-induced stress in maize. Plos One 15(5):e0232269

Tieman D, Zeigler M, Schmelz E, Taylor MG, Rushing S, Jones JB, Klee HJ (2010) Functional analysis of a tomato salicylic acid methyl transferase and its role in synthesis of the flavor volatile methyl salicylate. Plant J 62(1):113–123

Tiwari S, Gupta SC, Chauhan PS, Lata C (2020a) An OsNAM gene plays important role in root rhizobacteria interaction in transgenic *Arabidopsis* through abiotic stress and phytohormone crosstalk. Plant Cell Rep 5:1–13

Tiwari S, Lata C (2018) Heavy metal stress, signaling, and tolerance due to plant-associated microbes: an overview. Front Plant Sci 9:452

Tiwari S, Lata C, Chauhan PS et al (2016) *Pseudomonas putida* attunes morphophysiological, biochemical and molecular responses in *Cicer arietinum* L. during drought stress and recovery. Plant Physiol Biochem 99:108–117

Tiwari S, Lata C, Chauhan PS et al (2017b) A functional genomic perspective on drought signalling and its crosstalk with phytohormone-mediated signalling pathways in plants. Curr Genet 18(6): 469–482

Tiwari S, Muthamilarasan M, Lata C (2021) Genome-wide identification and expression analysis of *Arabidopsis* GRAM-domain containing gene family in response to abiotic stresses and PGPR treatment. Aust J Biotechnol 325:7–14

Tiwari S, Prasad V, Chauhan PS et al (2017a) *Bacillus amyloliquefaciens* confers tolerance to various abiotic stresses and modulates plant response to phytohormones through osmoprotection and gene expression regulation in rice. Front Plant Sci 8:1510

Tiwari S, Prasad V, Lata C (2019) *Bacillus*: plant growth promoting bacteria for sustainable agriculture and environment. In: New and future developments in microbial biotechnology and bioengineering. Elsevier, Amsterdam, pp 43–55

Tiwari S, Shweta S, Prasad M, Lata C (2020b) Genome-wide investigation of GRAM-domain containing genes in rice reveals their role in plant-rhizobacteria interactions and abiotic stress responses. Int J Biol Macromol 156:1243–1257

Vlot AC, Dempsey DMA, Klessig DF (2009) Salicylic acid, a multifaceted hormone to combat disease. Annu Rev Phytopathol 47:177–206

Wael MS, Mostafa R, Taia AAE, Saad MH, Magdi TA (2015) Alleviation of cadmium toxicity in common bean (*Phaseolus vulgaris* L.) plants by the exogenous application of salicylic acid. J Hortic Sci Biotech 90:83–91

Wang L, Fan L, Loescher W, Duan W, Liu G, Cheng J, Luo H, Li S (2010) Salicylic acid alleviates decreases in photosynthesis under heat stress and accelerates recovery in grapevine leaves. BMC Plant Biol 10:34. https://doi.org/10.1186/1471-2229-10-34

Wang W, Wang X, Huang M, Cal J, Zhou Q, Dai T, Jiang D (2020) Alleviation of field low-temperature stress in winter wheat by exogenous application of salicylic acid. J Plant Growth Regul 40:811

Westfall CS, Sherp AM, Zubieta C, Alvarez S, Schraft E, Marcellin R, Ramirez L, Jez JM (2016) *Arabidopsis thaliana* GH3. 5 acyl acid amido synthetase mediates metabolic crosstalk in auxin and salicylic acid homeostasis. Proc Natl Acad Sci U S A 113(48):13917–13922

Weyrich LS, Duchene S, Soubrier J, Arriola L, Llamas B, Breen J, Morris AG, Alt KW, Caramelli D, Dresely V, Farrell M (2017) Neanderthal behaviour, diet, and disease inferred from ancient DNA in dental calculus. Nature 544(7650):357–361

Yadu S, Dewangan TL, Chandrakar V, Keshavkant S (2017) Imperative roles of salicylic acid and nitric oxide in improving salinity tolerance in *Pisum sativum* L. Physiol Mol Biol Plants 23(1): 43–58

Yan Y, Pan C, Du Y, Li D, Liu W (2018) Exogenous salicylic acid regulates reactive oxygen species metabolism and ascorbate–glutathione cycle in *Nitraria tangutorum* Bobr. under salinity stress. Physiol Mol Biol Plants 24(4):577–589

Zengin F (2014) Exogenous treatment with salicylic acid alleviating copper toxicity in bean seedlings. Proc Nat Acad Sci U S A 84(3):749–755

Zhang F, Zhang H, Xia Y, Wang G, Xu L, Shen Z (2011) Exogenous application of salicylic acid alleviates cadmium toxicity and reduces hydrogen peroxide accumulation in root apoplasts of *Phaseolus aureus* and *Vicia sativa*. Plant Cell Rep 30:1475–1483

Zhang Y, Zhao L, Zhao J, Li Y, Wang J, Guo R, Gan S, Liu CJ, Zhang K (2017) S5H/DMR6 encodes a salicylic acid 5-hydroxylase that fine-tunes salicylic acid homeostasis. Plant Physiol 175(3):1082–1093

Zhang Z, Li Q, Li Z, Staswick PE, Wang M, Zhu Y, He Z (2007) Dual regulation role of GH3. 5 in salicylic acid and auxin signaling during *Arabidopsis-Pseudomonas syringae* interaction. Plant Physiol 145(2):450–464

JA and Abiotic Stress Tolerance

17

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Abstract

Advancement in the field of molecular and biochemical biology has generated huge amount of data that has helped in gaining insight of phytohormonal signalling under abiotic stress. Here in this chapter, we have discussed about a new class of fatty acid-derived hormone, jasmonates (JAs), that includes several members like JA, methyl jasmonate and jasmonyl-isoleucine and their biosynthetic pathways. Endogenous JAs have shown to act in plant survival and maintenance under harsh conditions by enhancing their production inside plant cells, while exogenous JA have further helped the plants in coping with different stress and alleviating the symptoms of stress. In recent times, the role of JAs has been considered to play an important role under several abiotic stresses, viz. salinity, heavy metal, UV-B, temperature, etc. The chapter elucidates the mechanism of action and role of JAs in dealing with alleviation of various abiotic stresses in crop plants.

Keywords

12-Oxo-phytodienoic acid · Abiotic stress · Biosynthetic pathway · Jasmonates · Methyl jasmonate · Phytohormone

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17.1 Introduction

Plants have adapted to different mechanisms in response to environmental stresses. As they are prone to these harmful conditions, they exhibit various physiological, biochemical and molecular responses (Ghassemi-Golezani and Farhangi-Abriz 2019). This may include changes in hormonal signalling and antioxidative enzymes, biosynthesis of diverse secondary metabolites, and modification in gene expression patterns. Gene expression in plants is mainly guided by phytohormones (Khan et al. 2019). Phytohormones include auxins, cytokinin, abscisic acid, gibberellins, JA, ethylene, salicylic acid and few others (Wani et al. 2016; Ghassemi-Golezani and Nikpour-Rashidabad 2017). Phytohormones facilitate/modulate overall growth and development though cascades of diverse responses during favourable and unfavourable conditions.

JA (JA) and its cyclopentanone derivatives produced in plants are collectively called as jasmonates (JAs). The recent researches have demonstrated that JAs are involved in various developmental and defence mechanisms (Siddiqi and Husen 2019; Huang et al. 2017; Per et al. 2018; Fig. 17.1). Through the octadecanoid pathway, JA can be attached to isoleucine (Ile) to form Ile–JA or get transformed to methyl jasmonate (MeJA) or other like components (Wasternack 2014). Ile–JA is the active form of JA. With exposure of plants to biotic and abiotic stresses, drastic enhancement in JA levels has been recorded. Overall, JAs help the plants to alleviate the harmful effects of environmental stresses.

Table 17.1 enlists some key researches establishing role of JAs in defence mechanisms against abiotic stresses. The investigations indicate alterations in various phytohormones vis-à-vis expression of specific genes inside plant cells under normal and stress conditions (Per et al. 2018). JAs are responsible for plant adaptation in a variety of abiotic stresses such as salinity, drought, UV-B, and toxicity of heavy metals (Ghassemi-Golezani and Farhangi-Abriz 2018a, b; Parihar et al. 2018; Raju et al. 2020).

17.1.1 Synthesis of Jasmonates in Plants

In the past few decades, biosynthesis of JAs has been extensively studied in different monocots and dicots. For better understanding of its role and functions, model plants like *Arabidopsis thaliana* and *Solanum lycopersicum* (tomato) have been investigated. Recent discoveries have led to identification of different enzymes in JA pathway, and its relation with other metabolic pathways has been clarified. Basically, three pathways exist in *Arabidopsis*, where the octadecane pathway starts from α-linolenic acid (18:3) and the hexadecane pathway begins with hexadecatrienoic acid (16:3) (Chini et al. 2018). All three pathways engage cytoplasm, chloroplast and peroxisomes as three reaction sites. In the chloroplast, 12-oxo-phytodienoic acid (12-OPDA) synthesis takes place which is finally converted to JA in the peroxisome. JA is converted into different forms by various

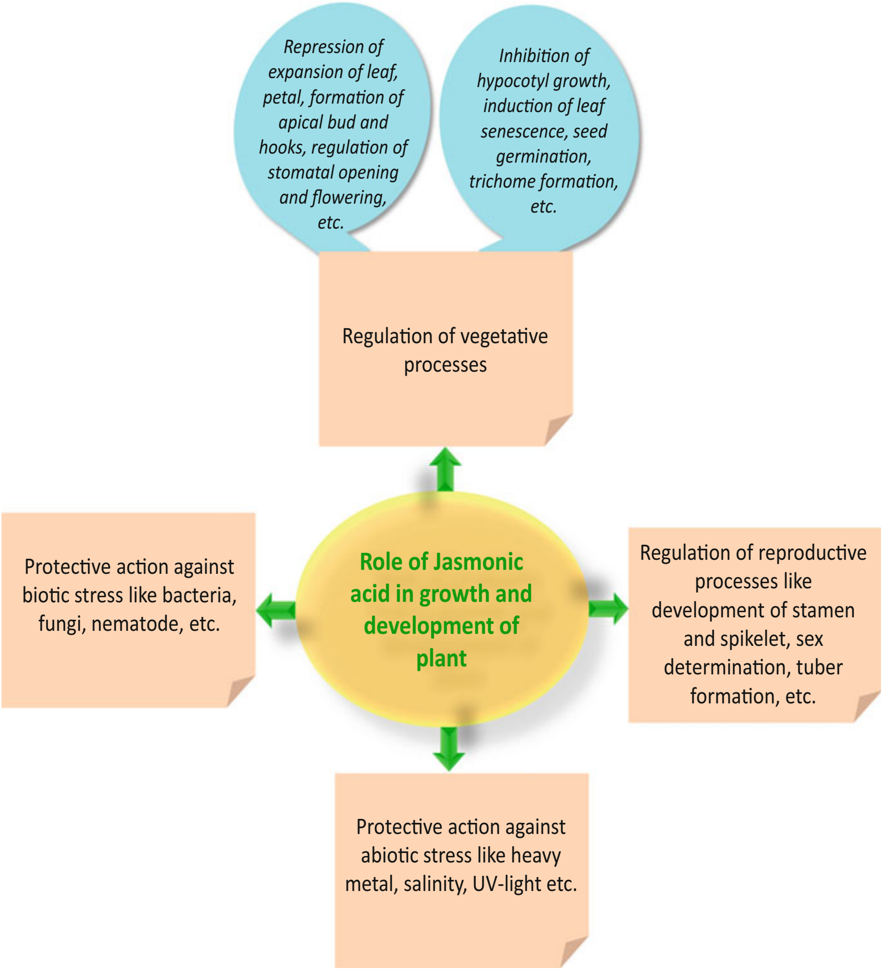

Fig. 17.1 Role of JA in growth and development of plants

chemical reactions like MeJA, *cis*-jasmone (CJ), JA-Ile and 12-hydroxyJA (12-OH-JA) in the cytoplasm (Fig. 17.2).

17.2 The Role of Jasmonate Under Abiotic Stress

Environmental stress tolerance in one major area where JAs have shown immense role in plants as reported in several studies (Ahmad et al. 2016; Riemann et al. 2015; Farhangi-Abriz and Ghassemi-Golezani 2018). JA confers adaptation to a variety of abiotic stresses such as salinity (Farhangi-Abriz and Ghassemi-Golezani 2018), heavy metals (Dar et al. 2015), drought (Wasternack 2014) and thermal stress

Table 17.1 Compilation of different studies on the role of exogenous or endogenous JA and their derivatives under abiotic stress

Stress factor	Concentration of JA and its derivatives	Studied plant	Response	Reference
Heavy metal	Exogenous MeJA (10^{-6} Mol/L and 10^{-5} Mol/L)	*Arabidopsis*	Showed protective effect against copper and cadmium metals by protecting photosynthetic apparatus	Maksymiec and Krupa (2002)
	Exogenous JA (JA; 25 μmol/L)	*Brassica napus*	Damaging effect of Cd was declined by enhancing the gas exchange as well as pigments content. Moreover, JA strengthened the antioxidant system that further helped in improving the growth of test seedling	Ali et al. (2018)
	Endogenous	*Phaseolus coccineus* and *Arabidopsis thaliana*	Cadmium and copper treatment induced the accumulation of JA in leaves of both the studied plants. Although the accumulation was in biphasic manner.	Maksymiec et al. (2005)
	Exogenous methyl jasmonate (MeJA; 10 μM)	*Brassica juncea*	The negative effect of Cd was alleviated by MeJA treatment by enhancing the photosynthetic rate, assimilation of sulphur and content of reduced glutathione (GSH)	Per et al. (2016)
	Exogenous methyl jasmonate (MeJA;0.1 and 1 μM)	*Brassica napus*	MeJA supplementation declined the oxidative stress by lowering the content of hydroxyl and H_2O_2 as well as increased the activities of antioxidant enzymes like SOD, POD, CAT, APX, and secondary metabolites.	Farooq et al. (2016)

(continued)

Table 17.1 (continued)

Stress factor	Concentration of JA and its derivatives	Studied plant	Response	Reference
			Moreover, MeJA also regulated multi-gene in response to as stress	
	Exogenous methyl jasmonate (MeJA; 0, 0.01 and 0.1 mM)	*Triticum aestivum*	MeJA at applied concentrations declined the Cd accumulation in plants as well as increased the expression of allene oxide synthase (AOS).	Alikhani and Abbaspour *(*2019*)*
Water stress	Exogenous methyl jasmonate (MeJA 0.01 and 0.1 mM)	*Fragaria vesca*	Reduction in transpiration rate as well as peroxidation of lipid-membrane as observed by malondialdehyde content. Moreover, alleviation in degree of unsaturation as well as the ratio of linolenic (18:3) to linoleic acid (18:2) was also observed	Wang (1999)
	Endogenous 12-oxo-phytodienoic acid (OPDA)	*Arabidopsis thaliana*	Drought stress led to accumulation of OPDA in three ecotypes of studied plant that suggests towards the drought-responsive regulatory role of OPDA	Savchenko et al. (2014)
	Endogenous JA (JA)	*Oryza sativa*	Transcriptomic study revealed the expression of genes involved in JA biosynthesis	Fu et al. (2017)
	Endogenous JA (JA)	*Prunus armeniaca*	Accumulation of JA was observed in both drought tolerant as well as drought sensitive varieties but the accumulation was threefold higher in case of drought tolerant	Ge et al. (2010)

(continued)

Table 17.1 (continued)

Stress factor	Concentration of JA and its derivatives	Studied plant	Response	Reference
	Exogenous methyl jasmonate (MeJA; 20 μM)	*Glycine max*	MeJA improved the tolerance of studied plant by enhancing the secondary metabolites as well as solutes. Moreover among the two genotypes Giza 35 was found to be more prone to water stress	Mohamed and Latif (2017)
Salinity stress	Exogenous 12-oxo-phytodienoic acid (OPDA; 0.01 μM)	*Luffa*	OPDA declined the negative impact of NaCl stress by strengthening the photosynthetic machinery, pigments content and also enhanced the content of secondary metabolites	Parihar et al. (2018)
	Exogenous methyl jasmonate (MeJA; 0.01 μM)	*Luffa*	Exogenous MeJA supplementation declined the NaCl stress and promoted growth by enhancing photosynthetic process and production of secondary metabolites	Parihar et al. (2018)
	Exogenous JA (JA; (0, 5, 25 and 50 μM)	*Zea mays*	Exogenous treatment with JA to different varieties of maize lead to improved growth under salt stress	Shahzad et al. (2015)
	Exogenous JA (JA; 2 mM)	*Triticum aestivum*	Exogenous JA declined the negative impact of salt stress by enhancing the transcription and activity of enzymes, i.e. SOD, POD, CAT and APX while declined the content of reactive oxygen species (ROS)	Qiu et al. (2014)

(continued)

Table 17.1 (continued)

Stress factor	Concentration of JA and its derivatives	Studied plant	Response	Reference
	Endogenous JA	*Arabidopsis*	Upregulation in the JA-responsive genes under NaCl stress was observed	Valenzuela et al. (2016)
	Endogenous JA	*Solanum lycopersicum*	Accumulation of JA was observed in the wild type in comparison to the mutant variety and the accumulation of JA leads to better ROS homeostasis	Abouelsaad and Renault (2018)
UV-B/ozone stress	Exogenous 12-oxo-phytodienoic acid (OPDA; 0.01 µM)	*Luffa*	OPDA declined the negative impact of UV-B stress by strengthening the photosynthetic machinery, pigments content and also enhanced the content of secondary metabolites	Parihar et al. (2018)
	Exogenous methyl jasmonate (MeJA; 50, 100 and 200 µM)	*Arabidopsis thaliana*	MeJA improved the damaging impact of ozone stress on studied plant by declining the oxidative stress	Rao et al. (2000)
	Endogenous JA (JA)	*Nicotiana*	UV-B stress elicited the expression of genes involved in phenylpropanoid pathway as well the genes involved in regulation of stress by JA	Demkura et al. (2009)
	Exogenous methyl jasmonate (MeJA; 0.01 µM)	*Luffa*	Exogenous MeJA supplementation declined the UV-B induced negative effect on growth, pigments and photosynthesis and promoted the production of secondary metabolites	Parihar et al. (2018)

(continued)

Table 17.1 (continued)

Stress factor	Concentration of JA and its derivatives	Studied plant	Response	Reference
	Exogenous JA (JA; 1 and 2.5 mM)	*Triticum aestivum*	Pretreatment with JA ameliorated the impact of UV-B stress by improving the functioning of photosynthetic apparatus substantiated by PSII functioning as well as by strengthening the antioxidant machinery and contents of proline and phenolics	Liu et al. (2012)
Temperature stress	Endogenous JA (JA)	*Arabidopsis thaliana*	JA upregulated the C-repeat binding factor and the genes involved in providing cold tolerance	Hu et al. (2017)
	Exogenous methyl jasmonate (0.1 mM)	*Musa acuminata*	Enhancement in the C-repeat binding factor as well as other genes involved in cold tolerance	Zhao et al. (2013)
	Endogenous JA (JA)	*Zoysia japonica*	Upregulation of ZjCBF, ZjDREB1 and ZjLEA genes as well as accumulation in JA was observed	Li et al. (2018)
	Exogenous methyl jasmonate (MeJA; 10 μmol/L)	*Eriobotrya japonica*	MeJA induced the chilling tolerance by strengthening the antioxidant system as well as improving the ratio of unsaturated/ saturated fatty acid	Cao et al. (2009)

(Sharma and Laxmi 2016). Application of JAs through foliar spray or hydroponically can be useful in enhancing stress tolerance mechanism in various plants. In this chapter, the role of JAs in coping different abiotic stresses and possible mechanism of action are discussed briefly.

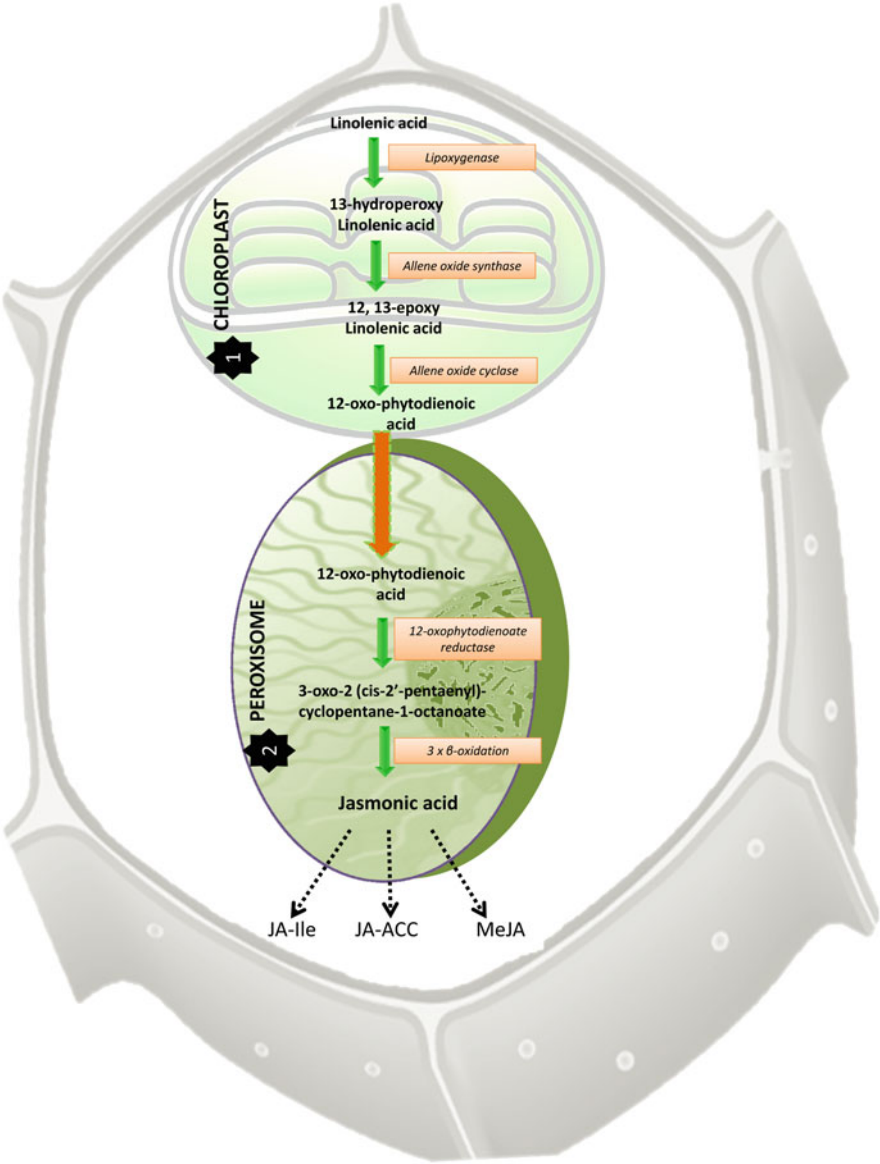

Fig. 17.2 Biosynthesis of JA takes place in two organelles: (1) chloroplast and (2) peroxisome. In the chloroplast, 12-oxo-phytodienoic acid (12-OPDA) synthesis takes place which is finally converted to JA in the peroxisome. JA is converted into different forms by various chemical reactions like jasmonyl-1-amino-1-cyclopropane carboxylic acid (JA-ACC), methyl-jasmonate (MeJA), *cis*-jasmone (CJ), jasmonyl-isoleucine (JA-Ile) and 12-hydroxyJA (12-OH-JA) in the cytoplasm

17.2.1 Salt Stress

Soil salinity has become a major global problem and hinders crop productivity around the world (Raju et al. 2020). Salinization causes increase in sodium (Na^+) and chloride (Cl^-) content which disrupt the normal functioning of plants and affects growth and development (Parihar et al. 2015). About 20% of irrigated land is affected by salinity, and this could increase up to 50% by 2050 (Raju et al. 2020). Salinity in soil and water severely affects membrane permeability, nutrient delivery, chlorophyll synthesis, nitrogen and carbon metabolism which lead to enhancement in the toxicity of ions and respiration rate in the plant cells (Ahmad et al. 2013; Kumar et al. 2018). Toxicity of salt also results in formation of reactive oxygen species (ROS) that culminates into oxidative stress causing damage to DNA and proteins, deactivation of enzymes as well as peroxidation of lipids (Raju et al. 2020).

Salt toxicity symptoms are significantly lowered through foliar spray of JA in soybean seedlings (Yoon et al. 2009). In *Carthamus* seedlings exposed to salt stress, foliar spray of JA enhances physiological attributes via enhanced relative water content, chlorophyll content, the maximum quantum yield of photosystem II (F_v/F_m) and grain yield (Ghassemi-Golezani and Hosseinzadeh-Mahootchi 2015). When JA is given externally in plants, activity of antioxidant enzymes and potassium level elevates with reduced lipid peroxidation under salt stress (Faghih et al. 2017; Farhangi-Abriz and Ghassemi-Golezani 2018). Lipoxygenase activity is enhanced by foliar spray of JA which in turn increases the percentages of total oil and linoleic acid formation from oleic acid significantly under exposure to salt stress (Ghassemi-Golezani and Farhangi-Abriz 2018a). It majorly affects the quality of soybean oil by enhancing the unsaturated index of oil. Foliar spray of JA reduces uptake of sodium by stimulating H^+-ATPase activity in root tonoplast in soybean seedlings (Ghassemi-Golezani and Farhangi-Abriz 2018b). In salt-stressed pea seedlings, MeJA improves growth attributes by restoring the F_v/F_m ratio for proper functioning of PS II (Velitchkova and Fedina 1998). Seed priming by JA is an effective way in enhancing stress tolerance in plants. Walia et al. (2007) have reported that seed priming with JA in barley seedlings expresses resistant to salt toxicity by a decrease in Na^+ accumulation and adequacy of nutrients. Hassawi okra seedlings develop salt tolerance by seed priming with 50 μM JA (Azooz et al. 2015). Rapeseed seedlings elicit resilience to salinity on seed priming with JA vis-à-vis significant enhancement of sugar accumulation (Harpreet et al. 2013).

17.2.2 Temperature Stress

17.2.2.1 Cold Stress

Cold stress (chilling and freezing) is one of the major stresses faced by the plants due to harsh environmental conditions and hampers crop productivity as these plants are intolerant to low temperature. Chilling and freezing stress affect the plant cells causing damage to the membranes, chlorosis, necrosis and alteration in enzyme activities and viscosity of cytoplasm due to which plant dies (Ruelland and

Zachowski 2010). Plants tend to adapt themselves to cold stress by evolving several tolerance mechanisms for their survival in harsh conditions (Shinozaki et al. 2003). A variation exists in levels of JA and other hormones in *Arabis alpina* seedlings under cold stress (Kolaksazov et al. 2013). Both tolerant and non-tolerant plants at normal room temperature exhibit high JA levels. Nevertheless, an exposure to chilling stress at 4 °C reduces JA level by tenfold in non-tolerant plants and very minutely in JA level in tolerant plants. Upon frost exposure, the content of JA drops heavily in tolerant plants whilst non-tolerant ones have the same amount of JA. This study indicates that JA acts as a jasmonate mediator of freezing stress in *Arabis* seedlings.

MeJA can diminish the negative impact of chilling injuries in plants. MeJA also induces production of many compounds which are beneficial for the pharmaceutical industries as well as antioxidants like vitamins and flavonoids (Martin et al. 2013). In *Cucurbita* seedlings, MeJA diminish chilling injuries through its regulation by ABA and polyamine levels (Wang and Buta 1994). MeJA-treated plants enhance their ABA levels when exposed to 5 °C which correspond to stimulation of ABA synthesis at freezing temperatures. Here, MeJA displays a signalling role in activating other hormone orchestrating response to cold stress. That is why MeJA and ABA maintain a parity of responses to cold stress (Parthier et al. 1992). Similarly, in Zucchini squash, ABA accumulation occurs in exocarp tissue by supplementation of MeJA (Wang and Buta 1994). MeJA is believed to introduce changes in tissue metabolism promoting ABA synthesis in response to cold stress. Therefore, MeJA predominately acts as a secondary messenger for crop plants for expression of stress genes in adapting to different stresses (Farmer et al. 1992).

17.2.2.2 Heat Stress

Heat stress also affects growth and development of plants to a great extent. This extreme variation in temperature causes plants to develop protective mechanisms for normal functioning of its cells. Undesirable alteration occurs in plant cells causing impairment in cell homeostasis due to heat stress (Bokszczanin and Fragkostefanakis 2013). Boston et al. (1996) have earlier reported that high temperatures elicit synthesis of heat shock proteins by the plants which assist refolding of disrupted proteins and thus prevent denaturation. It has subsequently been confirmed by Clarke et al. (2009) that JAs confer thermotolerance in plants. External application of MeJA in low concentration maintains cell viability and prevents electrolyte leakage in *Arabidopsis* seedlings exposed to heat stress and helps express JA inducible gene *PDF1.2* (Clarke et al. 2009). Involvement of JA in thermotolerance has also been confirmed from the analysis of salicylic acid and JA signalling mutants, namely, *opr3*, *coi1–1* and *jar1–1cpr5–1* (Clarke et al. 2009). Interestingly, various genes involved in JA biosynthesis are induced by drought and cold stress. However, the expression of same genes is suppressed in rice seedlings exposed to heat stress (Du et al. 2013). In conclusion, the endogenous levels of JA elevate due to cold and drought stress, whilst heat stress decreases JA levels. Zhang et al. (2015) have also contemplated the interplay of HSP90 and HSP70 in JACOR responses in HSP90 RNAi lines defining decrease in transcript levels of JA in *Arabidopsis* seedlings. Recently, MeJA has been demonstrated to stimulate lipoxygenase that positively contributes to heat stress. Further, the exogenous MeJA promotes endogenous accumulation of phytohormones in red alga *Gracilariopsis lemaneiformis* (Hou et al. 2018).

17.2.3 Drought Stress

Among various abiotic stresses, drought plays a major role for destruction of million tonnes of agricultural produce (Pandey et al. 2017). Normal growth and development of plants is altered due to drought stress by chain of biochemical, physiological and molecular changes that results in loss of crop productivity (Pandey et al. 2017). This environmental stress also causes a reduction in cell water potential and turgor, which elevates inter- or intra-cellular solute concentrations due to decrease in cell water potential and cause other harmful effects on plants (Todaka et al. 2015). Role of JA in response to drought has been neither fully understood nor studied by the researchers compared to other abiotic stresses. Kiribuchi et al. (2005) have demonstrated enhancement of JA levels in plant leaves and roots under drought stress. Further, an overexpression of JA carboxyl methyltransferase gene (AtJMT) responsible for JA level elevation has been reported in rice seedlings by Kim et al. (2009). These studies can be attributed to the fact of JA working as signalling molecule as well as a stress hormone in combating drought stress conditions.

Exogenous supplementation of JA as foliar spray or in hydroponics can be an aid to plants in combating harmful effects of drought. Reports from various researches have suggested that JA when externally given to the plants alleviates stress symptoms via stimulation of activities of antioxidant enzymes. In maize seedlings, exogenous JA application diminishes oxidative stress via stimulating activity of antioxidant enzymes (Abdelgawad et al. 2014). Exogenous JA reduces oxidative stress not only by increasing activity of antioxidant enzymes but also preventing membrane damage due to peroxidation of lipids in peanut seedlings (Kumari et al. 2006). In another study, exogenous application of JA has been demonstrated to facilitate the activities of enzymes like glutathione peroxidase, ascorbate peroxidase and catalase vis-à-vis reduction of ROS production in *Brassica* seedlings exposed to drought stress (Alam et al. 2014). The mechanism of JA in response to stress by modification of antioxidant systems is not very precise. This might be possible due to the modifications in gene transcription, translation or post-transcription through JA-induced activities of enzymes. But some studies also suggest organ-specific nature of JA that specifically controls and regulates sub-cellular changes in metabolism (Comparot et al. 2002).

JA adjusts cell water potential and alleviates drought stress in plants (Shan et al. 2015). JA might be responsible for upregulation of genes which have a prominent role in adaptation to drought conditions via stimulating the synthesis of cell wall formation, secondary metabolites, defence proteins and solutes like cysteine and proline (Abdelgawad et al. 2014). Exogenous application of JA to barley genotypes ameliorates synthesis of proline under drought stress (Bandurska et al. 2003).

Osmotic modifications induced by JA accumulate other osmoregulators like proteins and soluble carbohydrates (Abdelgawad et al. 2014). Under water stress, JA appears to promote invertase activity leading to accumulation of soluble sugars in seedlings and ascorbate and glutathione metabolism in leaves of *Agropyron cristatum* experiencing drought stress (Shan and Liang 2010).

17.2.4 Heavy Metal Stress

Various metal ions are beneficial for the normal growth and functioning of plants, but there are some heavy metals which are toxic in even minute concentrations and cause huge reduction in growth (Asgher et al. 2015; Iqbal et al. 2015). Even essential metals and metalloid can induce toxicity in plants when present in excess causing oxidative stress and membrane damage (Dhankar and Solanki 2011). JA supplementation enhances accumulation of osmolytes boosting synthesis of carotenoids which are responsible for increased activity of antioxidant enzymes vis-à-vis prevention from heavy metal toxicity (Poonam et al. 2013). Seedlings of pigeon pea supplemented with JA and exposed to copper stress significantly gain contents of proteins and chlorophyll pigments (total chlorophyll, carotenoids) and alleviate the stress symptoms. Cadmium toxicity causes generation of reactive oxygen species such as superoxide radicals and hydrogen peroxide which are responsible for oxidative stress in plants (Gallego et al. 2012). However, exogenous supplementation of JA diminishes about one-third of the damage caused by oxidative stress in runner bean and *Arabidopsis* exposed to copper and cadmium stress (Maksymiec et al. 2005). Boron toxicity causes visible destruction in plants like leaf burns, reduced size of fruits (Paull et al. 1992; Nable et al. 1997) and oxidative stress via generation of ROS in tomato (Cervilla et al. 2007), wheat (Gunes et al. 2007) and barley (Inal et al. 2009). When MeJA is sprayed onto the plants, stress symptoms get alleviated by stimulation of antioxidant defence system which prevents peroxidation of lipids. Alleviation of toxicity of copper and cadmium by supplementation of MeJA can be explained by the formation of metal ions complex due to accumulation of chelating ligands in *Arabidopsis* and thus preventing availability of these toxic metal ions to the plants (Poonam et al. 2013). Exogenous application of MeJA has shown significant enhancement in activities of SOD, GR and CAT and increased glutathione levels (Singh and Shah 2014). In another study, MeJA supplementation in *Capsicum* seedlings exposed to Cd stress augments dry weight of plant, chlorophyll pigment contents, enzymatic activities of APX and CAT (Yan et al. 2013). Similarly, exogenous application of MeJA at 1.0 and 10 μM concentrations enhances APX activity and reduces uptake of Cd in seedlings of *Avicennia marina* (Yan et al. 2015). Interestingly, exogenous supplementation MeJA retains endogenous JA levels, decreases photosynthetic damage and rate of transpiration and controls stomatal closure, finally preventing Cd uptake in *Kandelia* seedlings (Chen et al. 2014). JA alleviates the toxic effects of Cd stress by enhancing the activity of APX, GR, SOD, CAT, glycine betaine and proline and reducing the accumulation of ROS species such as H_2O_2 and MDA. As a result, *Vicia faba* roots prevent accumulation of Cd (Ahmad et al. 2017). In As-stressed *Brassica napus* seedlings, exogenous MeJA alleviates the stress symptoms and restores photosynthetic activity and overall growth of the plant (Farooq et al. 2018).

17.2.5 Flooding Stress

In our environment, water is essential for plants, but excess water due to flooding can have adverse effects on the normal growth and development of plants. Various adaptive mechanisms like development of aerenchyma and adventitious root and control of shoot growth are present in plants to manage absence of oxygen under waterlogging (Sachs 2008). When plant roots are exposed to excess water by which gas dispersal in the rhizosphere is restricted, it is known as flooding (Armstrong et al. 1994; Setter and Waters 2003). Dispersion of oxygen in water is 10,000 times slower as compared to that of atmosphere (Armstrong et al. 1994). Therefore, crops get damaged due to waterlogging or submergence caused by absence of oxygen (Colmer and Voesenek 2009).

The interplay of ethylene and JA production is crucial for the development of aerenchyma and adventitious roots under submergence. Zimmerman and Hitchcock (1933) were the first to recognise the role of ethylene in aerenchyma formation. Now, it is well known about the positive effect of ethylene on aerenchyma development (Verstraeten et al. 2014). Ethylene stimulation induced by flooding stress is responsible for the formation of aerenchyma (Vidoz et al. 2010). In one study, foliar spray as exogenous application of JAs has been conclusively established to enhance the production of ethylene (Hudgins and Franceschi 2004). Therefore, we can assume that JA can also have an impact in coping with flooding stress as it helps in increasing ethylene production. By altering the proteomic profile, JAs exhibit the ability to reduce toxic effects caused by flooding stress and has benefitted growth of *Glycine max* seedlings (Kamal and Komatsu 2016).

17.2.6 Light Stress

Various capabilities have been acquired by the plants in sensing the environment and adapt themselves according to their requisite of growth and development. Such exceptional instance of this diversification can be seen in solar light utilization for photosynthesis as well as signalling role for organising physiological responses to the environment. Alteration of light quality and quantity inputs into developmental output is majorly seen via signalling pathways of various hormones (Svyatyna and Riemann 2012). Thus, plant growth regulators play a vital role for photon inputs conversion into assemblies that assort growth and development of plant. Moreno et al. (2009) have reported the relationship between JA biosynthesis and light quality. Shade avoidance syndrome (SAS) is one of the light depended responses developed by plants. Regulation of this response is done by various plant growth regulators like cytokinin, JAs, auxin, brassinosteroids and ethylene. Recent works also suggest the vital role of JA in light-depended response in plants including that of SAS. The study also concludes the alteration of gene expression due to JA signalling exposed to shade and dim light stress.

Secondary metabolites like phenolic components are also enhanced with increase in biosynthesis of JAs under shade stress (Li and Kubota 2009). Leaf thickness also increases with JA accumulation in plants exposed to shade stress. JAZ (Jasmonate Zim-Domain) peptides are family of low-weight proteins which have been recently detected in sensing of JA signals related to its morphological, biochemical and molecular events (Kazan and Manners 2011). These quick-action mechanisms could be necessary for evading attacks of pathogen as shade condition provides favourable environment for population burst of pest and pathogen, while the shade limits the light requirement for plant slowing the rate of photosynthesis.

Sunlight is essential for plant and one of the important energy inputs, but in excess, it harms photosynthetic apparatus. Expression of light-responsive gene takes place in excess light which helps the plant to alleviate light stress. Endogenous JA content is enhanced by extreme sunlight which affects the growth of the plant positively. Extreme light can overexpress Zinc-finger transcription factor (ZAT 10) in *Arabidopsis* seedlings (Rossel et al. 2007). ZAT 10 is an intermediate in biosynthesis of JA which is made by 12-OPDA (Taki et al. 2005). This suggests biosynthesis of JA is regulated by ZAT 10 in extreme intensity of light that positively affects the growth and development of plants. Excess light is well-known to form reactive oxygen species oxidising polyunsaturated membrane fatty acids like a-linolenic acid peroxidation. Extreme light can cause the production of precursors of JAs from chloroplast lipids via non-enzymatic reactions as biosynthesis of JA is regulated by substrate accessibility (Wasternack 2014). Earlier, it has been reported that biosynthesis of JAs is induced by light stress through fibrillin proteins (Youssef et al. 2010). These structural plastid proteins show an ameliorative feedback in response to extreme light in plants. Some genes like VSP2 and LOX2 that respond to JAs have been shown to have decreased expression in JA-applied fibrillin RNAi plants (Youssef et al. 2010). Anthocyanin is regulated both by endogenous JA and light intensity in plants (Devoto et al. 2005). Chen et al. (2007) have also confirmed this coordination by demonstrating coronatine-insensitive 1 being vital for JA-induced anthocyanin formation in plant cells, revealing a correlation between JA signalling pathways and light intensity. Regulation of phenylpropanoid in cells of plant requires JAs and some transcription factors responding to light like PAP2 (MYB90), PAP1 (MYB75), GL3 (GLABROUS3) and bHLH (Shan et al. 2009).

Ultraviolet-B (UV–B) radiation is a major stress in plants that is reliant on light. Plants are very sensitive to ultraviolet-B radiation because of their eco-physiological nature, and among different species and genotypes, this response is varied. This difference happens because plants mechanism of protection against UV-B radiation depends on the physiological, biochemical and molecular responses (Li et al. 1993). Plant physiology and phenology is regulated by the actions of high UV-B radiation. Gene expression in plants is upregulated and downregulated which causes alteration in flowering and growth by UV-B radiation (Jordan 2002). High level energy photons of ultraviolet B inflict damage to the cell membrane and stress-inducible genes, orchestrating activation of lipases for release of the initial signal-transduction that activates the octadecanoid pathway (Hidema et al. 2000). Therefore, we can say that UV-B radiation response might be regulated by JAs resulted from linolenic acid via the octadecanoid pathway. Formation of some phenylpropanoid components like polyamines was enhanced by JAs which is mediated by MeJA-induced transcription factor under the exposure of UV-B radiation in seedlings of *Nicotiana tabacum* (Galis et al. 2006). We know as to how JA endogenously benefits plants under the influence of light stress (Riemann et al. 2007). However, very less is known about the UV-B radiation affecting the growth of plants. Recently, it has been concluded that exogenous MeJA enhances antioxidant defence system, photosynthetic activity and proline synthesis and helps recover from ill effects of UV-B radiation in seedlings of barley (Fedina et al. 2009).

17.3 Conclusion

JAs can easily be said as the quick action team of the plant defence as they act for quick injuries against the various biotic and abiotic stresses. Now, we know that JAs are also responsible for plant defence in harsh environmental conditions. JA and its methyl ester play prominent roles in stress tolerance and benefit plants under various abiotic stresses via physiological and molecular changes. Endogenous JAs have shown to act in plant survival and maintenance under harsh conditions, while exogenous JA have further helped the plants in coping with different stress and alleviating the symptoms of stress. Several studies suggest that antioxidant defence system gets activated via JA which alleviates oxidative stress caused by reactive oxygen species under abiotic stresses. It has also been observed that JAs upregulate and downregulate gene expression due to which physiological and molecular alteration occurs, leading to tolerance to various abiotic stresses. Plant growth regulators like abscisic acid and ethylene are also stimulated by JA in plants under exposure to environmental stresses. Future works can focus on JA effect on other hormones through crosstalk in aiding plants to strengthen their defence system. A proper physiological understanding of JA synthesis and its involvement in gene expressions needs elucidation that may help engineer crop plants to cope with various abiotic stresses and restore high productivity in adverse climatic conditions.

References

Abdelgawad ZA, Khalafaallah AA, Abdallah MM (2014) Impact of methyl jasmonate on antioxidant activity and some biochemical aspects of maize plant grown under water stress condition. Agric Sci 5:1077–1088

Abouelsaad I, Renault S (2018) Enhanced oxidative stress in the JA-deficient tomato mutant *def-1* exposed to NaCl stress. J Plant Physiol 226:136–144

Ahmad P, Alyemeni MN, Wijaya L, Alam P, Ahanger MA, Alamri SA (2017) JA alleviates negative impacts of cadmium stress by modifying osmolytes and antioxidants in faba bean (*Vicia faba* L.). Arch Agron Soil Sci 63:1889–1899

Ahmad P, Azooz MM, Prasad MNV (2013) Salt stress in plants. Springer, Heidelberg

Ahmad P, Rasool S, Gul A, Sheikh SA, Akram NA, Ashraf M, Kazi AM, Gucel S (2016) Jasmonates: multifunctional roles in stress tolerance. Front Plant Sci 7:813

Alam MM, Nahar K, Hasanuzzaman M, Fujita M (2014) Exogenous JA modulates the physiology, antioxidant defense and glyoxalase systems in imparting drought stress tolerance in different *Brassica* species. Plant Biotechnol Rep 8:279–293

Ali E, Hussain N, Shamsi IH, Jabeen Z, Siddiqui MH, Jiang LX (2018) Role of JA in improving tolerance of rapeseed (*Brassica napus* L.) to Cd toxicity. J Zhejiang Univ Sci B 19(2):130–146. https://doi.org/10.1631/jzus.B1700191

Alikhani O, Abbaspour H (2019) Effects of methyl jasmonate and cadmium on growth traits, cadmium transport and accumulation, and allene-oxide cyclase gene expression in wheat seedlings. Revista de Agricultura Neotropical Cassilândia-MS 6:20–29

Armstrong W, Brändle R, Jackson MB (1994) Mechanisms of flood tolerance in plants. Acta Bot Neerl 43:307–358

Asgher M, Khan MIR, Anjum NA, Khan NA (2015) Minimising toxicity of cadmium in plants-role of plant growth regulators. Protoplasma 252:399–413

Azooz MM, Metwally A, Abou-Elhamd MF (2015) Jasmonate-induced tolerance of Hassawi okra seedlings to salinity in brackish water. Acta Physiol Plant 37:77

Bandurska H, Stroiński A, Kubiś J (2003) The effect of JA on the accumulation of ABA, proline and spermidine and its influence on membrane injury under water deficit in two barley genotypes. Acta Physiol Plant 25:279–285

Bokszczanin KL, Fragkostefanakis S (2013) Perspectives on deciphering mechanisms underlying plant heat stress response and thermotolerance. Front Plant Sci 4:315

Boston RS, Viitanen PV, Vierling E (1996) Molecular chaperones and protein folding in plants. Plant Mol Biol 32:191–222

Cao S, Zheng Y, Wang K, Jin P, Rui H (2009) Methyl jasmonate reduces chilling injury and enhances antioxidant enzyme activity in postharvest loquat fruit. Food Chem 115(4):1458–1463

Cervilla LM, Blasco B, Rios JJ, Romero L, Ruiz JM (2007) Oxidative stress and antioxidants in tomato (*Solanum lycopersicum*) plants subjected to boron toxicity. Ann Bot 100:747–756

Chen J, Yan Z, Li X (2014) Effect of methyl jasmonate on cadmium uptake and ntioxidative capacity in *Kandelia obovata* seedlings under cadmium stress. Ecotoxicol Environ Saf 104: 349–356

Chen QF, Dai LY, Xiao S, Wang YS, Liu XL, Wang GL (2007) The COI1 and DFR genes are essential for regulation of jasmonate-induced anthocyanin accumulation in *Arabidopsis*. J Integr Plant Biol 49:1370–1377

Chini A, Monte I, Zamarreño AM, Hamberg M, Lassueur S, Reymond P, Weiss S, Stintzi A, Schaller A, Porzel A et al (2018) An OPR3-independent pathway uses 4,5 didehydrojasmonate for jasmonate synthesis. Nat Chem Biol 14:171–178

Clarke SM, Cristescu SM, Miersch O, Harren FJ, Wasternack C, Mur LA (2009) Jasmonates act with salicylic acid to confer basal thermotolerance in *Arabidopsis thaliana*. New Phytol 182: 175–187

Colmer TD, Voesenek LACJ (2009) Flooding tolerance: suites of plant traits in variable environments. Funct Plant Biol 36:665–681

Comparot SM, Graham CM, Reid DM (2002) Methyl jasmonate elicits a differential antioxidant response in light-and dark-grown canola (*Brassica napus*) roots and shoots. Plant Growth Regul 38:21–30

Dar TA, Uddin M, Khan MMA, Hakeem KR, Jaleel H (2015) Jasmonates counter plant stress: a review. Environ Exp Bot 115:49–57

Demkura PV, Abdala G, Baldwin IT, Ballare CL (2009) Jasmonate-dependent and independent pathways mediate specific effects of solar ultraviolet B radiation on leaf phenolics and antiherbivore defense. Plant Physiol 152(2):1084–1095

Devoto A, Ellis C, Magusin A, Chang HS, Chilcott C, Zhu T, Turner JG (2005) Expression profiling reveals COI1 to be a key regulator of genes involved in wound and methyl jasmonate-induced secondary metabolism, defence, and hormone interactions. Plant Mol Biol 58:497–513

Dhankar R, Solanki R (2011) Effect of copper and zinc toxicity on physiological and biochemical parameters in *Vigna mungo* (L.). Hepper. Int J Pharm Bio Sci 2:553–565

Du H, Liu H, Xiong L (2013) Endogenous auxin and JA levels are differentially modulated by abiotic stresses in rice. Front Plant Sci 4:397

Faghih S, Ghobadi C, Zarei A (2017) Response of strawberry plant cv. 'Camarosa' to salicylic acid and methyl jasmonate application under salt stress condition. J Plant Growth Regul 36:1–9

Farhangi-Abriz S, Ghassemi-Golezani K (2018) How can salicylic acid and JA mitigate salt toxicity in soybean plants? Ecotoxicol Environ Saf 147:1010–1016

Farmer EE, Johnson RR, Ryan CA (1992) Regulation of expression of proteinase inhibitor genes by methyl jasmonate and JA. Plant Physiol 98:995–1002

Farooq MA, Gill RA, Islam F, Ali B, Liu H, Xu J, He S, Zhou W (2016) Methyl jasmonate regulates antioxidant defense and suppresses arsenic uptake in *Brassica napus* L. Front Plant Sci 7:468

Farooq MA, Islam F, Yang C, Nawaz A, Gill RA, Ali B, Song W, Zhou W (2018) Methyl jasmonate alleviates arsenic-induced oxidative damage and modulates the ascorbate–glutathione cycle in oilseed rape roots. Plant Growth Regul 84:135–148

Fedina I, Nedeva D, Georgieva K, Velitchkova M (2009) Methyl jasmonate counteract UV-B stress in barley seedlings. J Agron Crop Sci 195:204–212

Fu J, Wu H, Ma SQ, Xiang DH, Liu RY, Xiong LZ (2017) OsJAZ1 attenuates drought resistance by regulating JA and ABA signaling in rice. Front Plant Sci 8:1–13

Galis I, Šimek P, Narisawa T, Sasaki M, Horiguchi T, Fukuda H, Matsuoka K (2006) A novel R2R3 MYB transcription factor NtMYBJS1 is a methyl jasmonate-dependent regulator of phenylpropanoid-conjugate biosynthesis in tobacco. Plant J 46:573–592

Gallego SM, Pena LB, Bracia RA, Azpilicueta CE, Lannone MF, Rosales EP, Zawoznik MS, Groppa MD, Benavides MP (2012) Unravelling cadmium toxicity and tolerance in plants: insight into regulatory mechanisms. Environ Exp Bot 8:33–46

Ge YX, Zhang LJ, Li FH, Chen ZB, Wang C, Yao YC, Han ZH, Zhang J, Shi ZS (2010) Relationship between JA accumulation and senescence in drought-stress. Afr J Agric Res 5: 1978–1983

Ghassemi-Golezani K, Farhangi-Abriz S (2018a) Changes in oil accumulation and fatty acid composition of soybean seeds under salt stress in response to salicylic acid and JA. Russ J Plant Physiol 65:229–236

Ghassemi-Golezani K, Farhangi-Abriz S (2018b) Foliar sprays of salicylic acid and JA stimulate H^+-ATPase activity of tonoplast, nutrient uptake and salt tolerance of soybean. Ecotoxicol Environ Saf 166:18–25

Ghassemi-Golezani K, Farhangi-Abriz S (2019) Biochar alleviates fluoride toxicity and oxidative stress in safflower (*Carthamus tinctorius* L.) seedlings. Chemosphere 223:406–415

Ghassemi-Golezani K, Hosseinzadeh-Mahootchi A (2015) Improving physiological performance of safflower under salt stress by application of salicylic acid and JA. WALIA J 31:104–109

Ghassemi-Golezani K, Nikpour-Rashidabad N (2017) Seed pretreatment and salt tolerance of dill: osmolyte accumulation, antioxidant enzymes activities and essence production. Biocatal Agric Biotechnol 12:30–35

Gunes A, Inal A, Bagci EG, Coban S, Sahin O (2007) Silicon increases B tolerance and reduces oxidative damage of wheat grown in soil with excess B. Biol Plant 51:571–574

Harpreet K, Poonam S, Geetika S (2013) Sugar accumulation and its regulation by JA in *Brassica napus* L. under salt stress. J Stress Physiol Biochem 9:53–64

Hidema J, Kumagai T, Sutherland BM (2000) UV radiation–sensitive norin 1 rice contains defective cyclobutane pyrimidine dimer photolyase. Plant Cell 12:1569–1578

Hou S, Lin L, Lv Y, Xu N, Sun X (2018) Responses of lipoxygenase, JA, and salicylic acid to temperature and exogenous phytohormone treatments in *Gracilariopsis lemaneiformis* (Rhodophyta). J Appl Phycol 30:3387–3394

Hu Y, Jiang Y, Han X, Wang H, Pan J, Yu D (2017) Jasmonate regulates leaf senescence and tolerance to cold stress: crosstalk with other phytohormones. J Exp Bot 68(6):1361–1369

Huang H, Liu B, Liu L, Song S (2017) Jasmonate action in plant growth and development. J Exp Bot 68:1349–1359

Hudgins JW, Franceschi VR (2004) Methyl jasmonate-induced ethylene production is responsible for conifer phloem defense responses and reprogramming of stem cambial zone for traumatic resin duct formation. Plant Physiol 135:2134–2149

Inal A, Pilbeam DJ, Gunes A (2009) Silicon increases tolerance to B toxicity and reduces oxidative damage in barley. J Plant Nutr 32:112–128

Iqbal M, Ahmad A, Ansari MKA, Qureshi MI, Aref IM, Khan PR, Hegazy SS, El-Atta H, Husen A, Hakeem KR (2015) Improving the phytoextraction capacity of plants to scavenge metal (loid)-contaminated sites. Environ Rev 23:44–65

Jordan BR (2002) Molecular response of plant cells to UV-B stress. Funct Plant Biol 29:909–916

Kamal AHM, Komatsu S (2016) JA induced protein response to biophoton emissions and flooding stress in soybean. J Proteome 133:33–47

Kazan K, Manners JM (2011) The interplay between light and jasmonate signalling during defence and development. J Exp Bot 62:4087–4100

Khan MS, Akther T, MubarakAli D, Hemalatha S (2019) An investigation on the role of salicylic acid alleviate the saline stress in rice crop *Oryza sativa* (L). Biocatal Agric Biotechnol 18:56. https://doi.org/10.1016/j.bcab.2019.101027

Kim EH, Kim YS, Park SH, Koo YJ, Do Choi Y, Chung YY, Lee IJ, Kim JK (2009) Methyl jasmonate reduces grain yield by mediating stress signals to alter spikelet development in rice. Plant Physiol 149:1751–1760

Kiribuchi K, Jikumaru Y, Kaku H, Minami E, Hasegawa M, Kodama O, Seto H, Okada K, Nojiri H, Yamane H (2005) Involvement of the basic helix-loop-helix transcription factor RERJ1 in wounding and drought stress responses in rice plants. Biosci Biotechnol Biochem 69:1042–1044

Kolaksazov M, Laporte F, Ananieva K, Dobrev P, Herzog M, Ananiev ED (2013) Effect of chilling and freezing stresses on jasmonate content in *Arabis alpina*. Bulgarian J Agri Sci 19:15–17

Kumar M, Kumar R, Jain V, Jain S (2018) Differential behavior of the antioxidant system in response to salinity induced oxidative stress in salt-tolerant and salt-sensitive cultivars of *Brassica juncea* L. Biocatal Agric Biotechnol 13:12–19

Kumari GJ, Reddy AM, Naik ST, Kumar SG, Prasanthi J, Sriranganayakulu G, Reddy PC, Sudhakar C (2006) JA induced changes in protein pattern, antioxidative enzyme activities and peroxidase isozymes in peanut seedlings. Biol Plant 50:219–226

Li J, Ou-Lee TM, Raba R, Amundson RG, Last RL (1993) *Arabidopsis* flavonoid mutants are hypersensitive to UV-B irradiation. Plant Cell 5:171–179

Li Q, Kubota C (2009) Effects of supplemental light quality on growth and phytochemicals of baby leaf lettuce. Environ Exp Bot 67:59–64

Li S, Yang Y, Zhang Q, Liu N, Xu Q, Hu L (2018) Differential physiological and metabolic response to low temperature in two zoysiagrass genotypes native to high and low latitude. PLoS One 13(6):0198885

Liu X, Chi H, Yue M, Zhang X, Li W, Jia E (2012) The regulation of exogenous JA on UV-B stress tolerance in wheat. J Plant Growth Regul 31(3):436–447. https://doi.org/10.1007/s00344-011-9253-5

Maksymiec W, Krupa Z (2002) JA and heavy metals in *Arabidopsis* plants—a similar physiological response to both stressors? J Plant Physiol 159(5):509–515

Maksymiec W, Wianowska D, Dawidowicz AL, Radkiewicz S, Mardarowicz M, Krupa Z (2005) The level of JA in *Arabidopsis thaliana* and *Phaseolus coccineus* plants under heavy metal stress. J Plant Physiol 162(12):1338–1346

Martin C, Zhang Y, Tonelli C, Petroni K (2013) Plants, diet, and health. Annu Rev Plant Biol 64: 19–46

Mohamed HI, Latif HH (2017) Improvement of drought tolerance of soybean plants by using methyl jasmonate. Physiol Mol Biol Plants 23:545–556

Moreno JE, Tao Y, Chory J, Ballaré CL (2009) Ecological modulation of plant defense via phytochrome control of jasmonate sensitivity. Proc Natl Acad Sci USA 106:4935–4940

Nable RO, Bañuelos GS, Paull JG (1997) Boron toxicity. Plant Soil 193:181–198

Pandey N, Iqbal Z, Pandey BK, Sawant SV (2017) Phytohormones and drought stress: plant responses to transcriptional regulation. In: Mechanism of plant hormone signaling under stress. Wiley, Hoboken, pp 477–504

Parihar P, Singh R, Prasad SM (2018) Regulatory role of oxylipins on growth and secondary metabolites under simultaneous treatments of NaCl and UVB stress in *Luffa* seedlings. Int J Agri Sci 9(1):30–36

Parihar P, Singh S, Singh R, Singh VP, Prasad SM (2015) Effect of salinity stress on plants and its tolerance strategies: a review. Environ Sci Pollut Res 22:4056–4075

Parthier B, Brückner C, Dathe W, Hause B, Herrmann G, Knöfel HD, Kramell HM, Kramell R, Lehmann J, Miersch O, Reinbothe S (1992) Jasmonates: metabolism, biological activities, and modes of action in senescence and stress responses. Prog Plant Growth Regul 13:276–285

Paull JG, Nable RO, Lake AWH, Materne MA, Rathjen AJ (1992) Response of annual medics (*Medicago* spp.) and field peas (*Pisum sativum*) to high concentrations of boron: genetic variation and mechanism of tolerance. Aust J Agric Res 43:203–213

Per TS, Khan MIR, Anjum NA, Masood A, Hussain SJ, Khan NA (2018) Jasmonates in plants under abiotic stresses: crosstalk with other phytohormones matters. Environ Exp Bot 145:104–120

Per TS, Khan NA, Masood A, Fatma M (2016) Methyl jasmonate alleviates cadmium-induced photosynthetic damages through increased S-assimilation and glutathione production in mustard. Front Plant Sci 2016:7. https://doi.org/10.3389/fpls.2016.01933

Poonam S, Kaur H, Geetika S (2013) Effect of JA on photosynthetic pigments and stress markers in *Cajanus cajan* (L.) Millsp. Seedlings under copper stress. Am J Plant Sci 4:817–823

Qiu Z, Guo J, Zhu A, Zhang L, Zhang M (2014) Exogenous JA can enhance tolerance of wheat seedlings to salt stress. Ecotoxicol Environ Saf 104:202–208

Raju AD, Parihar P, Singh R, Prasad SM, Kumar J (2020) Synergistic action of indole acetic acid with homobrassinolide in easing the NaCl-induced toxicity in *Solanum melongena* L. seedlings. Acta Physiol Plant 42:68. https://doi.org/10.1007/s11738-020-03054-8

Rao MV, Lee H, Creelman RA, Mullet JE, Davis KR (2000) JA signaling modulates ozone-induced hypersensitive cell death. Plant Cell 12:1633–1646. https://doi.org/10.1105/tpc.12.9.1633

Riemann M, Dhakarey R, Hazman M, Miro B, Kohli A, Nick P (2015) Exploring jasmonates in the hormonal network of drought and salinity responses. Front Plant Sci 6:1077

Riemann M, Gutjahr C, Korte A, Danger B, Muramatsu T, Bayer U, Waller F, Furuya M, Nick P (2007) GER1, a GDSL motif-encoding gene from rice is a novel early light- and jasmonate-induced gene. Plant Biol 9:32–40

Rossel JB, Wilson PB, Hussain D, Woo NS, Gordon MJ, Mewett OP, Howell KA, Whelan J, Kazan K, Pogson BJ (2007) Systemic and intracellular responses to photooxidative stress in *Arabidopsis*. Plant Cell 19:4091–4110

Ruelland E, Zachowski A (2010) How plants sense temperature. Environ Exp Bot 69:225–232

Sachs MM (2008) Flooding-stress in plants. Wiley, Hoboken

Savchenko T, Kolla VA, Wang CQ, Nasafi Z, Hicks DR, Phadungchob B, Chehab WE, Brandizzi F, Froehlich J, Dehesh K (2014) Functional convergence of oxylipin and abscisic acid pathways controls stomatal closure in response to drought. Plant Physiol 164:1151–1160

Setter TL, Waters I (2003) Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. Plant Soil 253:1–34

Shahzad AN, Pitann B, Ali H, Qayyum MF, Fatima A, Bakhat HF (2015) Maize genotypes differing in salt resistance vary in JA accumulation during the first phase of salt stress. J Agro Crop Sci 201(6):443–451

Shan C, Liang Z (2010) JA regulates ascorbate and glutathione metabolism in *Agropyron cristatum* leaves under water stress. Plant Sci 178:130–139

Shan C, Zhou Y, Liu M (2015) Nitric oxide participates in the regulation of the ascorbate-glutathione cycle by exogenous JA in the leaves of wheat seedlings under drought stress. Protoplasma 252:1397–1405

Shan X, Zhang Y, Peng W, Wang Z, Xie D (2009) Molecular mechanism for jasmonate-induction of anthocyanin accumulation in *Arabidopsis*. J Exp Bot 60:3849–3860

Sharma M, Laxmi A (2016) Jasmonates: emerging players in controlling temperature stress tolerance. Front Plant Sci 6:1129

Shinozaki K, Yamaguchi-Shinozaki K, Seki M (2003) Regulatory network of gene expression in the drought and cold stress responses. Curr Opinion Plant Biol 6:410–417

Siddiqi KS, Husen A (2019) Plant response to jasmonates: current developments and their role in changing environment. Bull Natl Res Cent 43:153. https://doi.org/10.1186/s42269-019-0195-6

Singh I, Shah K (2014) Exogenous application of methyl jasmonate lowers the effect of cadmium-induced oxidative injury in rice seedlings. Phytochemistry 108:57–66

Svyatyna K, Riemann M (2012) Light-dependent regulation of the jasmonate pathway. Protoplasma 249:137–145

Taki N, Sasaki-Sekimoto Y, Obayashi T, Kikuta A, Kobayashi K, Ainai T, Yagi K, Sakurai N, Suzuki H, Masuda T, Takamiya KI (2005) 12-oxo-phytodienoic acid triggers expression of a distinct set of genes and plays a role in wound-induced gene expression in *Arabidopsis*. Plant Physiol 139:1268–1283

Todaka D, Shinozaki K, Yamaguchi-Shinozaki K (2015) Recent advances in the dissection of drought-stress regulatory networks and strategies for development of drought-tolerant transgenic rice plants. Front Plant Sci 6:84

Valenzuela CE, Acevedo-Acevedo O, Miranda GS, Vergara-Barros P, Holuigue L, Figueroa CR, Figueroa PM (2016) Salt stress response triggers activation of the jasmonate signaling pathway leading to inhibition of cell elongation in *Arabidopsis* primary root. J Exp Bot 67(14):4209–4220. https://doi.org/10.1093/jxb/erw202

Velitchkova M, Fedina I (1998) Response of photosynthesis of *Pisum sativum* to salt stress as affected by methyl jasmonate. Photosynthetica 35:89–97

Verstraeten I, Schotte S, Geelen D (2014) Hypocotyl adventitious root organogenesis differs from lateral root development. Front Plant Sci 5:495

Vidoz ML, Loreti E, Mensuali A, Alpi A, Perata P (2010) Hormonal interplay during adventitious root formation in flooded tomato plants. Plant J 63:551–562

Walia H, Wilson C, Condamine P, Liu X, Ismail AM, Close TJ (2007) Large-scale expression profiling and physiological characterization of JA-mediated adaptation of barley to salinity stress. Plant Cell Environ 30:410–421

Wang CY, Buta JG (1994) Methyl jasmonate reduces chilling injury in *Cucurbita pepo* through its regulation of abscisic acid and polyamine levels. Environ Exp Bot 34:427–432

Wang SY (1999) Methyl jasmonate reduces water stress in strawberry. J Plant Growth Regul. 18(3):127–134

Wani SH, Kumar V, Shriram V, Sah SK (2016) Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. Crops J 4:162–176

Wasternack C (2014) Action of jasmonates in plant stress responses and development—applied aspects. Biotechnol Adv 32:31–39

Yan Z, Chen J, Li X (2013) Methyl jasmonate as modulator of cd toxicity in *Capsicum frutescens* var: *fasciculatum* seedlings. Ecotoxicol Environ Saf 98:203–209

Yan Z, Zhang W, Chen J, Li X (2015) Methyl jasmonate alleviates cadmium toxicity in *Solanum nigrum* by regulating metal uptake and antioxidative capacity. Biol Plant 59:373–381

Yoon JY, Hamayun M, Lee SK, Lee IJ (2009) Methyl jasmonate alleviated salinity stress in soybean. J Crop Sci Biotechnol 12:63–68

Youssef A, Laizet YH, Block MA, Maréchal E, Alcaraz JP, Larson TR, Pontier D, Gaffé J, Kuntz M (2010) Plant lipid-associated fibrillin proteins condition jasmonate production under photosynthetic stress. Plant J 61:436–445

Zhang XC, Millet YA, Cheng Z, Bush J, Ausubel FM (2015) Jasmonate signalling in *Arabidopsis* involves SGT1b–HSP70–HSP90 chaperone complexes. Nat Plants 1:15–49

Zhao ML, Wang JN, Shan W, Fan JG, Kuang JF, Wu KQ, Li XP, Chen WX, He FY, Chen JY, Lu W-J (2013) Induction of jasmonate signalling regulators MaMYC2s and their physical interactions with *MaICE1* in methyl jasmonate-induced chilling tolerance in banana fruit. Plant Cell Environ 36:30–51

Zimmerman PW, Hitchcock AE (1933) Initiation and stimulation of adventitious roots caused by unsaturated hydrocarbon gases. Contrib Boyce Thompson Inst 5:351–369

ABA: Metabolism, Regulation, and Functions in Crop Abiotic Stress Tolerance

18

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Abstract

Abiotic stresses exert negative effect on crop plantBs development and yield, and they are a major obstacle in catering to the global food demand. Plants have different tactics to deal with various kinds of stresses. ABA plays critical part in plant responses to different kinds of stresses. ABA acts as a mediator in signaling pathway of plant responses to stress. ABA acts by altering osmotic conditions of affected plants exposed to stress conditions. During stress conditions, ABA starts a signal transduction chain that stimulates expression of different stress resistance genes helpful in adaptation of plants to different kinds of stresses. The abiotic stress tolerance mechanism is composed of sophisticated signal transduction pathway having phoshorylating, dephosphorylating compounds, transcription factors, and other regulatory elements. Epigenetic regulations are also an important part of ABA-mediated stress adaptation mechanisms. Methylation of DNA, changes in chromatin besides post-transcriptional, post-translational control are different regulatory levels of ABA-mediated stress gene expression network. Because ABA has a central role in crop plant's abiotic stress tolerance strategy, genetic engineering at the level of ABA-mediated signal transduction pathway could be very useful in augmenting crop plants adaptation responses to stress. This review takes into account biosynthesis of ABA, its transport, and elements of ABA-directed signal transduction pathway. It also takes into account role of transcription factors in controlling ABA-directed signal transduction during

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abiotic stress, plant's reactions to abiotic stress at different steps of genetic biosynthesizing machinery, and part played by microRNAs.

Keywords

Abscisic acid · Abiotic stress · Biosynthesis · Phosphorylation · Regulation

18.1 Introduction

The world population is increasing at a rapid pace (United Nations Department of Economic and Social Affairs, and Population Division 2015), and for hunger requirements, global food generation through plants has to be enhanced significantly (Wani and Sah 2014). Extra food production in challenging climatic conditions and in limited resources has become the need of the recent times. However, challenges given by water shortage, saline conditions, and very high and decreased temperature conditions cause serious setback to crop yield, thus having adverse effect on fulfilling ever increasing food requirements globally (Tuteja 2007; Qin et al. 2011; Bailey-Serres et al. 2012). Abiotic stresses exert negative effect on yield due to adaptive responses in cells at physiolochemical and molecular levels (Hasanuzzaman et al. 2013). Therefore, encountering stress and devising strategies for stress-resistant crops, these stress resistance mechanism have to be understood in finer details (Wu et al. 2016).

Phytohormones are important in adaption to different stresses. Abscisic acid (ABA), a phytohormone, initiates adaptive responses, thus helpful in preventing crop plants yield losses (Sreenivasulu et al. 2012). Frederick Addicott first isolated ABA from cotton fruits which was observed to promote abscission (Ohkuma et al. 1963). ABA is observed in many lower and advanced plant groups. In cyanobacteria, salt stress enhanced ABA (Wolfram 2010). Many algal species possess ABA (Wolfram 2010). Salinity and drought induced ABA control stress-responsive genes. ABA initiates stomatal closure during water stress, thus preventing water loss (Sah et al. 2016). ABA mediates initiation and sustenance of seed dormancy (Matilla-Vázquez and Matilla 2009). SnRK2D/E/I, ABI5, LEA, PP2C, and HSP are some important compounds in regulation of seed development during water shortage (Trebichalský et al. 2017). ABA is involved in adaptation in root architecture in plants exposed to various stresses (Sah et al. 2016). ABA has positive effect on root length and decreases reactive oxygen species (ROS) (Harris 2015). ABA mediates initiation of senescence genes expression. Receptor kinase (RPK1), NAC-like, functionalized by apetala3/pistillata and SAG113, controlled ABA-mediated senescence (Sah et al. 2016). While encountering water shortage, ABA plays important role in changing ion equilibrium in stomatal guard cell, thus preventing unnecessary water scarcity (Kim et al. 2010). Strategy of preventing or reducing stomatal opening under drought stress includes protein kinases, anion channel and potassium channel proteins and CAT3 enzyme all of which are important in ABA mediated signaling especially stomatal response (Sah et al. 2016). CAT3 protects cellular damage from toxicity of hydrogen peroxide (Du et al. 2008). The membrane water channels aquaporins help in increased inflow of water and H_2O_2 in guard cells for ABA-stimulated closing of stomata (Verma et al. 2016). ABA can change functionality of aquaporins by changing their gene expression or alterations at post-transcriptional level (Sharipova et al. 2016).

ABA is helpful for plants in encountering stresses. Different osmotic stresses result in water loss at cellular level and stimulate plant ABA metabolism and enhancing transport of enzymes, generating osmo-protectants and subsequently reducing water loss at cellular level (Vishwakarma et al. 2017). Under environmental stress, in plants there is enhancement in induction in mRNA and corresponding increase in the enzymes of ABA biosynthesis, thus causing increase in level of ABA. The binding of enhanced ABA to its receptor starts signal transduction which subsequently results in cellular reactions (Ng et al. 2014). The plant growth regulator ABA exerts a positive regulatory effect on transcription factors, kinases, and phosphatases which are important in adaptative responses (Tuteja 2007). These compounds transmit many stress signals, subsequently controlling stress-stimulated genes (Pandey et al. 2017). ABA and various stresses cause elevation of calcium levels and calcium acts as secondary messenger during interactions in various types of stresses (Vishwakarma et al. 2017). Application of ABA to crops infested them with better adaptive responses (Khadri et al. 2006; Wei et al. 2015). Gaining detailed knowledge of ABA's importance in stress tolerance will contribute toward generating stress-tolerant crop plants which will be very much helpful in solving hunger problem globally (Hashiguchi and Komatsu 2016).

In the current review, biosynthesis, transport, signaling, and regulation of ABA and ABA-controlled gene networks in abiotic stress responses of crop plants have been discussed. Besides this, ABA regulation at epigenetic and post-transcriptional level and role of micro RNAs in ABA-mediated abiotic stress responses in crop plants has also been taken into account.

18.2 Metabolism of ABA

18.2.1 Biosynthesis of ABA

ABA is synthesized in plants in chloroplasts in fungi and animals (Li et al. 2011). ABA biosynthesis starts from plastids, and finally this process culminates in cytosol. In higher plants, ABA biosynthesis takes place through mevalonic acid-independent pathway (Nambara and Marion-Poll 2005). In abovementioned biosynthetic pathway, there is splitting of carotenoid precursor (C_{40}), originating through MEP pathway; after this there is change of xanthoxin to ABA (Seo and Koshiba 2002). Figure 18.1 exhibits ABA biosynthesis. The initial step in ABA biosynthetic sequence of reactions is the change of zeaxanthin and antheraxanthin to all trans-violaxanthin (Marin et al. 1996). Later, all trans-violaxanthin is transformed to 9-*cis*-violaxanthin or 9-*cis*-neoxanthin by an enzyme, knowledge about which is not deciphered (Seiler et al. 2011). Then, splitting of 9-cis-violaxanthin and/or 9-cis-neoxanthin results in the generation of xanthoxin (C_{15}). Xanthoxin is then shifted to cytosol (Nambara and Marion-Poll 2005) and transformed to ABA in two

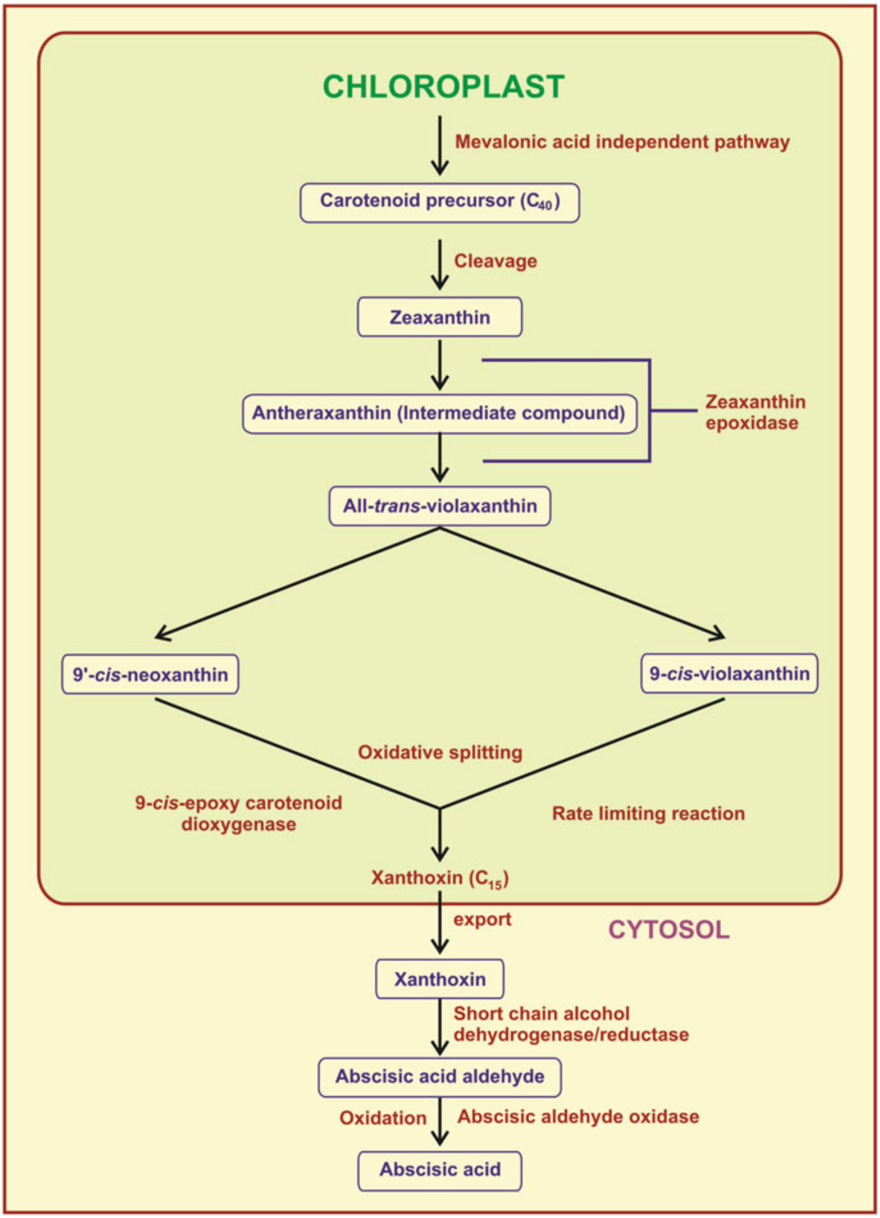

Fig. 18.1 Abscisic acid biosynthetic pathway in plants

steps. Initially, xanthoxin is transformed to ABA aldehyde (Cheng et al. 2002; Gonzalez-Guzman et al. 2002), and then abscisic aldehyde oxidizes to ABA.

18.2.2 ABA Catabolism

When plants are no more encountering stress, ABA is inactivated (Ng et al. 2014). The conversion of ABA into inactive products involves hydroxylation and conjugation (Nambara and Marion-Poll 2005).

Hydroxylation of ABA takes place through oxidation of C-70, C-80, and C-90 methyl groups. C-80 pathway is the main catalytic pathway (Okamoto et al. 2009). Phaseic acid and dihydrophaseic acid are chief ABA catabolites observed in the 80-hydroxylation pathway (Saito et al. 2004). Cytochrome P450 type enzyme (CYP707A) is involved in ABA metabolism (Kushiro et al. 2004). When enough water levels are restored, stomatal and foliar *CYP707A* gene expression controls the metabolism (Okamoto et al. 2011). The functional ABA is enhanced by glucosidase functionalization through stress-stimulated polymerization (Lee et al. 2006). Okamoto et al. (2009) observed that CYP707A3 decreases vascular systematic ABA. Under enhanced humidity conditions, CYP707A1 degrades local ABA in guard cells. Conjugation is another method for inactivation of ABA. It is operative under normal as well as in water loss scenarios (Xu et al. 2012). Glycosyltransferase enzyme is involved in formation of ABA glucosyl ester (ABA-GE). ABA-GE is stored in vacuoles (Boursiac et al. 2013). When encountering abiotic stress, ABA from ABA glucosyl ester is released by enzymatic hydrolysis. The glycosidase enzyme is involved in this hydrolytic transformation. This enzyme has been observed in barley (Dietz et al. 2000) and in *Arabidopsis* (Xu et al. 2012).

The equilibrium in biosynthetic and degrading reactions decides the quantity of endogenous ABA. ABA glucosyl ester and phaseic acid, obtained after catabolic reactions, release bound ABA (catalyzed by glucosidase) during water shortage, resulting in closure of stomata.

18.3 Transport of ABA

While encountering stress conditions, the availability of ABA in plants is critical to the adaptive response of plants to stress. ABA transporters are associated with ABA transport (passive and active transport). Besides specific transporters, process of diffusion is also involved in entry of ABA into cells. Weak acid ABA being protonated can cross biological membranes in a passive mode (Ng et al. 2014). Even when specific transporter is not available, ABA can pass to the exterior of cells upon sensing pH changes (Seo and Koshiba 2011).

ATP-binding cassettes (ABC) having transporter proteins are involved in movement of ABA in case of *Arabidopsis* (Kuromori et al. 2010). Many ABA transporter genes of the ABC group are observed in *A. thaliana*. A half-dimension ABC transporter protein coded by *Arabidopsis* ABA exporter gene *(*At ABCG25*)* is involved in export of ABA from vascular tissues (Kuromori et al. 2010), while *Arabidopsis* ABA importer gene (AtBCG40) encodes a full-dimension ABC transporter, which is part of ABA import system in plants (Kang et al. 2010). AtABCG22 also helps in ABA transport and stomatal control (Kuromori et al. 2011). Subsequently, ABCG16 was observed to be part of ABA tolerance machinery (Ji et al. 2014). Four AtABCG proteins have been observed to work cumulatively to make ABA available in developed imbibed seeds (Kang et al. 2015). They showed that AtABCG25 and AtABCG31 work as exporter proteins, and they are helpful in exporting ABA from endosperm to embryo; on the other hand, AtABCG30 and AtABCG40 are importer proteins, involved in influx of ABA inside the embryo. Besides ABA transporters of the ABC group, other kinds of ABA transporters have also been observed, the example of which is ABA-importing transporter (AIT1) which is a type of transporter of the NRT1 (nitrate transporter1) transporter family (Kanno et al. 2012). Another transporter, AtDTX50, was also observed to be involved in ABA movement in *Arabidopsis* (Zhang et al. 2014). Therefore, many kinds of transporters are found to be associated with ABA movement in plants.

18.4 ABA Signaling

ABA signaling is very important in ABA-mediated responses. The mechanism of ABA signaling has been elucidated by many relevant studies done previously (Umezawa et al. 2010; Liu 2012). ABA signaling system consists of PYR/PYL/RCAR, PP2C (negative controller), and SnRK2 (positive regulator). They aggregate in a signaling complex named "ABA signalosome." While ABA is present, PYR/PYL/RCAR-PP2C aggregate results in adverse effect on PP2C, resulting in functionalization of SnRK2 (Danquah et al. 2014). Functional SnRK2 then phosphorylates transcription factors, and subsequently transcription of ABA-mediated genes is resulted.

18.5 ABA Receptors

Ma et al. (2009) and Park et al. (2009) separately reported ABA receptor. They observed *Arabidopsis* PYR1, PYL, or RCAR proteins as ABA receptors. *Arabidopsis* harbors 14 PYR/PYL/RCAR genes (Ma et al. 2009; Park et al. 2009). Several PYR/PYL/RCAR group of proteins (collectively referred to as PYLs) directly attach to ABA (Miyazono et al. 2009; Santiago et al. 2009). Associated with ABA, above-mentioned PYL receptors can attach to PP2C, enzymes adversely affecting ABA signaling. The PP2C group includes ABI1 (ABA-insensitive1) and ABI2 (Nishimura et al. 2010). Many *pyr* and *pyl* mutants have exhibited insensitivity to ABA which points toward the fact that abovementioned ABA receptors are involved in ABA sensing (Gonzalez-Guzman et al. 2012). They show less sensitivity in germination, root growth adaptations to ABA (Gonzalez-Guzman et al. 2012). Enhanced expression of PYL5, PYL8/PYL9 corresponds with heightened ABA responses and drought hardiness in *A. thaliana* (Santiago et al. 2009; Saavedra et al. 2010). Increased RCAR1/PYL1, PYL5/RCAR8 or PYL8/RCAR3 expression imparts elevated drought adaptiveness in *A. thaliana*. PYR/PYL/RCAR group in *Arabidopsis* can stimulate ABA signaling, which points toward the fact that almost all members of this family are ABA receptors (Fujii et al. 2009). PYR/PYL/RCAR can correspond with ABI1 in ABA-dependent way or in a constitutive fashion. Similar observations are exhibited in *A. thaliana* (Nishimura et al. 2010). Structural and molecular investigations have strengthened the fact that PYR/PYL/RCAR receptors are critically involved in ABA sensing (Ma et al. 2009; Nishimura et al. 2009; Park et al. 2009).

When encountered with water and salinity stress, the ABA levels are enhanced, thus transmitting signal induced by stress. The genes whose expression is controlled by ABA are named as ABA-responsive genes. ABA-directed stress genes have cis-elements like ABRE, found at their upstream region with core sequence PyACGTGGC and coupling elements. AREB protein interacts with this sequence. The distance between ACGT cis-elements has a significant bearing on their induction by different compounds (Mehrotra and Mehrotra 2010). Specificity in attachment of bZIP group members to ACGT core sequence is provided by flanking sequences (Suzuki et al. 2005).

18.6 PP2C

Protein phosphorylation is an important cellular control mechanism which involves activation/deactivation of various enzymes and receptors by phosphorylation and dephosphorylation. The kinase enzymes catalyze phosphorylation, while phosphatase enzymes are involved in dephosphorylation events. Thus, reversible protein phosphorylation is at the center of cellular signal transduction. This signal transduction phenomenon is responsible for the conduction of signals to the inside of the cell, thus causing cellular changes in response to stimulus like different kinds of stresses.

In *A. thaliana,* genes for PP2Cs belong to ten categories (A–J). PP2Cs are basically related to a kind of PPM group of phosphatases. PP2Cs like ABI1, ABI2, AHG3/PP2CA, AHG1, HAB1, and HAB2 belong to group A (Schweighofer et al. 2004; Yoshida et al. 2006b). Many APP2Cs members especially ABI1, ABI2, and HAB1 help in ABA signaling. ABI1, ABI2, and HAB1 are involved in ABA signaling in tissue-specific manner (Ng et al. 2014). HAB1 negatively controls ABA signaling. This is strengthened by observations in recessive *hab1–1* mutants having increased ABA-responsive gene expression including enhanced closing of stomata and heightened ABA-sensitivity in seed germination (Saez et al. 2004; Hirayama and Shinozaki 2007). Group APP2Cs members adversely affect ABA signaling, and this is strengthened by observations of significant ABA hypersensitivity in functional knockdown mutants of APP2C members (Yoshida et al. 2006b; Antoni et al. 2012). The overexpression of a group APP2C from rice gene (*OsPP108*) under salinity and drought stresses results in loss of response to ABA and resistance to salinity and osmotic stress (Singh et al. 2015). *A. thaliana* PP2C, AP2C1 negatively control MAPK (MAPK4 and MAPK6) (Schweighofer et al. 2004), thus indicating toward involvement of PP2Cs in cold and drought stress adaptive responses. The adverse effect of PP2Cs on ABA signaling is universal. It has been corroborated by the observation of non-functionalization of stress-induced MAPK (SAMK) pathway by a PP2C coding gene MP2C through storage of MP2C phosphatase, thus stopping signal transmission (Meskiene et al. 1998).

18.7 SnRK2 Protein Kinases

Protein kinase enzymes are important in ABA signaling. The SnRK2 are serine/threonine kinases important in plants facing water shortage scenarios (Saruhashi et al. 2015).

ABA functionalized first protein kinase AAPK was reported in *Vicia faba*. AAPK positively controls ABA-stimulated stomatal closing (Li et al. 2000). *Arabidopsis* AAPK ortholog, OST1/SnRK2.6, is associated with ABA-directed control of stomata (Yoshida et al. 2002). These protein kinases propagate ABA signaling by adding phosphate group to their substrate proteins (Fujita et al. 2013). The ABA-activated protein kinases PKABA1 and AAPK phosphorylate and functionalize transcription factor TaABF (related to ABA signaling in seeds) and an RNA-binding protein AKIP1 (resulting into its influx into guard cells), respectively (Johnson et al. 2002; Li et al. 2000, 2002).

The SnKR2 family consists of three subgroups. Subgroup I shows no response to ABA; on the other hand, subgroup III shows active response to ABA and plays important role in ABA-mediated gene expression, subgroup II less weakly reacts to or shows no reaction to ABA (Kulik et al. 2011). In *A. thaliana*, 10 SnRK2 members were observed. Among the abovementioned members, SnRK 2.2, SnRK2.3, SnRK2.6, SnRK2.7, and SnRK2.8 exhibit active response to ABA. Almost all of the SnRK2 members except SnRK 2.9 can be functionalized upon encountering osmotic stress, which points toward their critical role in ABA and stress signaling (Furihata et al. 2006; Yoshida et al. 2006a). Because SnRK 2.2, SnRK 3.3, and SnRK 2.6 (subgroup III) have been observed to most strongly functionalize ABA, they have been designated as primary regulators of ABA (Boudsocq et al. 2004). OST1/SnRK2.6, included in *Arabidopsis* SnRK2 family, is a positive controller of stomatal response to ABA signaling, which is supported by observations that mutant *snrk2.6* (*ost1*) does not show ABA-directed stomatal closure (Mustilli et al. 2002). ABA-functionalized SnRK2 kinases add phosphate groups to ABFs/AREBs and ABA15 transcription factors. ABFs/AREBs transcription factors control ABA-responsive genes (Wang et al. 2014).

Observations in research studies in *Arabidopsis* point toward strong possibility that at least these 3SnRK2s, ABI1, and many receptor proteins of PYR/PYL/RCARs may constitute a core signaling aggregate (Nishimura et al. 2010; Joshi-Saha et al. 2011). It was observed that addition of phosphate group to the activation site is important for functionalizing SnRK2s, e.g., activation of SnRK2.6 in presence of ABA. On the other hand, PP2C, by dephosphorylating activation site of SnRK2.6

without ABA, causes non-functionalization of SnRK2.6 (Umezawa et al. 2009; Vlad et al. 2010). It was observed that osmotic stress also enhances site phosphorylation (Vlad et al. 2010). Plasma membrane proteins important in stomatal movements are phosphorylated by SnRK2, e.g., SLAC1, KAT1, and NADPH oxidase AtrbohF (Sato et al. 2009; Sirichandra et al. 2009). ABA- or stress-functionalized SnRK2s are observed in many crop plants, *Arabidopsis*, and algae (Li et al. 2010; Mao et al. 2010; Zhang et al. 2010).

18.8 SnRK2 Regulation

ARK kinase controls SnRK2 in terrestrial vegetation in response to osmotic changes. ARK could functionalize SnRK2B and ABA signaling by phosphorylating SnRK2B (Saruhashi et al. 2015). CK2 kinase, which adversely affects SnRK2, is involved in the development and DNA repair in plants (Mulekar and Huq 2014; Vilela et al. 2015).

18.9 Transcription Factors in ABA-Mediated Responses

Transcription factors are chief regulators coordinating and helping in transmitting different types of signals in plants (Jaradat et al. 2013). By their specific attachment to *cis*-elements in promoters of concerned target genes, a transcription factor controls numerous genes (Udvardi et al. 2007). Some of transcription factors playing critical part in control of ABA-mediated responses are discussed in Table 18.1. High salinity, water stress, or ABA results in induction of AREB1/ABF2, AREB2/ABF4, and ABF3 transcription factors in vegetative tissues (Yoshida et al. 2010). Enhanced expression of ABF3 results in adaptive responses to low and elevated temperature and drought (Kim et al. 2004). Transcription factor ABP9 which belongs to bZIP group takes part in water shortage and heat adaptive responses, and it positively affects photosynthesis under stress scenarios in *Arabidopsis* (Zhang et al. 2008). ABI5, included in *Arabidopsis* bZIP transcription factor subfamily (Jakoby et al. 2002), plays critical part in responses to ABA or water stress in developed seeds and juvenile seedling (Lopez-Molina et al. 2001). ABI5 attaches to ABRE in its target genes and positively affects ABA-controlled transcription complexes (Finkelstein and Lynch 2000). Overexpression of rice ABI5 (OsABI5) results in adaptive responses to enhanced salinity conditions (Zou et al. 2008). MYC and MYB transcription factors, included in bHLH (basic helix loop helix) subfamily, affect ABA signaling (Abe et al. 2003).

AtMYB60, AtMYB44, and AtMYB15 of the MYB group have been shown to control stomatal movements and ABA-directed responses to water shortage and salinity in *Arabidopsis* (Jaradat et al. 2013). AtMYC2 work as activator of transcription in ABA-stimulated gene expression in plants exposed to water shortage conditions in *Arabidopsis* (Abe et al. 2003). NAC transcription factors possibly play critical part in ABA transcriptional complex. AtNAC controls ABA- and

Table 18.1 Some important transcription factors in ABA-mediated responses

Transcription factor	Family/ subfamily	Adaptive responses affected by transcription factor	References
ABF3 (ABRE binding factors 3)	bZIP (basic leucine zipper) subfamily	Low temperature, elevated temperature, and drought	Kim et al. (2004)
ABP9 (ABA-responsive-element binding protein 9)	bZIP subfamily	Drought and heat stress positively affect photosynthesis in *Arabidopsis*	Zhang et al. (2008)
ABI5 (ABA-insensitive 5)	bZIP subfamily	Responses to ABA or water stress in mature seeds and juvenile seedling; adaptive response to increased salinity in rice	Finkelstein and Lynch (2000), Zou et al. (2008)
MYB (myeloblastosis) group (AtMYB60, AtMYB44, and AtMYB15)	bHLH (basic helix loop helix) subgroup	Stomatal movements, ABA-mediated responses to drought and salinity in *Arabidopsis*	Jaradat et al. (2013)
Arabidopsis MYC (myelocytomatosis) (AtMYC2)	bHLH subgroup	Activating transcription in ABA-stimulated gene expression during dehydration	Abe et al. (2003)
Arabidopsis NAC-type (AtNAC)	NAC family	Regulates ABA and senescence	Zhang and Gan (2012)
RAV1(related to *ABI3/ VP1*)	Ethylene-responsive factor (ERF) family	Negatively controls ABA signaling, decreases expression of ABA-responsive genes	Feng et al. (2005), Feng et al. (2014)

senescence-related genes (Zhang and Gan 2012). ABA in turn can stimulate expression of NAC transcription factors (Takasaki et al. 2015). Other transcription factors that control ABA signaling and ABA-mediated responses are *RhNAC3* transcription factor and ERF-type transcription factors (Song et al. 2005; Jiang et al. 2014).

In *Arabidopsis*, ABA-functionalized SnRK2s targets RAV1 transcription factor. On the other hand, it was observed that RAV1 negatively regulates ABA signaling and diminishes expression of ABA-responsive genes (Feng et al. 2005, 2014).

18.10 Post-Transcriptional and Post-Translational Control of ABA-Mediated Responses

RNA-binding proteins control gene expression at post-transcriptional level (Ambrosone et al. 2012), and in this way, they also take part in ABA-mediated responses. Mutation in *HYL1* gene encoding a RNA-binding protein resulted in heightened response to ABA during seed germination stage (Lu and Fedoroff 2000). Likewise, mutation in *SAD1* gene encoding a protein resembling to snRNP involving nuclear mRNA processing, enhanced responsiveness to ABA, and water shortage (Xiong et al. 2001). *Arabidopsis* mutant having abnormalities in mRNA cap-attaching protein, ABH1, exhibits ABA-hypersensitive control of seed germination and stomatal movements (Hugouvieux et al. 2001, 2002). Mutation in DEAD box RNA helicase gene *LOS4* caused increased ABA sensitivity and low temperature adaptiveness (Gong et al. 2005). ABA and abiotic stresses resulted in decreased expression of other DEAD-box RNA helicase genes (Kant et al. 2007).

AKIP1 is a hnRNP in *Vicia faba* which attaches to RNA and critically involved in ABA-mediated responses in crops (Li et al. 2000, 2002). SR proteins are another type of RNA-attaching proteins controlling splicing at post-transcriptional level and in ABA-mediated responses (Carvalho et al. 2010; Cruz et al. 2014). Regulation of targeted proteins by ubiquitination is also important in ABA-mediated responses (Yu et al. 2016).

18.11 Control of ABA Responses by Alterations at Epigenetic Level

Various chemical alterations of DNA and its associated proteins and modifications in functionality of genes due to these alterations are called epigenetics (Bonasio et al. 2010). DNA methylation, alterations of DNA associated histone proteins, and generation of microRNAs comes under category of epigenetic alterations (Yaish et al. 2011). Addition of methyl group to DNA (catalyzed by DNA methyltransferase) is designated as DNA methylation. Very low or enhanced DNA methylation results in decreased gene expression, while moderate methylation corresponds to enhance gene expression (Zemach et al. 2010). MicroRNAs (miRNAs) are few nucleotides long non-coding RNAs taking part in post-transcriptional regulation of gene expression either by target mRNA destruction or through repression at translational level (Bartel 2009). miRNAs can negatively regulate key epigenetic controllers like DNA methyltransferases and histone deacetylases, and in this way they take part in epigenetic control of gene expression (Sato et al. 2011). According to some important observations by researchers, epigenetic alterations like DNA methylation (Khraiwesh et al. 2010; Gohlke et al. 2013), histone alterations involving histone acetylation and deacetylation (Chen et al. 2010; Chen and Wu 2010), chromatin changes and nucleosome assembly proteins (Han et al. 2012; Liu et al. 2009), and micro-RNAs (Wei et al. 2009; Shen et al. 2010; Guo and Wang 2012) are important ways through which epigenetic control is exerted on ABA-related stress signaling complexes.

18.12 Interconnections Between ABA and MAPK Signaling Cascade

The mitogen-activated protein kinase (MAPK) cascade is a signaling method which exerts its control on cellular functions by sensing different stimuli like changes in osmotic levels of cells during stress (Hamel et al. 2012). This cascade is made up of kinases MAPK, MAPKK, and MAPKKK which take part in a phosphorylation transmission relay (Colcombet and Hirt 2008). ABA alters transcriptional control, protein aggregation, and stability of various components in MAPK cascade indicating toward their role in ABA signaling. The significance of MAPK cascade in ABA-mediated stress responses of plants will be further unveiled when functions of MAPK pathway genes will be elucidated (Wang et al. 2010; Danquah et al. 2014).

18.13 Conclusions

Due to growing population and climate change, food demand is increasing. Thus, enhanced food production including through crops exposed to abiotic stress conditions is required. Therefore, deciphering abiotic stress tolerance in crops has everlasting consequences. ABA is a phytohormone controlling various abiotic plant stresses. Due to molecular genetics, genomics, and proteomics, significant knowledge about the role of ABA in stress adaptation, especially to abiotic stress, has been achieved, although more is yet to be revealed. On the other hand, abiotic stress-altered expression of ABA biosynthetic genes is needed to be known in detail. ABA-mediated functionalization of genes at transcriptional level caused enhanced expression of other stress genes, thus contributing to stress adaptation. Transcription factors are significantly involved in crop abiotic stress adaptive responses. A detailed knowledge of role of epigenetics in mediating genome-environment interactions will be important in improving plant resistance to abiotic stresses. Deciphering interactions between RNA-binding proteins and targets will be helpful in elucidating ABA action during post-transcriptional control of ABA-mediated abiotic stress adaptive responses. The research progress in ABA signaling and regulation has further enriched the knowledge of molecular interactions during stress especially abiotic stress, which will be helpful in improving crop productivity.

References

Abe H, Urao T, Ito T, Seki M, Shinozaki K, Yamaguchi-Shinozaki K, Shinozaki KY (2003) *Arabidopsis* AtMYC2(bHLH) and AtMYB2(MYB) function as transcriptional activators in abscisic acid signaling. Plant Cell 15:63–78

Ambrosone A, Costa A, Leone A, Grillo S (2012) Beyond transcription: RNA-binding proteins as emerging regulators of plant response to environmental constraints. Plant Sci 182:12–18

Antoni R, Gonzalez-Guzman M, Rodriguez L, Rodrigues A, Pizzio GA, Rodriguez PL (2012) Selective inhibition of clade A phosphatases type 2C by PYR/PYL/RCAR abscisic acid receptors. Plant Physiol 158:970–980

Bailey-Serres J, Lee SC, Brinton E (2012) Waterproofing crops: effective flooding survival strategies. Plant Physiol 160:1698–1709. https://doi.org/10.1104/pp.112.208173

Bartel DP (2009) MicroRNAs: target recognition and regulatory functions. Cell 136:215–233

Bonasio R, Tu S, Reinberg D (2010) Molecular signals of epigenetic states. Science 330:612–616

Boudsocq M, Barbier-Brygoo H, Lauriere C (2004) Identification of nine sucrose nonfermenting1-related protein kinases2 activated by hyperosmotic and saline stresses in *Arabidopsis thaliana*. J Biol Chem 279:41758–41766

Boursiac Y, Leran S, Corratge-Faillie C, Gojon A, Krouk G, Lacombe B (2013) ABA transport and transporters. Trends Plant Sci 18:325–333

Carvalho RF, Carvalho SD, Duque P (2010) The plant-specific SR45 protein negatively regulates glucose and ABA signaling during early seedling development in *Arabidopsis*. Plant Physiol 154:772–783

Chen LT, Luo M, Wang YY, Wu K (2010) Involvement of *Arabidopsis* histone deacetylase HDA6 in ABA and salt stress response. J Exp Bot 61:3345–3353

Chen LT, Wu K (2010) Role of histone deacetylases HDA6 and HDA19 in ABA and abiotic stress response. Plant Signal Behav 5:1318–1320

Cheng WH, Endo A, Zhou L, Penney J, Chen HC, Arroyo A, Leon P, Nambara E, Asami T, Seo M, Koshiba T, Sheen J (2002) A unique short-chain dehydrogenase/reductase in *Arabidopsis* glucose signaling and abscisic acid biosynthesis and functions. Plant Cell 14:2723–2743

Colcombet J, Hirt H (2008) *Arabidopsis* MAPKs: a complex signaling network involved in multiple biological processes. Biochem J 413:217–226

Cruz TMD, Carvalho RF, Richardson DN, Duque P (2014) Abscisic acid (ABA) regulation of *Arabidopsis* SR protein gene expression. Int J Mol Sci 15:17541–17564

Danquah A, de Zelicourt A, Colcombet J, Hirt H (2014) The role of ABA and MAPK signaling pathways in plant abiotic stress responses. Biotechnol Adv 32:40–52

Dietz KJ, Sauter A, Wichert K, Messdaghi D, Hartung W (2000) Extracellular beta-glucosidase activity in barley involved in the hydrolysis of ABA-glucose conjugate in leaves. J Exp Bot 51: 937–944

Du Y-Y, Wang P-C, Chen J, Song C-P (2008) Comprehensive functional analysis of the catalase gene family in *Arabidopsis thaliana*. J Integr Plant Biol 50(10):1318–1326

Feng CZ, Chen Y, Wang C, Kong YH, Wu WH, Chen YF (2014) *Arabidopsis* RAV1 transcription factor, phosphorylated by SnRK2 kinases, regulates the expression of ABI3, ABI4, and ABI5 during seed germination and early seedling development. Plant J 80:654–668

Feng JX, Liu D, Pan Y, Gong W, Ma LG, Luo JC, Deng XW, Zhu YX (2005) An annotation update via cDNA sequence analysis and comprehensive profiling of developmental, hormonal or environmental responsiveness of the *Arabidopsis* AP2/EREBP transcription factor gene family. Plant MolBiol 59:853–868

Finkelstein RR, Lynch TJ (2000) The *Arabidopsis* abscisic acid response gene ABI5 encodes a basic leucine zipper transcription factor. Plant Cell 12:599–609

Fujii H, Chinnusamy V, Rodrigues A, Rubio S, Antoni R, Park S-Y, Cutler SR, Sheen J, Rodriguez PL, Zhu JK (2009) In vitro reconstitution of an abscisic acid signaling pathway. Nature 462: 660–664

Fujita Y, Yoshida T, Shinozaki KY (2013) Pivotal role of the AREB/ABF-SnRK2 pathway in ABRE-mediated transcription in response to osmotic stress in plants. Physiol Plant 147:15–27

Furihata T, Maruyama K, Fujita Y, Umezawa T, Yoshida R, Shinozaki K, Shinozaki KY (2006) Abscisic acid-dependent multisite phosphorylation regulates the activity of a transcription activator AREB1. Proc Natl Acad Sci U A 103:1988–1993

Gohlke J, Scholz C-J, Kneitz S, Weber D, Fuchs J, Hedrich R, Deeken R (2013) DNA methylation mediated control of gene expression is critical for development of crown gall tumors. PLoS Genet 9:e1003267

Gong Z, Dong CH, Lee H, Zhu J, Xiong L, Gong D, Stevenson B, Zhu JK (2005) A DEAD box RNA helicase is essential form RNA export and important for development and stress responses in *Arabidopsis*. Plant Cell 17:256–267

Gonzalez-Guzman M, Apostolova N, Belles JM, Barrero JM, Piqueras P, Ponce MR, Micol JL, Serrano R, Rodriguez PL (2002) The short-chain alcohol dehydrogenase ABA2 catalyzes the conversion of xanthoxin to abscisic aldehyde. Plant Cell 14:1833–1846

Gonzalez-Guzman M, Pizzio GA, Antoni R, Vera-Sirera F, Merilo E, Bassel GW, Fernandez MA, Holdsworth MJ, Perez-Amador MA, Kollist H, Rodriguez PL (2012) *Arabidopsis* PYR/PYL/RCAR receptors play a major role in quantitative regulation of stomatal aperture and transcriptional response to abscisic acid. Plant Cell 24:2483–2496

Guo L, Wang X (2012) Cross talk between phospholipase D and sphingosine kinase in plant stress signaling. Front Plant Sci 3:51

Hamel LP, Nicole MC, Duplessis S, Ellis BE (2012) Mitogen-activated protein kinase signaling in plant-interacting fungi: distinct messages from conserved messengers. Plant Cell 24:1327–1351

Han SK, Sang Y, Rodrigues A, Wu MF, Rodriguez PL, Wagner D (2012) The SWI2/SNF2 chromatin remodeling ATPase BRAHMA represses abscisic acid responses in the absence of the stress stimulus in *Arabidopsis*. Plant Cell 24:4892–4906

Harris JM (2015) Abscisic acid: hidden architect of root system structure. Plan Theory 4:548–572

Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M (2013) Physiological, biochemical and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci 14:9643–9684. https://doi.org/10.3390/ijms14059643

Hashiguchi A, Komatsu S (2016) Impact of post-translational modifications of crop proteins under abiotic stress. Proteomes 4:42

Hirayama T, Shinozaki K (2007) Perception and transduction of abscisic acid signals: keys to the function of the versatile plant hormone ABA. Trends Plant Sci 12:343–351

Hugouvieux V, Kwak JM, Schroeder JI (2001) An mRNA cap binding protein, ABH1, modulates early abscisic acid signal transduction in *Arabidopsis*. Cell 106:477–487

Hugouvieux V, Murata Y, Young JJ, Kwak JM, Mackesy DZ, Schroeder JI (2002) Localization, ion channel regulation, and genetic interactions during abscisic acid signaling of the nuclear mRNA cap-binding protein, ABH1. Plant Physiol 130:1276–1287

Jakoby M, Weisshaar B, Dröge-Laser W, Vicente-Carbajosa J, Tiedemann J, Kroj T, Parcy F, bZIP Research Group (2002) bZIP transcription factors in *Arabidopsis*. Trends Plant Sci 7:106–111

Jaradat MR, Feurtado JA, Huang D, Lu Y, Cutler AJ (2013) Multiple roles of the transcription factor AtMYBR1/AtMYB44 in ABA signaling, stress responses, and leaf senescence. BMC Plant Biol 13:192

Ji H, Peng Y, Meckes N, Allen S, Stewart CN Jr, Traw MB (2014) ATP dependent binding cassette transporter G family member 16 increases plant tolerance to abscisic acid and assists in basal resistance against *Pseudomonas syringae* DC 3000. Plant Physiol 166:879–888

Jiang X, Zhang C, Lü P, Jiang G, Liu X, Dai F, Gao J (2014) RhNAC3, a stress-associated NAC transcription factor, has a role in dehydration tolerance through regulating osmotic stress-related genes in rose petals. Plant Biotechnol J 12:38–48

Johnson RR, Wagner RL, Verhey SD, Walker-Simmons MK (2002) The abscisic acid-responsive kinase PKABA1 interacts with a seed-specific abscisic acid response element-binding factor, TaABF, and phosphorylates TaABF peptide sequences. Plant Physiol 130:837–846

Joshi-Saha A, Valon C, Leung J (2011) A brand new START: abscisic acid perception and transduction in the guard cell. Sci Signal 4:re4

Kang J, Hwang JU, Lee M, Kim YY, Assmann SM, Martinoia E, Lee Y (2010) PDR-type ABC transporter mediates cellular uptake of the phytohormone abscisic acid. Proc Natl Acad Sci U S A 107:2355–2360

Kang J, Yim S, Choi H, Kim A, Lee KP, Lopez-Molina L, Martinoia E, Lee Y (2015) Abscisic acid transporters cooperate to control seed germination. Nat Commun 6:8113

Kanno Y, Hanada A, Chiba Y, Ichikawa T, Nakazawa M, Matsui M, Koshiba T, Kamiya Y, Seo M (2012) Identification of an abscisic acid transporter by functional screening using the receptor complex as a sensor. Proc Natl Acad Sci U S A 109:9653–9658

Kant P, Kant S, Gordon M, Shaked R, Barak S (2007) STRESS RESPONSE SUPPRESSOR1 and STRESS RESPONSE SUPPRESSOR2, two DEAD-box RNA helicases that attenuate *Arabidopsis* responses to multiple abiotic stresses. Plant Physiol 145:814–830

Khadri M, Tejera NA, Lluch C (2006) Alleviation of salt stress in common bean (*Phaseolus vulgaris*) by exogenous abscisic acid supply. J Plant Growth Regul 25:110–119

Khraiwesh B, Arif MA, Seumel GI, Ossowski S, Weigel D, Reski R, Frank W (2010) Transcriptional control of gene expression by microRNAs. Cell 140:111–122

Kim S, Kang J-Y, Cho D-I, Park JH, Kim SY (2004) ABF2, an ABRE-binding bZIP factor, is an essential component of glucose signaling, and its overexpression affects multiple stress tolerance. Plant J 40:75–87

Kim TH, Bohmer M, Hu H, Nishimura N, Schroeder JI (2010) Guard cell signal transduction network: advances in understanding abscisic acid, CO_2, and Ca^{2+} signaling. Annu Rev Plant Biol 61:561–591

Kulik A, Wawer I, Krzywinska E, Bucholc M, Dobrowolska G (2011) SnRK2 protein kinases-key regulators of plant response to abiotic stresses. OMICS 15:859–872

Kuromori T, Miyaji T, Yabuuchi H, Shimizu H, Sugimoto E, Kamiya A, Moriyama Y, Shinozaki K (2010) ABC transporter ATABCG25 is involved in abscisic acid transport and responses. PNAS 107:2361–2366

Kuromori T, Sugimoto E, Shinozaki K (2011) *Arabidopsis* mutants of AtABCG22, an ABC transporter gene, increase water transpiration and drought susceptibility. Plant J 67:885–894

Kushiro T, Okamoto M, Nakabayashi K, Yamagishi K, Kitamura S, Asami T, Nobuhiro H, Tomokazu K, Kamiya U, Nambara E (2004) The *Arabidopsis* cytochrome P450CYP707A encodes ABA 8′- hydroxylases: key enzymes in ABA catabolism. EMBO J 23:1647–1656

Lee KH, Piao HL, Kim HY, Choi SM, Jiang F, Hartung W, Hwang I, Kwak JM, Lee I-J, Hwang I (2006) Activation of glucosidase via stress-induced polymerization rapidly increases active pools of abscisic acid. Cell 126:1109–1120

Li H-H, Hao R-L, Wu S-S, Guo P-C, Chen C-J, Pan L-P, Ni H (2011) Occurrence, function and potential medicinal applications of the phytohormone abscisic acid in animals and humans. Biochem Pharmacol 82:701–712

Li J, Kinoshita T, Pandey S, Ng CK-Y, Gygi SP, Shimazaki KI, Assmann SM (2002) Modulation of an RNA-binding protein by abscisic-acid activated protein kinase. Nature 418:793–797

Li J, Wang XQ, Watson MB, Assmann SM (2000) Regulation of abscisic acid-induced stomatal closure and anion channels by guard cell AAPK kinase. Science 287:300–310

Li L-B, Zhang YR, Liu KC, Ni ZF, Fang ZJ, Sun QX, Gao JW (2010) Identification and bioinformatics analysis of SnRK2 and CIPK family genes in sorghum. Agric Sci China 9:19–30

Liu Y (2012) Roles of mitogen-activated protein kinase cascades in ABA signaling. Plant Cell Rep 31:1–12

Liu ZQ, Gao J, Dong AW, Shen WH (2009) A truncated *Arabidopsis* NUCLEOSOME ASSEMBLY PROTEIN1, AtNAP1;3T, alters plant growth responses to abscisic acid and salt in the Atnap1;3-2 mutant. Mol Plant 2:688–699

Lopez-Molina L, Mongrand S, Chua NH (2001) A post germination developmental arrest checkpoint is mediated by abscisic acid and requires the ABI5 transcription factor in *Arabidopsis*. Proc Natl Acad Sci U S A 98:4782–4787

Lu C, Fedoroff N (2000) A mutation in the *Arabidopsis* HYL1 gene encoding a dsRNA binding protein affects responses to abscisic acid, auxin, and cytokinin. Plant Cell 12:2351–2365

Ma Y, Szostkiewicz I, Korte A, Moes D, Yang Y, Christmann A, Grill E (2009) Regulators of PP2C phosphatase activity function as abscisic acid sensors. Science 324:1064–1068

Mao X, Zhang H, Tian S, Chang X, Jing R (2010) TaSnRK2.4*, an SNF*1-type serine/threonine protein kinase of wheat (*Triticum aestivum* L.), confers enhanced multistress tolerance in *Arabidopsis*. J Exp Bot 61:683–696

Marin E, Nussaume L, Quesada A, Gonneau M, Sotta B, Hugueney P, Frey A, Marion-Poll A (1996) Molecular identification of zeaxanthin epoxidase of *Nicotiana plumbaginifolia*, a gene involved in abscisic acid biosynthesis and corresponding to the ABA locus of *Arabidopsis thaliana*. EMBO J 15:2331–2342

Matilla-Vázquez M, Matilla A (2009) Seed dormancy and ABA signaling: the breakthrough goes on. Plant Signal Behav 4:1035–1049

Mehrotra R, Mehrotra S (2010) Promoter activation by ACGT in response to salicylic and abscisic acids is differentially regulated by the spacing between two copies of the motif. J Plant Physiol 167:1214–1220

Meskiene I, Boegre L, Glaser W, Balog J, Brandstoetter M, Zwerger K, Ammerer G, Hirt H (1998) MP2C, a plant protein phosphatase 2C, functions as a negative regulator of mitogen-activated protein kinase pathways in yeast and plants. Proc Natl Acad Sci U S A 95:1938–1943

Miyazono K-I, Miyakawa T, Sawano Y, Kubota K, Kang H-J, Asano A, Miyauchi Y, Takahashi M, Zhi Y, Fujita Y, Yoshida T, Kodaira KS, Shinozaki KY, Tanokura M (2009) Structural basis of abscisic acid signaling. Nature 462:609–614

Mulekar JJ, Huq E (2014) Expanding roles of protein kinase CK2 in regulating plant growth and development. J ExpBot 65:2883–2893

Mustilli A-C, Merlot S, Vavasseur A, Fenzi F, Giraudat J (2002) Arabidopsis OST1 protein kinase mediates the regulation of stomatal aperture by abscisic acid and acts upstream of reactive oxygen species production. Plant Cell 14:3089–3099

Nambara E, Marion-Poll A (2005) Abscisic acid biosynthesis and catabolism. Annu Rev Plant Biol 56:165–170

Ng LM, Melcher K, The BT, Xu HE (2014) Abscisic acid perception and signaling: structural mechanisms and applications. Acta Pharmacol Sin 35:567–584

Nishimura N, Hitomi K, Arvai AS, Rambo RP, Hitomi C, Cutler SR, Schroeder JI, Getzoff ED (2009) Structural mechanism of abscisic acid binding and signaling by dimeric PYR1. Science 326:1373–1379

Nishimura N, Sarkeshik A, Nito K, Park SY, Wang A, Carvalho PC, Lee S, Caddell DF, Cutler SR, Chory J, Yates JR, Schroeder JI (2010) PYR/PYL/RCAR family members are major *in-vivo* ABI1 protein phosphatase 2C-interacting proteins in *Arabidopsis*. Plant J 61:290–299

Ohkuma K, Lyon JL, Addicott FT, Smith OE (1963) AbscisinII, an abscission-accelerating substance from young cotton fruit. Science 142:1592–1593

Okamoto M, Kushiro T, Jikumaru Y, Abrams SR, Kamiya Y, Seki M, Nambara E (2011) ABA 9′-hydroxylation is catalyzed by CYP707A in *Arabidopsis*. Phytochemistry 72:717–722

Okamoto M, Tanaka Y, Abrams SR, Kamiya Y, Seki M, Nambara E (2009) High humidity induces abscisic acid 8′-hydroxylase in stomata and vasculature to regulate local and systemic abscisic acid responses in *Arabidopsis*. Plant Physiol 149:825–834

Pandey N, Iqbal Z, Pandey BK, Sawant SV (2017) Phytohormones and drought stress: plant responses to transcriptional regulation. In: Pandey GK (ed) Mechanism of plant hormone signaling under stress. Wiley, Hoboken, pp 477–504

Park S-Y, Fung P, Nishimura N, Jensen DR, Fujii H, Zhao Y, Lumba S, Santiago J, Rodrigues A, Chow T-FF, Alfred SE, Bonetta D, Finkelstein R, Provart NJ, Desveaux D, Rodriguez PL, McCourt P, Zhu JK, Schroeder JI, Volkman BF, Cutler SR (2009) Abscisic acid inhibits PP2Cs via the PYR/PYL family of ABA-binding START proteins. Science 324:1068–1071

Qin F, Shinozaki K, Yamaguchi-Shinozaki K (2011) Achievements and challenges in understanding plant abiotic stress responses and tolerance. Plant Cell Physiol 52:1569–1582

Saavedra X, Modrego A, Rodríguez D, González-García MP, Sanz L, Nicolás G, Lorenzo O (2010) The nuclear interactor PYL8/RCAR3 of *Fagus sylvatica* FsPP2C1 is a positive regulator of abscisic acid signaling in seeds and stress. Plant Physiol 152:133–150

Saez A, Apostolova N, Gonzalez-Guzman M, Gonzalez-Garcia MP, Nicolas C, Lorenzo O, Rodriguez PL (2004) Gain of function and loss of function phenotypes of the protein phosphatase 2C HAB1 reveal its role as a negative regulator of abscisic acid signaling. Plant J 37: 354–369

Sah SK, Reddy KR, Li J (2016) Abscisic acid and abiotic stress tolerance in crop plants. Front Plant Sci 7:571

Saito S, Hirai N, Matsumoto C, Ohigashi H, Ohta D, Sakata K, Mizutani M (2004) *Arabidopsis* CYP707As encode (+)-abscisic acid 8′-hydroxylase, a key enzyme in the oxidative catabolism of abscisic acid. Plant Physiol 134:1439–1449

Santiago J, Rodrigues A, Saez A, Rubio S, Antoni R, Dupeux F, Park SY, Marquez JA, Cutler SR, Rodriguez PL (2009) Modulation of drought resistance by the abscisic acid receptor PYL5 through inhibition of clade APP2Cs. Plant J 60:575–588

Saruhashi M, Ghosh TK, Arai K, Ishizaki Y, Hagiwara K, Komatsu K, Shiwa Y, Izumikawa K, Yoshikawa H, Umezawa T, Sakata Y, Takezawa D (2015) Plant Raf-like kinase integrates abscisic acid and hyperosmotic stress signaling upstream of SNF1-related protein kinase2. Proc Natl Acad Sci U S A 112:E6388–E6396

Sato A, Sato Y, Fukao Y, Fujiwara M, Umezawa T, Shinozaki K, Hibi T, Taniguchi M, Miyake H, Goto DB, Uozumi N (2009) Threonine at position 306 of the KAT1 potassium channel is essential for channel activity and is a target site for ABA-activated SnRK2/OST1/SnRK2.6 *protein kinase*. Biochem J 424:439–448

Sato F, Tsuchiya S, Meltzer SJ, Shimizu K (2011) MicroRNAs and epigenetics. FEBS J 278:1598–1609

Schweighofer A, Hirt H, Meskiene I (2004) Plant PP2C phosphatases: emerging functions in stress signaling. Trends Plant Sci 9:236–240

Seiler C, Harshavardhan VT, Rajesh K, Reddy PS, Strickert M, Rolletschek H, Scholz U, Wobus U, Sreenivasulu N (2011) ABA biosynthesis and degradation contributing to ABA homeostasis during barley seed development under control and terminal drought-stress conditions. J Exp Bot 62:2615–2632

Seo M, Koshiba T (2002) Complex regulation of ABA biosynthesis in plants. Trends Plant Sci 7: 41–48

Seo M, Koshiba T (2011) Transport of ABA from the site of biosynthesis to the site of action. J Plant Res 124:501–510

Sharipova G, Veselov D, Kudoyarova G, Fricke W, Dodd IC, Katsuhara M, Furuichi T, Ivanov I, Veselov S (2016) Exogenous application of abscisic acid (ABA) increases root and cell hydraulic conductivity and abundance of some aquaporin isoforms in the ABA-deficient barley mutant Az34. Ann Bot 118(4):777–785

Shen J, Xie K, Xiong L (2010) Global expression profiling of rice microRNAs by one-tube stem-loop reverse transcription quantitative PCR revealed important roles of microRNAs in abiotic stress responses. Mol Genet Genomics 284:477–488

Singh A, Jha SK, Bagri J, Pandey GK (2015) ABA inducible rice protein phosphatase 2C confers ABA insensitivity and abiotic stress tolerance in *Arabidopsis*. PLoS One 10:e0125168

Sirichandra C, Gu D, Hu HC, Davanture M, Lee S, Djaoui M, Valot B, Zivy M, Leung J, Merlot S, Kwak JM (2009) Phosphorylation of the *Arabidopsis* AtrbohF NADPH oxidase by OST1protein kinase. FEBS Lett 583:2982–2986

Song C-P, Agarwal M, Ohta M, Guo Y, Halfter U, Wang P, Zhu JK et al (2005) Role of an *Arabidopsis* AP2/EREBP-type transcriptional repressor in abscisic acid and drought stress responses. Plant Cell 17:2384–2396

Sreenivasulu N, Harshavardhan VT, Govind G, Seiler C, Kohli A (2012) Contrapuntal role of ABA: does it mediate stress tolerance or plant growth retardation under long-term drought stress? Gene 506:265–273

Suzuki M, Ketterling MG, McCarty DR (2005) Quantitative statistical analysis of cis-regulatory sequences in ABA/VP1- and CBF/DREB1-regulated genes of *Arabidopsis*. Plant Physiol 139: 437–440

Takasaki H, Maruyama K, Takahashi F, Fujita M, Yoshida T, Nakashima K, Myouga F, Toyooka K, Shinozaki KY, Shinozaki K (2015) SNAC-As, stress-responsive NAC transcription factors, mediate ABA-inducible leaf senescence. Plant J 84:1114–1123

Trebichalský P, Tóth T, Bajčan D, Harangozo Ľ, Vollmannová A (2017) Hormonal changes in spring barley after triazine herbicide treatment and its mixtures of regulators of polyamine biosynthesis. Potravinarstvo Slovak J Food Sci 11:156–161

Tuteja N (2007) Abscisic acid and abiotic stress signaling. Plant Signal Behav 2:135–138

Udvardi MK, Kakar K, Wandrey M, Montanari O, Murray J, Andriankaja A, Zhang JY, Benedito V, Hofer JMI, Chueng F, Town CD (2007) Legume transcription factors: global regulators of plant development and response to the environment. Plant Physiol 144:538–549

Umezawa T, Nakashima K, Miyakawa T, Kuromori T, Tanokura M, Shinozaki K, Shinozaki KY (2010) Molecular basis of the coreregulatory network in ABA responses: sensing, signaling and transport. Plant Cell Physiol 51:1821–1839

Umezawa T, Sugiyama N, Mizoguchi M, Hayashi S, Myouga F, Shinozaki KY, Ishihama Y, Hirayama T, Shinozaki K (2009) Type 2C protein phosphatases directly regulate abscisic acid-activated protein kinases in *Arabidopsis*. Proc Natl Acad Sci U S A 106:17588–17593

United Nations, Department of Economic and Social Affairs, and Population Division (2015) World population prospects: the 2015 revision, key findings and advance tables. Working paper, no. ESA/P/WP.241. United Nations Department of Economic and Social Affairs, New York

Verma V, Ravindran P, Kumar PP (2016) Plant hormone-mediated regulation of stress responses. BMC Plant Biol 16:86

Vilela B, Nájar E, Lumbreras V, Leung J, Pagès M (2015) Casein kinase2 negatively regulates abscisic acid-activated SnRK2s in the core abscisic acid-signaling module. Mol Plant 8:709–721

Vishwakarma K, Upadhyay N, Kumar N, Yadav G, Singh J, Mishra RK, Kumar V, Verma R, Upadhyay RG, Pandey M, Sharma S (2017) Abscisic acid signaling and abiotic stress tolerance in plants: a review on current knowledge and future prospects. Front Plant Sci 8:161

Vlad F, Droillard MJ, Valot B, Khafif M, Rodrigues A, Brault M, Michel Z, Rodriguez PL, Merlot S, Lauriere C (2010) Phospho-site mapping, genetic and *in planta* activation studies reveal key aspects of the different phosphorylation mechanisms involved in activation of SnRK2s. Plant J 63:778–790

Wang J, Ding H, Zhang A, Ma F, Cao J, Jiang M (2010) A novel mitogen-activated protein kinase gene in maize (*Zea mays*), ZmMPK3, is involved in response to diverse environmental cues. J Integr Plant Biol 52:442–452

Wang Y, Chang H, Hu S, Lu X, Yuan C, Zhang C, Wang P, Xiao W, Xiao L, Xue G-P, Guo X (2014) Plastid casein kinase 2 knockout reduces abscisic acid (ABA) sensitivity, thermotolerance, and expression of ABA- and heat-stress-responsive nuclear genes. J Exp Bot 65:4159–4175

Wani SH, Sah SK (2014) Biotechnology and abiotic stress tolerance in rice. J Rice Res 2:1105. https://doi.org/10.4172/jrr.1000e105

Wei L, Wang L, Yang Y, Wang P, Guo T, Kang G (2015) Abscisic acid enhances tolerance of wheat seedlings to drought and regulates transcript levels of genes encoding ascorbate-glutathione biosynthesis. Front Plant Sci 6:458

Wei L, Zhang D, Xiang F, Zhang Z (2009) Differentially expressed miRNAs potentially involved in the regulation of defense mechanism to drought stress in maize seedlings. Int J Plant Sci 170: 979–989

Wolfram H (2010) The evolution of abscisic acid (ABA) and ABA function in lower plants, fungi and lichen. Funct Plant Biol 37:806–810

Wu Y, Zhao J, Yan Z, Zhu Y (2016) Impact of imidacloprid seed dressing treatment on soil microorganisms and enzyme activities in the maize rhizosphere. Open Biotechnol J 10:266–271

Xiong L, Gong Z, Rock CD, Subramanian S, Guo Y, Xu W, Galbraith D, Zhu JK (2001) Modulation of abscisic acid signal transduction and biosynthesis by an Sm-like protein in *Arabidopsis*. Dev Cell 1:771–781

Xu ZY, Lee KH, Dong T, Jeong JC, Jin JB, Kanno Y, Kim DH, Kim SY, Seo M, Bressan RA, Yun DJ, Hwang I (2012) A vacuolar beta-glucosidase homolog that possesses glucose-conjugated abscisic acid hydrolyzing activity plays an important role in osmotic stress responses in *Arabidopsis*. Plant Cell 24:2184–2199

Yaish MW, Colasanti J, Rothstein SJ (2011) The role of epigenetic processes in controlling flowering time in plants exposed to stress. J Exp Bot 62:3727–3735

Yoshida R, Hobo T, Ichimura K, Mizoguchi T, Takahashi F, Aronso J, Ecker JR, Shinozaki K (2002) ABA-activated SnRK2 protein kinase is required for dehydration stress signaling in *Arabidopsis*. Plant Cell Physiol 43:1473–1483

Yoshida R, Umezawa T, Mizoguchi T, Takahashi S, Takahashi F, Shinozaki K (2006a) The regulatory domain of SRK2E/OST1/SnRK2.6 interacts with ABI1 and integrates ABA and osmotic stress signals controlling stomatal closure in *Arabidopsis*. J Biol Chem 281:5310–5318

Yoshida T, FujitaY SH, Kidokoro S, Maruyama K, Mizoi J, Shinozaki K, Shinozaki KY (2010) AREB1, AREB2, and ABF3 are master transcription factors that cooperatively regulate ABRE-dependent ABA signaling involved in drought stress tolerance and require ABA for full activation. Plant J 61:672–685

Yoshida T, Nishimura N, Kitahata N, Kuromori T, Ito T, Asami T, Shinozaki K, Hirayama T (2006b) ABA-hypersensitive germination3 encodes a protein phosphatase 2C (AtPP2CA) that strongly regulates abscisic acid signaling during germination among *Arabidopsis* protein phosphatase 2Cs. Plant Physiol 140:115–126

Yu F, Wu Y, Xie Q (2016) Ubiquitin-proteasome system in ABA signaling: from perception to action. Mol Plant 9:21–33

Zemach A, McDaniel IE, Silva P, Zilberman D (2010) Genome-wide evolutionary analysis of eukaryotic DNA methylation. Science 328:916–919

Zhang H, Mao X, Wang C, Jing R (2010) Overexpression of a common wheat gene TaSnRK2.8 enhances tolerance to drought, salt and low temperature in *Arabidopsis*. PLoS One 5:e16041

Zhang H, Zhu H, Pan Y, Yu Y, Luan S, Li L (2014) ADTX/MATE-type transporter facilitates abscisic acid efflux and modulates ABA sensitivity and drought tolerance in *Arabidopsis*. Mol Plant 7:1522–1532

Zhang K, Gan S-S (2012) An abscisic acid-AtNAP transcription factor-SAG113 protein phosphatase 2C regulatory chain for controlling dehydration in senescing *Arabidopsis* leaves. Plant Physiol 158:961–969

Zhang X, Wollenweber B, Jiang D, Liu F, Zhao J (2008) Water deficits and heat shock effects on photosynthesis of a transgenic *Arabidopsis thaliana* constitutively expressing ABP9, a bZIP transcription factor. J Exp Bot 59:839–848

Zou M, Guan Y, Ren H, Zhang F, Chen F (2008) A bZIP transcription factor, OsABI5, is involved in rice fertility and stress tolerance. Plant Mol Biol 66:675–683

Polyamines: Metabolism, Regulation, and Functions in Crop Abiotic Stress Tolerance

19

Swati Sinha and Maneesh Mishra

Abstract

Polyamines are small, positively charged, organic compounds containing more than two amino groups. They are omnipresent in plants and produced during various metabolic processes. Environmental fluctuations owing to greenhouse gases, pollution, deforestation, and global warming are known to hamper plants' normal growth, production, and developmental processes causing various forms of abiotic stresses such as drought, salinity, heat, cold, osmolarity, etc. Polyamines are considered important to plants as they provide support in maintaining normal growth and development of plants even during stressed conditions. They play crucial role whether present at endogenous levels or fortified exogenously to plants utilizing plant tissue culture or genetic transformation techniques. Although they are regarded important for plants, still their mode of action and regulation during plant stress conditions is still not well understood. In this chapter, their endogenous production, mode of action and regulation is described at length so as to facilitate a broader and clearer picture to the researchers to understand the importance of them in combating various abiotic stresses in plants.

Keywords

Polyamines · Abiotic stress tolerance · Putrescine · Spermidine · Spermine

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19.1 Introduction

Polyamines (PAs) are polycationic aliphatic amines. They are present in plants abundantly and take part in major plant growth and development processes. Spermidine (Spd), spermine (Spm) and putrescine (Put) are common polyamines apparently involved in plant responses to microbial symbionts that are critical for plant nutrition (El Ghachtoul et al. 1996), and are involved in molecular signaling events in interactions between plants and pathogens (Martin-Tanguy 1987). PAs are important for plant growth development and environmental stresses as well (Evans and Malmberg 1989; Galston and Kaur-Sawhney 1990). PAs are synthesized from the amino acids ornithine or arginine. Their capacities to neutralize acids and act as antioxidant agents—as well as their roles in membrane/cell wall stabilization—make them indispensable for normal functioning of cells. DNA has an overall negative charge due to phosphate group attached to it (Basu et al. 1990; Pohjanpelto and Höltta 1996), so PAs tend to bind with DNA, thereby providing stability to the DNA helix (Beigbeder 1995; Tassoni et al. 1996) and pectic polysaccharides (D'Oraci and Bagni 1987). They have been shown to be involved in protein phosphorylation (Ye et al. 1994), post-transcriptional modifications (Mehta et al. 1994), and conformational transition of DNA (Basu et al. 1990). There is direct evidence that they are essential for growth and development in prokaryotes and eukaryotes (Tabor and Tabor 1984; Heby and Persson 1990; Tiburcio et al. 1990; Slocum 1991). PAs are considered to be signaling molecules, especially in stress situations (Evans and Malmberg 1989; Galston and Kaur-Sawhney 1995).

Naturally occurring PAs play pivotal role in plant metabolism such as effects on the tolerance mechanism to abiotic stresses (Meloni et al. 2003; Zeid 2004; Jiuju and Shirong 2005; Duan et al. 2007; Roychoudhury et al. 2011).

Abiotic stresses such as soil salinity, cold, frost injury, drought, acidity, and heavy metal affect plant growth, development, and productivity. Since these conditions produce stress and result in extensive losses to many agriculturally important crops, they have been the main subject of intense research. The accumulation of some functional substances, such as compatible solute, protective proteins, and polyamines, is an important element of the physiological and biochemical response to the stressful conditions. Polyamines have been proposed as a new category of plant growth regulators which are active in physiological processes, such as embryogenesis, cell division, morphogenesis, and development (Bais and Ravishankar 2002; Liu et al. 2006a). Though the physiological significance of polyamines in stress is not thoroughly understood, much progress has been made. The focus in the present paper is on progress concerning the involvement and potential role of polyamines in plant responses to abiotic stresses.

19.2 Polyamine Biosynthesis and Metabolism in Plants

Polyamine biosynthesis in plants is documented. Put is produced either directly from ornithine-by-ornithine decarboxylase (ODC, EC 4.1.1.17) or indirectly from arginine-by-arginine decarboxylase (ADC, EC 4.1.1.19) with two intermediates, agmatine and *N*-carbamoyl putrescine, and two corresponding biosynthetic enzymes, agmatine iminohydrolase (EC 3.5.3.12) and *N*-carbamoylputrescine amidohydrolase (EC 3.5.1.53) (Malmberg et al. 1998; Martin-Tanguy 2001). Put is converted into Spd via spermidine synthase (SPDS, EC 2.5.1.16) with the addition of an aminopropyl moiety provided by decarboxylated *S*-adenosylmethionine (dcSAM), which is catalyzed by *S*-adenosylmethionine decarboxylase (SAMDC, EC 4.1.1.50) using *S*-adenosylmethionine (SAM) as the substrate. Similarly, Spm is produced from Spd via spermine synthase (SPMS, EC 2.5.1.22) with the same aminopropyl moiety rendered by dcSAM. Apart from biosynthesis, polyamine degradation plays a crucial role in cellular polyamine titers regulation, which is primarily ascribed to two amine oxidases, diamine oxidase (DAO, EC 1.4.3.6), and polyamine oxidase (PAO, EC 1.5.3.11). DAO catalyzes the oxidation of Put to give pyrroline, which is further metabolized to g-aminobutyric acid (Cona et al. 2006) and PAO, and acts as a catalyst in the conversion of Spd and Spm to pyrroline and 1-(3 aminopropyl)-pyrroline, respectively, along with 1,3-diaminopropane in plants (Martin-Tanguy 2001; Šebela et al. 2001).

19.3 Polyamines Transport in Plants

It is estimated that PAs can be transported in long distances; the presence of large amounts of PAs has been observed in exudates of xylem and phloem sap; the vacuolar membrane had the highest capacity to transport them (Vladimir and Shevyakova 2007).

As per a study carried out in carrot cells, PAs (Put and Spd) flow through the cell by a transmembrane electrochemical gradient. Other research with maize roots, whose application of Put was performed exogenously, indicated that Put is transported through the plasma membrane by a process regulated by a protein carrier (Kusano et al. 2008). This carrier TPO1 of PAs is mainly located in vacuolar membrane and plasma membrane. Among the four PA carriers, those which are encoded by TPO2 and TPO3 are specific for Spm, while for Put, Spd and Spm are encoded by TPO1 and TPO4 (Uemura et al. 2005). TPO1 is dependent of pH (Uemura et al. 2005); in some research with lichen (*Evernia prunastri*), it was shown that the uptake of PAs depends on this variable (Kakkar et al. 1998). Uptake of Spr and Spd is performed at alkaline pH ($pH = 8.0$), while inhibition of only Spd was observed at acidic pH ($pH = 5.0$), next to the pH of the vacuoles found internally. This suggests that TPO1 carrier acts as a catalyst for polyamine excretion at acidic pH (Uemura et al. 2005). Put uptake occurred under different conditions of concentration and pH in African violet petals (*Saint pauliaionantha*), at a relatively lower concentration gradient (0.5–1.1 micromoles, $pH = 5.0–5.5$) and to a high concentration gradient (from 0.1 to 100 millimolar, pH = 8.0) (Kakkar et al. 1998); therefore, PAs show the ability as buffers or regulators (Pandey et al. 2000).

19.4 Polyamines in Stress Responses

There is creditable evidence confirming the role of PAs in stress tolerance. Scavenging of excess reactive oxygen species (ROS) is a direct strategy by which plants adapt to adverse environments. However, altering metabolism and accumulating beneficial metabolites, including PAs, are another ways of plants' defense mechanism. Often changes in PA metabolism and expression levels of their pathway genes are positively linked with enhanced tolerance of abiotic stresses in plants (Shi and Chan 2014). For example, overexpression of *FcWRKY70* resulted in Put accumulation to provide drought tolerance in *Fortunella crassifolia* (Gong et al. 2015). Spd promotes biomass accumulation and upregulates proteins involved in cell rescue. Spd was involved in inducing antioxidant enzymes in tomato (*Lycopersicon esculentum*) seedlings subjected to high-temperature conditions (Sang et al. 2017). Exogenous Spm treatment induced defense mechanism and caused resistance against a root rot pathogen, *Phytophthora capsici,* in *Capsicum annuum* (Koc et al. 2017). Furthermore, Spd was found to be vital for adjustment of intracellular PA pathways and endogenous PA homeostasis, which enhanced salt tolerance in rice (Saha and Giri 2017).

19.5 Mode of Action of Polyamines in Stress Responses

PAs are reported to protect plants against stress through mechanisms including the following:

1. Polycationic PAs are known to bind anionic molecules such as nucleic acids and proteins, thus stabilizing them. This property may be important in preventing stress-induced damage to these macromolecules. Spd and Spm have been shown to prevent radiation and oxidative stress-induced strand breaks in DNA.
2. PAs are involved in the regulation of membrane transport in plants. They have been shown to block two slow and fast vacuolar cation channels. The effect of PAs is direct, and the channels open when PAs are withdrawn. PAs also affect vacuolar and plasma membrane H^+ and Ca^{2+} pumps and have been reported to bring about stomatal closure in response to drought stress by blocking the activity of a KAT1-like inward K^+ channel in the guard cell membrane. This is an indirect effect caused by low-affinity PA binding to the channel protein.
3. PAs are known to modulate ROS homeostasis. They are known for inhibiting metals auto-oxidation, thereby reducing the required electron supply for ROS generation. PAs are known to induce antioxidant enzymes in stress situations, as evidenced by use of inhibitors of PA biosynthesis or transgenics overexpressing enzymes involved in PA biosynthesis. For example, application of D-arginine,

which is an inhibitor of PA biosynthesis enzymes, resulted in reduced levels of PAs and increased levels of ROS. In addition, *ADC* overexpression influences increased tolerance to drought stress, causing reduced ROS generation in transgenic plants. PAs, especially Spm have roles as signaling molecules which activate the antioxidant machinery. Generation of H_2O_2 by PA catabolism, which may be promoted when PA levels are above a specific threshold, is known to play an essential role in signaling cascade regulation during abiotic and biotic stress conditions. Additionally, abiotic stresses often induce accumulation of abscisic acid (ABA) and nitric oxide (NO) and the interactions between them. PAs trigger protective responses, including regulation of the channels for ion homeostasis and stomatal responses to enhance and maintain water content, thereby inducing the antioxidant machinery to check excessive ROS generation, with compatible osmolytes synthesis and accumulation. All of these phenomena occur to cascade the abiotic stress tolerance of plants (Shi and Chan 2014).

19.6 Polyamines and Abiotic Stress

Polyamines modulate the plant's response to much broader range of abiotic stresses than expected, viz., drought, salinity, heavy metal toxicity, oxidative stress, chilling injury, high temperature, osmotic stress, water logging, and flooding tolerance as proved either by exogenous application of polyamines or by development of transgenic plants overexpressing the genes involved in polyamine biosynthesis (Gill and Tuteja 2010a, b). Increased or decreased levels of PAs either act as a signal or as a messenger (to transmit the perceived signals from the sensors) to articulate the plants' behavioral response spatially and temporally either to avoid or overcome stress. Modulated endogenous polyamine (free or conjugated or bound) levels are known to be involved in formation of polyamine-RNA complexes, thereby generating structural changes in RNA at physiological concentrations of potassium and magnesium ions (Igarashi and Kashiwagi 2000). Covalent linkage of polyamines to various enzymes or proteins (post-translational modification) involved in physiological processes under normal or stressed conditions was catalyzed by transglutaminase (TGase; EC 2.3.2.13) class of enzymes (Beninati et al. 1985; Folk 1980). Of various abiotic environmental stimuli under which polyamines get modulated and thereby its cellular functions were mineral nutrient deficiency (Richards and Coleman 1952; Coleman and Hegarty 1957), metal toxicity (Choudhary et al. 2012a, b), salinity (Lefèvre et al. 2001; Hummel et al. 2004), high (Oshima 2007) and low temperature (Hummel et al. 2004), drought (Bhatnagar et al. 2008; Alcazar et al. 2010), hypoxia (Moschou et al. 2008), osmotic (Lefèvre et al. 2001), and oxidative factors (Moschou et al. 2008; Bouchereau et al. 1999). PAs, also change ion channels (Takahashi and Kakehi 2010), stimulate special kind of protein synthesis, stimulate assembly of 30S ribosomal subunits, and stimulate Ile-tRNA formation (Igarashi and Kashiwagi 2000). Also, modulated titers of polyamines in combination with epibrassinolides, active form of brassinosteroids, were reported to regulate abscisic acid (ABA) and indole-3-acetic acid (IAA) pathways which in turn enhances tolerance to metal toxicity (Choudhary et al. 2012a, b). PAs in combination with brassinosteroids besides modulating ABA and IAA pathways with their cascading effects for heavy metal tolerance also modulate levels of antioxidants like glutathione, ascorbic acid, proline, glycine-betaine, and antioxidant enzymes like glutathione reductase, peroxidase, catalase, and superoxide dismutase to cause stress tolerance (Choudhary et al. 2012a, b). Enhanced levels of polyamines either through exogenous feeding (Gill and Tuteja 2010a, b) or through heterologous expression of polyamine biosynthetic genes in transgenic plants (Liu et al. 2007) were reported to increase abiotic stress tolerance. However, the use of constitutively expressed promoters like CaMV35S, ubiquitin, and actin with polyamine biosynthetic genes toward stress tolerance may produce modulated polyamine levels even under normal conditions resulting in deleterious effects which causes reduced plant yield special concern toward agricultural crops (Katiyar et al. 1999).

19.7 Polyamines Involvement in Regulation of Plant Stress Tolerance and Adaptation

Abiotic and biotic stresses cause alterations in the normal physiological processes of all plant organisms, including the economically important crops. Plant damage and productivity decrease are most often due to naturally occurring unfavorable factors of the environment—natural stress factors. Plant organisms are also imposed to a large scale with new stressors related to human activity—anthropogenic stress factors. Independent of the type of stress, an increased production of reactive oxygen species (ROS) occurs in plants that alter their normal physiological functions, decrease the biosynthetic capacity of plant organisms, and cause damage that may lead to plant death (Mittler 2002; Fujita et al. 2006; Ahmad et al. 2008; Gill and Tuteja 2010a, b; Potters et al. 2010). In plants, ROS are generated mainly as by-products of various processes requiring high metabolic activity or elevated electron flow by electron transport chains. The major targets of deleterious ROS action are cellular macromolecules as phospholipids, proteins, and nucleic acids. Plant organisms possess a complex of antioxidant protective systems in order to cope with destructive effects of the unfavorable environmental conditions. Beside enzymatic antioxidants and nonenzymatic antioxidants, a significant number of studies provided evidence that PAs also contribute to plant stress tolerance as a part of defense mechanisms or adaptation programs that help plants to mitigate the negative stress consequences. Since all stresses limit plant growth and crop productivity, the efforts of many scientists are focused to minimize the negative stress effects. A promising strategy to enhance plant tolerance and adaptation to an unfavorable environment is the use of a transgenic and molecular genetic approach to increase the cellular PA concentrations (Table 19.1).

Table 19.1 Enhanced stress tolerance in transgenic plants engineered to overproduce polyamines (PAs) Source: Todorova et al. (2014)

Gene	Gene source	Transgenic plant	Increased tolerance	PAs overproduction
ADC	Oat	Rice	Salt tolerance	Put
ADC	Oat	Eggplant	Multiple abiotic stress tolerance, fungus wilt tolerance	Put, Spd (particularly conjugated forms), and free Spm fraction
ADC	Datura	Rice	Drought tolerance	Put, facilitating synthesis of Spm and Spd
ADC1	*Arabidopsis*	*Arabidopsis*	Freezing tolerance	Put
ADC2	*Arabidopsis*	*Arabidopsis*	Drought and cold tolerance	Put
PtADC	*Trifoliate orange*	Tobacco tomato	Improvement in dehydration and drought tolerance	Put
PtADC	*Trifoliate orange*	*Arabidopsis* adc 1–1 mutant	High osmoticum, drought, low temperature tolerance	Put
ODC	Mouse	Tobacco	Salinity tolerance	Put
SAMDC	Tritordeum	Rice	Salt tolerance	Spm and Spd
SAMDC	Human	Tobacco	Salt, drought, fungal wilt tolerance	Spd, put especially conjugated fraction
SAMDC	Carnation	Tobacco	Salt, cold, acidic, ABA tolerance	Put, Spd, and Spm
ySAMDC	Yeast	Tomato	High temperature tolerance	Spm and Spd after exposure to high temperature
MdSAMDC2	Apple	Tobacco	Low temperature, salt, osmotic tolerance	Free put, Spd, and Spm
SAMDC1	*Arabidopsis*	*Arabidopsis*	Salt, dehydration, ozone tolerance	Spm
MdSAMDC1	Apple	European pear	Salt, osmotic tolerance	Spd
MdSAMDC1	Apple	European pear	Multiple abiotic stress (salt, osmotic, Cu) tolerance	Spd
MdSAMDC1	Apple	European pear	Al tolerance	Spd
MdSAMDC1	Apple	European pear	Heavy metal (Cd, Pb, Zn) tolerance	Spd
MdSAMDC1	Apple	Tomato	Salinity tolerance	Spd and Spm
SPDS	Figleaf gourd	*Arabidopsis*	Chilling, freezing, salinity, hyperosmosis, drought, paraquat tolerance	Conjugated Spd

(continued)

Table 19.1 (continued)

Gene	Gene source	Transgenic plant	Increased tolerance	PAs overproduction
SPDS (FSPD1)	Figleaf gourd	Sweet potato	Chilling heat	Spd
SAMS (SsSAMS2)	*Suaeda salsa*	Tobacco	Salt tolerance	Free Spm, Spd, and put

19.8 Abiotic Stress

19.8.1 Mineral Nutrient Deficiency

Since macro- and micronutrients are of paramount importance for normal plant growth and development, insufficient mineral nutrition affects all physiological processes in plants. To cope with mineral deficiency, plants usually augment PAs in response to nutrient shortage of potassium, boron, calcium, magnesium, and phosphorus (Wimalasekera et al. 2011). Boron deficiency caused an accumulation of free and conjugated Put and Spd (Camacho-Cristobal et al. 2005). Polyamines are also incremented by lower P-supply in roots and shoots of *Plantago lanceolata* L. (Bratek and Lang 2003). Plants grown on soils with low Ca concentration due to acidic deposition are exposed to multiple stress factors, and under these conditions, plants produce stress-related N-rich metabolites like Put, arginine, γ-aminobutyric acid, and proline in a species-particular manner for protection from toxic ammonia (Minocha et al. 2010). Potassium deficiency leads to increased levels of free PAs in *Betula pendula* and *Betula pubescens* (Sarjala and Kaunisto 2002) and cause a time-dependent pattern of Put accumulation during in vitro development of *Gentiana triflora* (Takahashi et al. 2012). Increased free-Put in potassium-deficient plants indicates that PAs are involved in maintenance of cation–anion balance in plant cells and conferred plant adaptation to ionic stress (Bouchereau et al. 1999).

19.8.2 Drought, Salt, Cold, and Osmotic Stress

Drought and salinity are widespread environmental constraints, and both cause reduced water potential and may lead to oxidative stress in plants (Lei 2008; Wang et al. 2011). The negative effects of salinity are deleterious involving complex mechanism, and they often come along ion toxicity. Drought increases accumulation of Na^+ in cells and also results in ion toxicity (Wang et al. 2003; Basu et al. 2010). An increase of PAs due to drought and osmotic stresses has been found in different plant tissues (Yang et al. 2007; Lei 2008; Sziderics et al. 2010; Ghosh et al. 2011). Moderate or severe drought increased lipid peroxidation but also proline and PAs in wheat seedlings (Todorova et al. 2008). Frequently, PA accumulation (primarily Spd and/or Spm) is associated with drought and salt tolerance, supporting the effect of

PAs in response to stress and tolerance mechanisms (Basu et al. 2010; Zhou and Yu 2010; Alet et al. 2011, 2012). Mutlu and Bozcuk (2007) noted that the concentrations of free, bound, and total Spm increased in roots of *Helianthus annuus* L. (salt-tolerant and salt-sensitive) treated with NaCl and assumed its role in diminishing the harsh consequences of salinity. Salt tolerance in sunflower plants was related to the excessive accumulation of PAs in roots which were grown under salt stress conditions. Accumulation of Spm and compatible solutes (sucrose, proline, mannitol, and raffinose) was shown to be main players in alleviating NaCl stress in *Populus tremula* (Jouve et al. 2004). The role of higher PAs in osmotic adjustment as compatible solutes has been suggested (Basu et al. 2010; Alcazar et al. 2011a; Hussain et al. 2011).

Recently, Gupta et al. (2012a) reported that NaCl and Spd spray in rice (salt-tolerant and salt- sensitive) led to phosphorylation of 42-kDa Ca^{+2}-independent SnRK2 in roots of rice because of Spd in response to NaCl. Gupta et al. (2012b) demonstrated the important role of Spd in regulation of salinity-mediated signaling in rice. The response of plant varieties differing in tolerance to drought or salinity includes Put accumulation for sensitive cultivars and increase of Spm and Spd for tolerant varieties of rice (Roy et al. 2005; Roychoudhury et al. 2008; Basu et al. 2010), wheat (Liu et al. 2004b), and barley (Liu et al. 2006). Zhou and Yu (2010) demonstrated that rise of free and conjugated Spd and Spm in vetiver grass leaves assist plants to cope with water deficit conditions. Conversely, withholding water for 1 week in the drought-sensitive crop pepper caused significant accumulation in Put and cadaverine in leaves of pepper (Sziderics et al. 2010). Legocka and Sobieszczuk-Nowicka (2012) documented reduced amounts of microsome- and thylakoid-associated PAs in *Zea mays* and *Phaseolus vulgaris* subjected to iso-osmotic concentrations of NaCl and sorbitol. The authors suggested that these cultivars are drought sensitive and noted that PAs associated with microsomes and thylakoids might be good markers of plant stress tolerance. In order to show the effect of ionic and osmotic components of salinity on free PAs, Lefèvre et al. (2001) studied short-term exposure of salt-resistant and salt-sensitive rice cultivars to PEG or iso-osmotic concentrations of NaCl and KCl. The authors demonstrated that both ion and PA concentrations were changed 3 h after ionic stresses and assumed that the ionic component may trigger short-term PA accumulation independent of the osmotic component. The authors reported that enhanced Put levels also depends on the plant tissue in rice treated with PEG, KCl, or NaCl; it was found in the roots of salt-resistant cultivar, whereas in shoots for salt-sensitive cultivar. Similarly, Hummel et al. (2004) showed that the major effect, even after long-term exposure of *Pringlea antiscorbutica* seedlings to salinity and osmotic stress, was the modification of PA distribution between roots and shoots. Higher PA content in roots was assumed to be a developmental response to stress, and their accumulation in roots facilitated reinitiation of root growth. In contrast, salinity resistance in rice exposed to short-term PEG, KCl, and NaCl was not related with Spm or Spd (Lefèvre et al. 2001). A relationship between stress-induced augmentation of Spd and Spm in transgenic plants and tolerance to drought stress was also demonstrated. In addition, Peremarti et al. (2009) generated transgenic rice plants overexpressing *DsSAMDC* in order to increase only higher PAs but not Put concentrations and noted accumulation of Spm, which facilitates drought recovery.

Alcazar et al. (2011b) analyzed *Arabidopsis* transcriptional profiles of PA biosynthetic genes and their metabolic fluxes through progressive drought acclimation with assessing the amounts of PAs in resurrection plant *Craterostigma plantagineum* and in PA biosynthetic mutants of *Arabidopsis*. The Put to Spm conversion in *Arabidopsis* coupled with Spm to Put back conversion has been proposed to participate in the drought stress response and to increase an effective PA recycling-loop during acclimation to water shortage. Involvement of Spm and Spd in maintaining ionic homeostasis by regulation of the activity of plasma membrane H^+-ATPase and vacuolar H^+-ATPase activities has been proposed as a general mechanism for salt tolerance and confirmed in different model systems (Roy et al. 2005; Liu et al. 2006; Janicka-Russak et al. 2010; Orsini et al. 2011). Similarly, due to experiments with PEG-treated drought-tolerant and drought-sensitive wheat cultivars, Liu et al. (2004a) reported that PAs conjugated to tonoplast vesicles correlate with maintenance of tonoplast H^+-ATPase and H^+-PPase activities in roots with enhanced osmotic stress tolerance in the plant. The authors could not detect Spm occurrence in wheat roots but free fractions of Spm- and Spd-enhanced osmotic stress tolerance in seedlings of the same cultivars (Liu et al. 2004b).

Yamaguchi et al. (2006, 2007) showed that the double knockout mutant of *Arabidopsis* (*acl5/spms*), which is unable to produce Spm, is hypersensitive to salinity and drought, but the addition of Spm specifically rescues the hypersensitive phenotype of mutant plants. The *acl5/spms* plant was shown to be Ca^{2+} deficient (Yamaguchi et al. 2006), and as a result of improper stomatal closure under drought conditions, it lost more water as compared to the control (Yamaguchi et al. 2007). The authors proposed a model for the defensive role of Spm in salinity and drought stress responses (Yamaguchi et al. 2006; Kusano et al. 2007).

The expression of certain genes is also induced by ABA treatment (Urano et al. 2003). The *ADC2*, *SPDS1*, and *SPMS* expression was examined in ABA-deficient (*aba2–3*) and ABA-insensitive (*abi1–1*) mutants exposed to water stress exhibiting decreased transcriptional induction in the stressed *aba2–3* and *abi1–1* mutants compared to the wild type, showing that ABA modulates polyamine metabolism at the transcription level by upregulating the expression of *ADC2*, *SPDS1*, and *SPMS* genes under water stress conditions (Alcázar et al. 2006a, b). In addition, Put accumulation, occurred as a result of drought, is also damaged in the *aba2–3* and *abi1–1* mutants in comparison with wild-type plants. All these observations show that upregulation of PA-biosynthetic genes and accumulation of Put under water stress are especially due to ABA-dependent responses. It is assumed that polyamine responses to salt stress are also ABA-dependent, since both *ADC2* and *SPMS* are produced by ABA. In fact, stress-responsive, drought-responsive (DRE), low temperature-responsive (LTR), and ABA-responsive elements (ABRE and/or ABRE related motifs) are there in the promoters of the polyamine biosynthetic genes (Alcázar et al. 2006). This strengthens the view that in response to drought and salt treatments, the expression of some of the genes in polyamine biosynthesis are controlled by ABA. Free Put levels are enhanced on cold treatment, and this corresponds with the introduction of *ADC* genes. Reduced expression of *NCED3* and several ABA-regulated genes was detected in the *adc1* mutants at low temperature. Complementation analyses of *adc1* mutants with ABA and mutual complementation of *aba2–3* mutant with Put supported the conclusion that diamine controls the levels of ABA in response to cold by modulating ABA biosynthesis at the transcriptional level (Cuevas et al. 2008, 2009). Certainly, Put and ABA are integrated in a positive feedback loop in which ABA and Put work synergistically for biosynthesis as a result of abiotic stress conditions that culminates a unique mode of operation of polyamines as regulators of ABA biosynthesis.

Liu et al. (2004a, b, c) reported that polyethylene glycol (PEG 6000) treatment (inducing water stress) significantly increased the free Spd and free Spm levels in the leaves of *Triticum aestivum* drought-tolerant cv. Yumai No. 18, whereas Yangmai No. 9 cv. (drought-sensitive) showed a significant increase of free Put. They suggested that free Spd, free Spm, and PIS-bound Put facilitated the osmotic stress tolerance of wheat seedlings. In response to PEG 6000 (20% w/v, 48 h)-mediated water stress condition in rice seedlings, Basu et al. (2010) showed that the salt-tolerant rice variety Pokkali accumulated the highest levels of Spd, Spm, and total PAs, while the Put level was the highest in the salt-sensitive variety IR-29 and induced maximally in the aromatic rice variety Pusa Basmati. In this respect, the aromatic variety behaved more closely to the sensitive variety. It was found that acquired tolerance to low water potential in potato cells leads to changes in Put biosynthesis and conjugation, which may be involved in ensuring cell survival (Gill and Tuteja 2010a, b). In case of *Theobroma cacao*, the expression of *TcODC*, *TcADC*, and *TcSAMDC* was induced with the onset of drought and correlated with the changes in stomatal conductance, photosynthesis, PSII efficiency, and leaf water potential. Induction of *TcSAMDC* in the leaves was more closely correlated with the changes in water potential (Bae et al. 2008). Yang et al. (2007) suggested that under drought conditions, the drought-resistant rice cultivars have the ability to respond early to water stress through increases in PA levels. Drought-resistant cultivars have higher SAMDC and SPDS activities and accumulated higher free Spd and free Spm in the leaves than drought-susceptible ones under water stress. The drought resistance in rice is therefore not only connected with PA levels but also with the response time at which PAs are significantly elevated. Vetiver grass can cope well with a moderate water-deficit conditions through maintenance of the total contents of free, conjugated, and bound Spd and Spm in leaves (Zhou and Yu 2010). In tolerant grapevine cultivars only, the higher PA-biosynthetic rate in the cellular compartment eliminates detrimental effects exerted by PAO-derived H_2O_2 in the apoplast. In the sensitive genotype, intracellular homeostasis of PAs is not restored, and their levels are insufficient to mitigate the intervening effects of H_2O_2 (Toumi et al. 2010). Endogenous levels of individual as well as total PAs in the roots of 7-day-old chickpea seedlings subjected to -0.8 MPa water stress increased significantly (Nayyar et al. 2005).

Using *Arabidopsis* has opened new vistas in functional dissection of the polyamine metabolic pathway and its role in the control of abiotic stress responses (Ferrando et al. 2004; Alcázar et al. 2006b; Kusano et al. 2008; Takahashi and

Kakehi 2010; Gill and Tuteja 2010a). Annotation of the *Arabidopsis* genome enabled complete compilation for the biosynthetic pathway of polyamine. Transcript prowling by using Q-RT-PCR has revealed that water stress induces the expression of *ADC2*, *SPDS1*, and *SPMS* genes (Alcázar et al. 2006a). The expression of some of these genes is also induced by ABA treatment (Perez-Amador et al. 2002; Urano et al. 2003). To get a further insight into ABA regulation of polyamine pathway, the expression of *SPMS, SPDS1*, and *ADC2* was investigated in the ABA-deficient (*aba2–3*) and ABA-insensitive (*abi1–1*) mutants subjected to water stress (Alcázar et al. 2006a). These three genes display reduced transcriptional induction in the stressed *aba2–3* and *abi1–1* mutants compared to the wild type, showing that ABA modulates polyamine metabolism at the transcription level by upregulating the expression of *ADC2*, *SPDS1*, and *SPMS* genes under water stress conditions (Alcázar et al. 2006a). In addition, Put accumulation in response to drought is also hampered in the *aba2–3* and *abi1–1* mutants compared to wild-type plants. This result is further supported by metabolomic studies showing that polyamine responses to dehydration are also impaired in *nced3* mutants (Urano et al. 2009). All these observations support the conclusion that upregulation of PA-biosynthetic genes and accumulation of Put under water stress are mainly ABA-dependent responses. Under salt stress conditions, there is a rapid increase in the expression of *ADC2* and *SPMS*, which is maintained during the 24-h treatment and results in increased Put and Spm levels (Urano et al. 2003). Spm-deficient mutants are salt sensitive, while the introduction of Spm suppresses the salt sensitivity, suggesting a protective role of Spm to high salinity (Yamaguchi et al. 2006).

It is evident that polyamine responses to salt stress are also ABA-dependent, since both *ADC2* and *SPMS* are induced by ABA (see above). In fact, stress-responsive, drought-responsive (DRE), low temperature-responsive (LTR), and ABA-responsive elements (ABRE and/or ABRE-related motifs) are available in the promoters of the polyamine biosynthetic genes (Alcázar et al. 2006b). This reinforces the view that in response to drought and salt treatments, the expression of some of the genes involved in polyamine biosynthesis are regulated by ABA. Transcript prowling has also revealed that cold enhances the expression of *ADC1*, *ADC2*, and *SAMDC2* genes (Urano et al. 2003; Cuevas et al. 2008, 2009). Free Put levels are enhanced on cold treatment, and this corresponds with the induction of *ADC* genes. Surprisingly, the levels of free Spd and Spm remain unchanged or even decrease in response to cold treatment. The absence of correlation between enhanced *SAMDC2* expression and the decrease of Spm levels could be a result of increased Spm catabolism (Cuevas et al. 2008). Since double mutants completely devoid of ADC activity are not viable in *Arabidopsis* (Urano et al. 2005), two independent mutant alleles for both *ADC1* and *ADC2* were used to study their response to freezing. As indicated in “polyamines and abiotic stress,” the *adc1* and *adc2* mutations caused higher sensitivity to freezing conditions, in both acclimated and non-acclimated plants, while addition of Put complemented this stress sensitivity (Cuevas et al. 2008, 2009). Reduced expression of *NCED3* and several ABA-regulated genes was found in the *adc1* mutants at low temperature. Complementation analyses of *adc1* mutants with ABA and reciprocal complementation of *aba2–3* mutant with Put supported the conclusion that this diamine controls the levels of ABA in response to cold by modulating ABA biosynthesis at the transcriptional level (Cuevas et al. 2008, 2009). All these results suggest that Put and ABA are integrated in a positive feedback loop, in which ABA and Put reciprocally promote each other's biosynthesis in response to abiotic stress. This highlights a novel mode of action of polyamines as regulators of ABA biosynthesis.

In general, cold-tolerant varieties show higher endogenous PA levels in response to low temperature than non-tolerant ones. Nayyar (2005) found that PA levels were enhanced by six to nine times in chickpea (*Cicer arietinum* L.) subjected to chilling temperatures. In poplar seedlings grown at 4 °C, Put accumulation occurred during the beginning of the cold treatment, while Spd and Spm accumulated after 4 or 7 days, respectively (Renaut et al. 2005). More recent quantitative expression analyses indicate that transcription of both *ADC1* and *ADC2* genes is produced as early as 30 min after cold exposure, the mRNA transcript levels of *ADC1* being higher than that of *ADC2*. The complementation analysis of *adc* mutants with ABA and reciprocal complementation tests of the *aba* 2–3 mutant with Put help the research finding of Put controls ABA levels in response to low temperature (Cuevas et al. 2008). However, data obtained by Kim et al. (2002) in tomato showed that ABA and Put affected cold-induced changes in cellular membranes of tomato leaves independently. The sequence analysis of the *ADC1* promoter revealed the presence of CRT/DRE, which could mediate the early and transient *ADC1* upregulation under cold stress (Alcázar et al. 2006b). Accumulation of Put was also observed in lucerne and wheat during cold hardening, in which a differential regulation of *ADC* activity could be detected between control and cold-treated plants. In a chilling-tolerant rice cultivar (Tainung 67), the *ADC* activity and Put levels increased during low temperature in both shoots and roots, while a chilling-sensitive cultivar (Taichung Native 1) showed a slight Put rise in shoots and a lowering in roots (Lee et al. 1997). Chilling induced the expression of all the three *ADC* genes (*MADC1, MADC2*, and *MADC3*) in *Brassica juncea*, whereas salt predominantly resulted in increased accumulation of *MADC3* transcript (Mo and Pua 2002). The low temperature also increased the Put level in cold-sensitive maize plants, especially when the stress occurred in light. Pillai and Akiyama (2004) suggested that the induction of the *OsSAMDC* gene in response to cold could be utilized as a molecular marker for the ability of rice seedlings to withstand low temperatures. In *Arabidopsis*, the expression of *SAMDC2* also increased after cold treatment. Cuevas et al. (2008) reported absence of correlation between enhanced *SAMDC2* expression and decrease of Spm levels in response to cold treatment, which may be a result of increased Spm catabolism. Shen et al. (2000) showed that chilling markedly increased Spd content concomitantly with a rise in SAMDC activity in the cold-tolerant cucumber cultivars (Jinchun No. 3) but not in sensitive ones (Suyo). This response is not mediated by ABA, since Spd pretreatment did not affect the content of ABA in cold-treated leaves of the cv. Suyo, and ABA content did not increase in the leaves of the cv. Jinchun No. 3. Imai et al. (2004) reported that a novel *SPDS* gene, *OsSPDS2* from rice, was involved in chilling response in roots. This gene is closely related to *AtSPDS3* or *At5g53120*, a putative *Arabidopsis SPDS* gene. Overexpression of *ZAT12*, a cold-inducible gene encoding a C2H2 zinc finger transcription factor (that contributes to an increased freezing tolerance), dampens the expression of the *CuAO* gene *At4G12280*, which shows sequence similarities to diamine oxidases. ZAT12 signaling promotes tolerance by activating a ZAT12 regulon, which includes *ADC1* and *ADC2* upregulation, leading to a resultant accumulation of Put (Alcázar et al. 2006b). Another cold inducible zinc finger protein called SCOF-1 has been reported from soybean (Kim et al. 2001).

Osmotic treatments using sorbitol induced high levels of Put and ADC in detached oat leaves (Flores and Galston 1984), whereas Spd and Spm show a dramatic decrease. Bouchereau et al. (1999) reported that osmotica with widely different assimilation routes, such as sorbitol, mannitol, proline, betaine, and sucrose, all induce a rise in Put. Such alterations are coincident with indications of stress, such as wilting and protein loss. Tiburcio et al. (1995) reported that when peeled oat leaves are incubated with sorbitol in the dark, they lose chlorophyll and senescence rapidly. Senescence could be slowed down by incorporating Spm in the incubation medium. The senescence-retarding effect of Spm was correlated with increase in the introduction of identified precursors into proteins, RNA, and DNA. They also inferred with rise in putrescine level and in particular its bound form to thylakoid membranes. A study by Schraudner et al. (1990) also discovered a correlation between ethylene emission, and PA biosynthesis was found in O^{3-} treated potato and tobacco plants, of which the leaves showed early senescence in response to the pollutant. In the presence of O_3, all compounds of ethylene biosynthetic pathway in tobacco leaves were upregulated. Put and Spd levels also increased, as did ornithine decarboxylase (ODC) activity (Bouchereau et al. 1999). Differences in PA (Put, Spd, Spm) response under salt stress have been reported among and within species. For example, according to Prakash and Prathapsenan (1988), endogenous levels of PAs (Put, Spd, and Spm) decreased in rice seedlings under NaCl stress, whereas Basu et al. (1988) found that salinity influences accumulation of such compounds in the same material (Bouchereau et al. 1999).

Santa-Cruz et al. (1997) reported that the (Spd + Spm):Put ratios increased with salinity in the salt-tolerant tomato species (*Lycopersicon pennellii*, Carrel D'Arcy) but not in the salt-sensitive tomato species (*L. esculentum*). In both species, stress treatments decreased the levels of Put and Spd. The Spm levels did not decrease with salinity in *L. pennellii* over the salinization period; however, it was found to decrease in *L. esculentum*. The effects of different NaCl concentrations on maize embryogenic cells obtained from immature embryo cultures of a salt-sensitive inbred line (cv. w64) and a resistant hybrid (cv, Arizona) have also been reported where increased salt concentration strongly reduced the growth of the calluses and resulted in a significant increase in the total PA (Put, Spd) content, especially caused by a rise in Put. A study conducted by Bouchereau et al. (1999) revealed that incorporating the inhibitors of Put synthesis, the ADC pathway in tomato plants functions appropriately in both stress and control conditions, whereas the ODC pathway is stimulated only under the stress conditions.

19.9 Heavy Metals

Metal contamination of soils has considerably increased due to human activities, and heavy metal excess also provoked changes in PA metabolism. Abundance of PAs in different plants cultivated on abundant heavy metals and their effect in regulation of plant tolerance and adaptation to metal stress is well studied. Cadmium excess led to increase in Put, which was accompanied by a respective decrease in higher PAs in *Potamogeton crispus* L. (Yang et al. 2010). The activities of PAO and DAO increased categorically with the rise in Cd concentrations, and authors suggested that some PAs and their forms impart an important role in the adaptation mechanism of *P. crispus* under Cd-stress.

In experiments with tobacco BY-2 cells exposed to Cd, a marked accumulation of total PAs during 3-day treatment was observed (Kuthanová et al. 2004). The increase in PA levels was because of Put which was coincident with DAO activity. Cd treatment increased PAs in roots and leaves of *Salix alba* L., whereas in *Populus nigra* L., only the Put content was significantly enhanced in roots (Zacchini et al. 2011). Lefèvre et al. (2009) also observed that the halophyte *Atriplex halimus* exposed to Cd accumulated free PAs. Probably the resistance of *A. halimus* to Cd toxicity was related to the improved tissue tolerance through increase in the synthesis of osmoprotective compounds like PAs. Polyamine concentrations in mung bean plants grown on medium supplied with Cd was also higher than these found in control plants and negatively correlated with the activity of DAO (Choudhary and Singh 2000).

Increased contents of Ni, Zn, Cu, and Cd in soil increased the accumulation of Put and Spm in spinach and barley (Bergmann et al. 2001). Groppa et al. (2007a, b, 2008) found that PA metabolism was differently affected in wheat and sunflower discs subjected to either Cu or Cd. Put content increased significantly in sunflower plants after Cd and Cu treatments, Spd was modified only by Cd, while Spm was affected by Cu or Cd and rose at 16 days after the germination of seeds (Groppa et al. 2007b). Both ADC and ODC activities were increased by Cd, whereas Cu enhanced ADC but reduced ODC activity. Furthermore, Groppa et al. (2007a) studied the PA metabolism in wheat leaves under Cd or Cu stress and showed that cadmium and copper increased Put, Spd remained unaltered either with Cd or Cu, while Spm was reduced as compared to control values by both heavy metal treatments. Copper also decreased ADC but did not modify ODC and DAO activities (Groppa et al. 2007a). Both metals caused significant increases in proline and Put and also in Spd and Spm at the highest concentration tested (1 mM), and these increments were more pronounced for Cd treatment of sunflower seedlings (Groppa et al. 2008). Additionally, the authors suggested that PAs are key biological compounds, probably involved in signaling pathways triggered under stress environmental conditions. Similarly, Zhang et al. (2010) found that Cu treatment increased Put and lowered the Spd and Spm levels, thereby reducing the Put/(Spd + Spm) ratio in leaves of grafted and non-grafted cucumber seedlings. Grafting markedly reversed these Cu-induced effects for all Spd, Spr, and Put and partly regained the Put/(Spd + Spm) ratio in leaves. These results suggest that grafting can enhance the tolerance of cucumber seedlings to Cu stress by increasing the activities of antioxidants and the levels of Spd and Spm, decreasing the Put/(Spd + Spm) ratio and the levels of ROS, promoting free proline and soluble protein synthesis in cucumber seedling leaves (Zhang et al. 2010).

In *Erica andevalensis* hydroponically grown with supplied increasing Cu concentration (1 to 500 μM) in the nutrient medium, the heavy metal led to a significant rise of PAs in shoots (Rossini Oliva et al. 2010). High levels of PAs in shoots helped the authors to conclude that PAs impart a defensive mechanism in plant cells at high metal concentration. Accordingly, Choudhary et al. (2009) showed that Cu treatment resulted in to a marked increase in PAs in *R. sativus* seedlings. Szafranska et al. (2011) examined the effect of Cu on the regeneration of *Daucus carota* L. androgenic embryos of var. Feria and 1014 breeding line and also on PAs, proline contents, lipid peroxidation, and Cu accumulation after 16 and 24 weeks and found that the higher tolerance of Feria to oxidative stress may result from increased content of proline and higher contents of the Put and Spd. The authors concluded that variations in PA levels depend not only on the concentrations of heavy metal but also on plant species and cultivars, and PAs point to better protection of such cultivars that possess higher constitutive PA levels. Zhao et al. (2008) investigated the phytotoxic effect of Ni on *Hydrocharis dubia* leaves and showed that Ni induced lipid peroxidation, destroyed the structure and functions of membranes, altered the balance of nutrient elements, and caused the toxicity of *H. dubia*. Ni stress significantly increased Put and lowered Spd and Spm levels, thus significantly reducing the ratio of free (Spd + Spm)/Put in leaves, which has been considered as a signal under stress. The changes of PAs content and physiological and biochemical responses in *H. dubia* leaves at high metal concentrations led the authors to conclude that PAs may be involved in the adaptation of plants to Ni-induced stress. Pb treatment of *Potamogeton crispus* L. significantly increased the free Put and changed dynamically other PAs levels.

The activities of PAO and ADC were initially decreased and then enhanced with the increase in the Pb concentration (Xu et al. 2011). Accumulation of PAs in shoot tissue of *Trifolium pratense* L. was affected by arsenic (Mascher et al. 2002) when metal was supplied in concentration 10 mg/kg soil. Extra accumulation of Spm seemed to be a part of a protective mechanism against the destruction of membranes caused by arsenate. In vitro shoots of a transgenic European pear, overexpressing *MdSPDS1*, performed attenuated susceptibility to heavy metal (Zn, Pb, Cu, Al, Cd) stress in conjunction with the wild plant (Wen et al. 2008, 2009, 2010). The authors supposed that abundance of Spd in transgenic plants could play an important role in the tolerance to heavy metals in long-term experiments. In this line Spd reduced the toxic effects of supplied metals mainly via alleviating oxidative status, by affecting mineral element balance and/or by its specific feature to act as metal chelator as well (Løvaas 1997; Lomozik et al. 2005). Thus, there is an indication that PAs acts as antioxidants and/or metal chelators (Kuthanová et al. 2004).

19.10 Herbicides

The extensive use of herbicides is a common practice in modern agriculture. However, their application usually provokes oxidative stress not only in sensitive but also in tolerant plants. Most of the herbicides are known to generate ROS by direct involvement in radical production or by inhibition of key biosynthetic pathways (Prasad and Rengel 1998). Enhancing free higher PAs in lotus prevented paraquat-induced superoxide production in vivo (Cuevas et al. 2004). However, because of the natural tolerance of *L. glaber* to the herbicide, it was not possible to correlate the content of free PAs with their hypothetical inhibitory role during oxidative stress. So, the authors tested for paraquat toxicity in tobacco plant and found that high concentrations of herbicide induced an increase of free PA levels in crude extracts and intercellular fluids, while low herbicide concentrations increased only the free PAs in the intercellular fluids. These results suggested that PA metabolism in the apoplast is involved in the physiological response to oxidative stress and subsequently in plant stress tolerance (Cuevas et al. 2004).

Deng (2005) found that chlorsulfuron and glyphosate directly regulated the levels of arginine and ornithine in *Datura stramonium* L. seedlings, which were increased two to three times. Recently, Kielak et al. (2011) investigated the effect of glyphosate-based herbicide (Roundup Ultra 360 SL) and showed significant positive correlation between Roundup dose and over-accumulation of Put and Spd as well as total PA in model plant duckweed. Putrescine was synthesized first within the plant cells and Spd later. Additionally, with augmentation of PAs, an increase in APX and CAT activities was recorded by herbicide which is the resultant of PA inclusion. These findings indicated that duckweed plants responded to herbicide stress by activating one or more components of the plant defense system, including PAs, which helps plants to mitigate the negative stress outcome.

19.11 Heat Tolerance

The amylose levels in rice are greatly decreased during elevated temperature conditions at the time of seed germination, changing the fine amylopectin structure and producing more chalky grains (Asaoka et al. 2010; Inouchi et al. 2000) which hampers the rice yield and seed quality (Krishnan and Ramakrishnan 2011; Peter 2011). The occurrence of chalky grains of rice is typically caused by the unusual expressions of genes encoding starch synthase enzymes (Nishi et al. 2001; Tanaka et al. 2010). As PAs are known to be involved in grain filling and they might contribute to build up heat resistance of some cereals, the hybrid rice “YLY 689” was taken in an experiment to find the effects of exogenous spermidine (Spd) on seed quality under high temperature during the grain filling stage (Fu et al. 2019). The concentration of Spm and Spd in superior grains of rice was remarkably higher than that of the inferior grains (Cao et al. 2016). In this investigation, just after pollination, spikes were treated with Spd or cyclohexylamine (CHA). Interestingly, CHA is its synthesis inhibitor.

Recently, Fu et al. (2019) revealed that when the rice plants were transferred to 40 °C for 5-day heat treatment, it resulted into significant enhancement in the germination index, percentage, germination index, seedling shoot height, vigor index, and dry weight of seeds in case of Spd pretreatment, harvested at 35 days after pollination. In contrast, the CHA significantly decreased the seed germination and seedling growth. Also, Spd categorically enhanced the peroxidase (POD) activity and reduced the malondialdehyde (MDA) content in seeds. Nevertheless, after spraying with Spd, the endogenous content of spermidine and spermine and the expression of their synthetic genes, *spermidine synthase* (*SPDSYN)*, and *spermine synthase* (*SPMS1* and *SPMS2*) remarkably enhanced, although, the accumulation of amylose, total starch, and the expression of their related synthase genes, *soluble starch synthase II-3* (*SS II-3*) and *granules bound starch synthase I* (*GBSSI*), also rose to some magnitude indicating that exogenous Spd pretreatment could diminish he high temperature stress on rice seed grain filling and improve the rice seed quality, which could possibly be induced by upregulating endogenous polyamines and starch metabolism (Fu et al. 2019). Recent report also suggests that Spd is involved in heat tolerance in higher plants, which provides membrane stability and increase the reactive oxygen species (ROS) scavenging system. Cao et al. (2016) found that the content of Spd and Spm in superior grains of rice was significantly higher than that in inferior grains (Cao et al. 2016). The content of Spm and Spd in grains works in synergy with grain plumpness during the grain filling stage.

19.12 Plant Senescence

The PA metabolic enzymes activities and PAs contents change throughout the stages of plant growth. In whole plants, endogenous PAs and PA synthetase activity were recorded to be highest in the meristem and growing cells and lowest in senescent tissues. As leaves senescence, the chlorophyll content slowly reduces and so does ADC and ODC activities, while PAO and hydrolases activities increase rapidly. All of these changes can be blocked by the inclusion of exogenous PAs (Duan 2000; Cai 2009). A reduction in PA levels seems to be a significant prelude to senescence signals, or it may be that a decrease in PAs content is the senescence signal (Duan et al. 2006). Exogenous Spd and Spm treatments can increase the content of PAs in cut flowers and prolong their senescence and improve quality (Yang and He 2001; Cao 2010). In *Anthurium andraeanum*, the introduction of GA_3 + Spm by spraying slowed down the senescence of cut flowers stored at 20 °C and augmented the quality of the inflorescences (Simões et al. 2018). Delayed leaf senescence was recorded to be linked with a rise in Spm concentration, reduced ROS production, and increased NO levels (Sobieszczuk-Nowicka 2017). Polyamines appeared to slow down the process of senescence by suppressing the ethylene biosynthesis (Woo et al. 2013; Anwar et al. 2015). 0.1 mM Spd application on gerbera flowers or gerbera vase flower fortification with 10 mM Spd resulted in slowing down the senescence, while those sprayed with 1 mM Spd, 10 mM Spd, 0.1 mM Spm, 1 mM Spm, or mixed solution of 0.1 mM each of Put, Spd, and Spm showed accelerated senescence, with brown spots and yellowing of the petal rims starting from day 2 of treatment (Bagni and Tassoni 2006). Legocka and Sobieszczuk-Nowicka (2012) found that chlorophyll rapidly degraded, and Put accumulation inhibited protein degradation and reduced chlorophyll losses (Serafini-Fracassini et al. 2010; Cai et al. 2015). In peony, a PA synthesis inhibitor (0.1 Mm) extended the lifespan and delayed the cut flowers senescence, while PAs lessened the flower lifespan and accelerated flower senescence (Han 2016).

19.13 Conclusion and Future Prospects

Many scientists have reported different plants defence mechanisms exhibited during its growth progression. However, the practical mode of action and regulations of many aspects still remain uncovered. The biosynthesis of PAs is present in every cell and tissue of plants; however, the number of enzymes involved in these processes is limited. That is why PA biosynthesis proves to be is an experimental model for studying how they act in protecting plants against various biotic and abiotic stresses. From several decades, PAs are being employed using mutants, inhibitors, plant tissue culture, exogenous application, genetic transformation techniques, etc. Various studies have been reported in order to illustrate the role of PAs such as Spm and Spd which have increased levels when plants get exposed to stress conditions enzymes, indicating the homeostatic equilibrium that is maintained inside the plant cells incorporating enzymes.

PAs' role in combating abiotic stress could easily be inferred by studies performed on *Arabidopsis*, wherein PAs were found to act antagonistically against salinity and cold stress conditions, thereby providing tolerance against such factors (Roy et al. 2005; Liu et al. 2006; Janicka-Russak et al. 2010; Orsini et al. 2011). Similarly, exogenous spray of Spd and Spm helped in delayed plant senescence in cut flowers and vase flowers (Yang and He 2001; Cao 2010). PA levels were found to be enhanced in plants experiencing mineral deficiencies such as potassium, boron, calcium, magnesium, and phosphorus (Wimalasekera et al. 2011). Likewise, there are reports from various researchers of how PAs play a pivotal role in plant stress conditions.

However, a lot had been studied and reported about PAs, but there still exists a lacuna of understanding the enzymes involved during biosynthesis of PAs, localization of PAs at cellular and subcellular levels, translocation and movements of free PAs, and their interaction with other plant hormones. Therefore, more research needs to be done under these niche areas so as to have a better understanding of polyamines as a whole.

References

Ahmad P, Sarwat M, Sharma S (2008) Reactive oxygen species, antioxidants and signaling in plants. J Plant Biol 51:167–173

Alcazar R, Altabella T, Marco F et al (2010) Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. Springer, New York

Alcázar R et al (2006a) Abscisic acid modulates polyamine metabolism under water stress in *Arabidopsis thaliana*. Physiol Plant 128:448–455

Alcázar R, Marco F, Cuevas JC, Patron M, Ferrando A, Carrasco P, Tiburcio AF, Altabella T (2006b) Involvement of polyamines in plant response to abiotic stress. Biotechnol Lett 28: 1867–1876

Alcazar R, Cuevas JC, Planas J, Zarza X, Bortolotti C, Carrasco P, Salinas J, Tiburcio AF, Altabella T (2011a) Integration of polyamines in the cold acclimation response. Plant Sci 180:31–38

Alcazar R, Bitrian M, Bartels D, Koncz C, Altabella T, Tiburcio AF (2011b) Polyamine metabolic canalization in response to drought stress in *Arabidopsis* and the resurrection plant *Craterostigma plantagineum*. Plant Signal Behav 6(2):243–250

Alcázar R et al (2006) Abscisic acid modulates polyamine metabolism under water stress in *Arabidopsis thaliana*. Physiol Plant 128:448–455

Alet A, Sánchez D, Ferrando A, Fernandez-Tiburcio A, Alcazar R, Cuevas JC, Altabella T, Pico FM, Carrasco P, Menéndez AB, Ruiz OA (2011) Homeostatic control of polyamine levels under long-term salt stress in *Arabidopsis*. Changes in putrescine content do not alleviate ionic toxicity. Plant Signal Behav 6:1–6

Alet AI, Sánchez DH, Cuevas JC, Marina M, Carrasco P, Altabella T, Tiburcio AF, Ruiz OA (2012) New insights into the role of spermine in *Arabidopsis thaliana* under long-term salt stress. Plant Sci 182:94–100

Anwar R, Mattoo AK, Handa AK (2015) Polyamine interactions with plant hormones: crosstalk at several levels. Int J Hydrogen Energy 38:1039–1051

Asaoka M et al (2010) Effect of environmental temperature during development of rice plants on some properties of endosperm starch. Starch-Starke 36:189–193

Bae H, Kim SH, Kim MS, Sicher RC, Lary D, Stream MD, Natarajan S, Bailey BA (2008) The drought response of *Theobroma cacao* (cacao) and the regulation of genes involved in polyamine biosynthesis by drought and other stresses. Plant Physiol Biochem 46:174–188

Bagni N, Tassoni A (2006) The role of polyamines in relation to flower senescence. Floricult Ornament Plant Biotechnol 1536:855–856

Bais HP, Ravishankar GA (2002) Role of polyamines in the ontogeny of plants and their biotechnological applications. Plant Cell Tiss Org Cult 69:1–34

Basu HS, Schwietert HCA, Feuerstein BG, Marton LJ (1990) Effect of variation in the structure of spermine on the association with DNA and the induction of DNA conformational changes. Biochem J 269:329–334

Basu R, Maitra N, Ghosh B (1988) Salinity results in polyamine accumulation in early rice (*Oryza sativa* L.) seedlings. Aust J Plant Physiol 15:777–786

Basu S, Roychoudhury A, Saha PP, Sengupta DN (2010) Comparative analysis of some biochemical responses of three indica rice varieties during polyethylene glycol-mediated water stress exhibits distinct varietal differences. Acta Physiol Plant 32:551–563

Beigbeder AR (1995) Influence of polyamine inhibitors on light independent and light dependent chlorophyll biosynthesis and on the photosyntetic rate. J Photochem Photobiol 28:235–242

Beninati S, Piacentini M, Argento-Ceru MP, Russo-Caia S, Autuori F (1985) Presence of di- and polyamines covalently bound to protein in rat liver. BBA-Gen Sub 841(1):120–126

Bergmann H, Machelett B, Lippmann B, Friedrich Y (2001) Influence of heavy metals on the accumulation of trimethylglycine, putrescine and spermine in food plants. Amino Acids 20: 325–329

Bhatnagar P, Vadez V, Sharma KK (2008) Transgenic approaches for abiotic stress tolerance in plants: retrospect and prospects. Plant Cell Rep 27(3):411–424

Bouchereau A, Aziz A, Larher F, Martin-Tanguy J (1999) Polyamines and environmental challenges: recent development. Plant Sci 140:103–125

Cai G, Sobieszczuknowicka E, Aloisi I, Al E (2015) Polyamines are common players in different facets of plant programmed cell death. Amino Acids 47:27–44

Cai Q (2009) Progress in physiology of plant polyamines. Fujian Sci Technol Rice Wheat 27:37–40

Camacho-Cristobal JJ, Maldonado JM, Gonzales-Fontes A (2005) Boron deficiency increases putrescine levels in tobacco plants. J Plant Physiol 162:921–928

Cao D (2010) Effects of polyamines on seed quality and germination of super sweet corn seeds during development. Zhejiang University, Hangzhou

Cao YY et al (2016) Growth characteristics and endosperm structure of superior and inferior spikelets of indica rice under high-temperature stress. Biol Plant 60:532–542

Choudhary A, Singh R (2000) Cadmium-induced changes in diamine oxidase activity and polyamine levels in *Vigna radiata* wilczek seedlings. J Plant Physiol 156:704–710

Choudhary S, Bhardway R, Gupta B, Dutt P, Kanwar M, Arora P (2009) Epibrassinolide regulated synthesis of polyamines and auxins in *Raphanus sativus* L. seedlings under cu metal stress. Braz J Plant Physiol 21(1):25–32

Choudhary SP, Kanwar M, Bhardwaj R, Yu JQ, Tran LP (2012b) Chromium stress mitigation by polyamine brassinosteroid application involves phytohormonal and physiological strategies in *Raphanus sativus* L. PLoS One 7(3):e33210

Choudhary SP, Oral HV, Bhardwaj R, Yu J, Tran LP (2012a) Interaction of brassinosteroids and polyamines enhances copper stress tolerance in *Raphanus sativus*. Oxford University Press, Oxford

Coleman RG, Hegarty MP (1957) Metabolism of dl-ornithine-2-14C in normal and potassium-deficient barley. Nature 179:376

Cona A, Rea G, Angelini R, Federico R, Tavladoraki P (2006) Functions of amine oxidases in plant development and defence. Trends Plant Sci 11:80–88

Cuevas J, Lopez-Cobollo R, Alcazar R, Zarza X, Koncz C, Altabella T, Salinas J, Tiburcio A, Ferrando A (2009) Putrescine as a signal to modulate the indispensable ABA increase under cold stress. Plant Signal Behav 4:219–220

Cuevas JC, Lopez-Cobollo R, Alcazar R, Zarza X, Koncz C, Altabella T, Salinas J, Tiburcio AF, Ferrando A (2008) Putrescine is involved in *Arabidopsis* freezing tolerance and cold acclimation by regulating abscisic acid levels in response to low temperature. Plant Physiol 148:1094–1105

Cuevas JC, Sánchez DH, Marina M, Ruiz OA (2004) Do polyamines modulate the *Lotus glaber* NADPH oxidation activity induced by the herbicide methyl viologen? Funct Plant Biol 31:921–928

D'Oraci D, Bagni N (1987) In vitro interactions between polyamines and pectic substances. Biochem Biophys Res Commun 148:1159–1163

Deng F (2005) Effects of glyphosate, chlorsulfuron, and methyl jasmonate on growth and alkaloid biosynthesis of jimsonweed (*Datura stramonium* L.). Pest Biochem Physiol 82:16–26

Duan G (2000) Effect of spermidine on protein contents and protease during senescence of excised wheat leaves. J Sichuan Teach Coll 21:44–47

Duan G, Huang Z, Lin H (2006) The role of polyamines in the ontogeny of higher plants. Acta Agric Boreali Occidentalis Sinica 15:190–194

Duan JJ, Guo SR, Kang YY, Jiao YS (2007) Effects of exogenous spermidine on polyamine content and antioxidant system in roots of cucumber under salinity stress. J Ecol Rural Environ 4(4): 11–17

El Ghachtoul N, Martin-Tangu J, Paynot M, Gianinazz S (1996) First report of the inhibition of arbuscular mycorrhizal infection of *Pisum sativum* by specific and irreversible inhibition of polyamine biosynthesis or by gibberellic treatment. FEBS Lett 385:189–192

Evans PT, Malmberg RL (1989) Do polyamines have roles in plant development? Annu Rev Plant Physiol Plant Mol Biol 40:235–269

Ferrando A, Carrasco P, Cuevas JC, Altabella T, Tiburcio AF (2004) Integrated molecular analysis of the polyamine pathway in abiotic stress signaling. In: Amancio S, Stulen I (eds) Nitrogen acquisition and assimilation in higher plants. Kluwer Academic Publishers, London, pp 207–230

Flores HE, Galston AW (1984) Osmotic stress-induced polyamine accumulation in cereal leaves: I. physiological parameters of the response. Plant Physiol 75:102–109

Folk JE (1980) Transglutaminases. Annu Rev Biochem 49:517–531

Fu Y et al (2019) Spermidine enhances heat tolerance of rice seeds by modulating endogenous starch and polyamine metabolism. Molecules 24:1395

Fujita M, Fujita Y, Noutoshi Y, Takahashi F, Narusaka Y, Yamaguchi-Shinozaki K, Shinozaki K (2006) Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signaling networks. Curr Opin Plant Biol 9:436–442

Galston AW, Kaur-Sawhney R (1995) Polyamines as endogenous growth regulators. In: Davies PJ (ed) Plant hormones: physiology, biochemistry and molecular biology, 2nd edn. Kluwer Academic Publishers, Dordrecht, pp 158–178

Galston AW, Kaur-Sawhney RK (1990) Polyamines in plant physiology. Plant Physiol 94:406–410

Ghosh N, Adak MK, Ghosh PD, Gupta S, Sen Gupta DN, Mandal C (2011) Differential responses of two rice varieties to salt stress. Plant Biotechnol Rep 5:89–103

Gill SS, Tuteja N (2010a) Polyamines and abiotic stress tolerance in plants. Plant Signal Behav 5: 26–33

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

Gong XQ, Zhang JY, Hu JB, Wang W, Wu H, Zhang QH, Liu JH (2015) FcWRKY70, a WRKY protein of *Fortunella crassifolia*, functions in drought tolerance and modulates putrescine synthesis by regulating arginine decarboxylase gene. Plant Cell Environ 38:2248–2262

Groppa MD, Ianuzzo MP, Tomaro ML, Benavides MP (2007b) Polyamine metabolism in sunflower plants under long-term cadmium or copper stress. Amino Acids 32:265–275

Groppa MD, Tomaro ML, Benavides MP (2007a) Polyamines and heavy metal stress: the antioxidant behavior of spermine in cadmium- and copper-treated wheat leaves. Biometals 20:185–195

Groppa MD, Zawoznik MS, Tomaro ML, Benavides MP (2008) Inhibition of root growth and polyamine metabolism in sunflower (*Helianthus annuus*) seedlings under cadmium and copper stress. Biol Trace Elem Res 126:246–256

Gupta B, Gupta K, Sengupta DN (2012a) Spermidine-mediated in vitro phosphorylation of transcriptional regulator OSBZ8 by SNF1-type serine/threonine protein kinase SAPK4 homolog in indica rice. Acta Physiol Plant 34:1321

Gupta K, Gupta B, Ghosh B, Sengupta DN (2012b) Spermidine and abscisic acid-mediated phosphorylation of a cytoplasmic protein from rice root in response to salinity stress. Acta Physiol Plant 34:29–40

Han L (2016) Studies on mechanism of low temperature storage and polyamine impact in cut flowers of herbaceous peony postharvest senescence. Shandong Agricultural University, Shandong

Heby O, Persson L (1990) Molecular genetics of polyamine synthesis in eukaryotic cells. Trends Biochem Sci 15:153–158

Hummel I, Gouesbet G, El Amrani A, Aïnouche A, Couée I (2004) Characterization of the two arginine decarboxylase (polyamine biosynthesis) paralogues of the endemic subantarctic cruciferous species *Pringlea antiscorbutica* and analysis of their differential expression during development and response to environmental stress. Gene 342:199–209

Hussain SS, Ali M, Ahmad M, Siddique KHM (2011) Polyamines: natural and engineered abiotic and biotic stress tolerance in plants. Biotechnol Adv 29:300–311

Igarashi K, Kashiwagi K (2000) Polyamines: mysterious modulators of cellular functions. Biochem Biophys Res Commun 271(3):559–564

Imai R, Ali A, Pramanik HR, Nakaminami K, Sentoku N, Kato H (2004) A distinctive class of spermidine synthase is involved in chilling response in rice. J Plant Physiol 161:883–886

Inouchi N et al (2000) The effect of environmental temperature on distribution of unit chains of rice amylopectin. Starch-Starke 52:8–12

Janicka-Russak M, KabaŁa K, Mlodzińska E, Klobus G (2010) The role of polyamines in the regulation of the plasma membrane and the tonoplast proton pumps under salt stress. J Plant Physiol 167:261–269

Jiuju D, Shirong G (2005) Effects of exogenous spermidine on salt tolerance of cucumber seedlings under NaCl stress. China Veg 12:8–10

Jouve L, Hoffmann L, Hausman J-F (2004) Polyamine, carbohydrate, and proline content changes during salt stress exposure of aspen (*Populus tremula* L.): involvement of oxidation and osmoregulation metabolism. Plant Biol 6:74–80

Kakkar R, Rai V, Nagar P (1998) Polyamine uptake and translocation in plants. Biología Plantarum 40(4):481–491

Katiyar SA, Agarwal M, Grover A (1999) Emerging trends in agricultural biotechnology research: use of abiotic stress-induced promoter to drive expression of a stress resistance gene in the transgenic system leads to high level stress. Curr Sci 77(12):1577

Kielak E, Sempruch C, Mioduszewska H, Klocek J, Leszczynski B (2011) Phytotoxicity of roundup ultra 360 SL in aquatic ecosystems: biochemical evaluation with duckweed (*Lemna minor* L.) as a model plant. Pestic Biochem Physiol 99:237–243

Kim JC, Lee SH, Cheong YH, Yoo CM, Lee SI, Chun HJ, Yun DJ, Hong JC, Lee SY, Lim CO, Cho MJ (2001) A novel cold-inducible zinc finger protein from soybean, SCOF-1, enhances cold tolerance in transgenic plants. Plant J 25:247–259

Kim TE, Kim SK, Han TJ, Lee JS, Chang SC (2002) ABA and polyamines act independently in primary leaves of cold-stressed tomato (*Lycopersicon esculentum*). Physiol Plant 115:370–376

Koc E, Islek C, Kasko Arici Y (2017) Spermine and its interaction with proline induce resistance to the root rot pathogen *Phytophthora capsici* in pepper (*Capsicum annuum*). Hortic Environ Biotechnol 58:254–267

Krishnan P, Ramakrishnan BJ (2011) Chapter three-high-temperature effects on rice growth, yield, and grain quality. Adv Agron 111:87–206

Kusano T, Berberich T, Tateda C, Takahashi Y (2008) Polyamines: essential factors for growth and survival. Planta 228:367–381

Kusano T, Yamaguchi K, Berberich T, Takahashi Y (2007) The polyamine spermine rescues *Arabidopsis* from salinity and drought stresses. Plant Signal Behav 2:251–252

Kuthanová A, Gemperlová L, Zelenková S, Eder J, Machá˘cková I, Opatrny Z, Cvikrová M (2004) Cytological changes and alterations in polyamine contents induced by cadmium in tobacco BY-2 cells. Plant Physiol Biochem 42(2):149–156

Lee T, Liu JJ, Pua EC (1997) Molecular cloning of two cDNAs (accession Nos. X95729 and U80916) encoding *S*-adenosyl-L methionine decarboxylase in mustard (*Brassica juncea* [L.] Czern & Coss). Plant Physiol 115:1287

Lefèvre I, Gratia E, Lutts S (2001) Discrimination between the ionic and osmotic components of salt stress in relation to free polyamine level in rice (*Oryza sativa*). Plant Sci 16:943–952

Lefevre I, Marchal G, Meerts P, Correal E, Lutts S (2009) Chloride salinity reduces cadmium accumulation by the Mediterranean halophyte species *Atriplex halimus* L. Environ Exp Bot 65: 142–152

Legocka J, Sobieszczuk-Nowicka E (2012) Sorbitol and NaCl stresses affect free, microsome associated and thylakoid-associated polyamine content in *Zea mays* and *Phaseolus vulgaris*. Acta Physiol Plant 34:1145–1151

Lei Y (2008) Physiological responses of *Populus przewalskii* to oxidative burst caused by drought stress. Russ J Plant Physiol 55:857–864

Liu H, Liu Y, Yu B, Liu Z, Zhang W (2004a) Increased polyamines conjugated to tonoplast vesicles correlate with maintenance of the H+-ATPase and H+-PPase activities and enhanced osmotic stress tolerance in wheat. J Plant Growth Regul 23:156–165

Liu HP, Dong BH, Zhang YY, Liu ZP, Liu YL (2004b) Relationship between osmotic stress and the levels of free, conjugated and bound polyamines in leaves of wheat seedlings. Plant Sci 166: 1261–1267

Liu HP, Dong BH, Zhang YY, Liu ZP, Liu YL (2004c) Relationship between osmotic stress and the levels of free, conjugated, and alterations in polyamine contents induced by cadmium in tobacco BY-2 cells. Plant Physiol Biochem 42(2):149–156

Liu J, Yu B-J, Liu Y-L (2006a) Effects of spermidine and spermine levels on salt tolerance associated with tonoplast H + -ATPase and H + -PPase activities in barley roots. Plant Growth Regul 49:119–126

Liu JH, Kitashiba H, Wang J, Ban Y, Moriguchi T (2007) Polyamines and their ability to provide environmental stress tolerance to plants. Plant Biotechnol 24:117–126

Liu JH, Nada K, Honda C, Kitashiba H, Wen XP, Pang XM, Moriguchi T (2006) Polyamine biosynthesis of apple callus under salt stress: importance of the arginine decarboxylase pathway in stress response. J Exp Bot 57:2589–2599

Lomozik L, Gasowska A, Bregier-Jarzebowska R, Jastrzab R (2005) Coordination chemistry of polyamines and their interactions in ternary systems including metal ions, nucleosides and nucleotides. Coord Chem Rev 249:2335–2350

Lovaas E (1997) Antioxidant and metal-chelating effects of polyamines. In: Sies H (ed) Advances in pharmacology, Vol. 38: antioxidants in disease mechanisms and therapy. Academic Press, Amsterdam, pp 119–149

Malmberg RL, Watson MB, Galloway GL, Yu W (1998) Molecular genetic analysis of plant polyamines. Crit Rev Plant Sci 17:5

Martin-Tanguy J (1987) Hydroxycinnamic acid amides, hypersensitivity, flowering and sexual organogenesis in plants. In: Von Wettstein D, Chua DN (eds) Plant molecular biology. Plenum Publishing Corporation, New York, pp 253–263

Martin-Tanguy J (2001) Metabolism and function of polyamines in plants: recent development (new approaches). Plant Growth 34:135

Mascher R, Lippmann B, Holzinger S, Bergmann H (2002) Arsenate toxicity: effects on oxidative stress response molecules and enzymes in red clover plants. Plant Sci 163:961–969

Mehta HS, Saftner RA, Mehta RA, Davies PJ (1994) Identification of post transcriptionally modified 18-kilodalton protein from rice as eukaryotic translocation initiation factor 5A. Plant Physiol 106:1413–1419

Meloni DA, Oliva MA, Martinez CA, Cambraia J (2003) Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress. Environ Exp Bot 49: 69–76

Minocha R, Long S, Thangavel P, Minocha SC, Eagar C, Driscoll CT (2010) Elevation dependent sensitivity of northern hardwoods to Ca addition at Hubbard Brook Experimental Forest, NH, USA. For Ecol Manage 260:2115–2124

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Mo H, Pua EC (2002) Up-regulation of arginine decarboxylase gene expression and accumulation of polyamines in mustard (*Brassica juncea*) in response to stress. Physiol Plant 114:439–449

Moschou PN, Paschalidis KA, Delis ID et al (2008) Spermidine exodus and oxidation in the apoplast induced by abiotic stress is responsible for H2O2 signatures that direct tolerance responses in tobacco. Plant Cell 20(6):1708–1724

Mutlu F, Bozcuk S (2007) Salinity-induced changes of free and bound polyamine levels in sunflower (*Helianthus annuus* L.) roots differing in salt tolerance. Pak J Bot 39:1097–1102

Nayyar H (2005) Putrescine increases floral retention, pod set and seed yield in cold stressed chickpea. J Agron Crop Sci 191:340–345

Nayyar H, Kaur S, Singh S, Kumar S, Singh KJ, Dhir KK (2005) Involvement of polyamines in the contrasting sensitivity of chickpea (*Cicer arietinum* L.) and soybean (*Glycine max* (L.) Merrill.) to water deficit stress. Bot Bull Acad Sin 46:333–338

Nishi A et al (2001) Biochemical and genetic analysis of the effects of amylose-extender mutation in rice endosperm. J Plant Physiol 127:459

Orsini F, Accorsi M, Gianquinto G, Dinelli G, Antognoni F, Ruiz Carrasco KB, Martinez EA, Alnayef M, Marotti I, Bosi S, Biondi S (2011) Beyond the ionic and osmotic response to salinity in *Chenopodium quinoa*: functional elements of successful halophytism. Funct Plant Biol 38(10):818–831

Oshima T (2007) Unique polyamines produced by an extreme thermophile, *Thermus thermophilus*. Amino Acids 33:2

Pandey S, Ranade S, Nagar P, Nikhil K (2000) Role of polyamines and ethylene as modulators of plant senescence. J Biosci 25(3):291–299

Paradi I, Bratek Z, Lang F (2003) Influence of arbuscular miccorhiza and phosphorus supply on polyamine content, growth and photosynthesis of *Plantago lanceolata*. Biologia Plantarum 46(4):563–569

Peremarti A, Bassie L, Christou P, Capell T (2009) Spermine facilitates recovery from drought but does not confer drought tolerance in transgenic rice plants expressing *Datura stramonium* S-adenozylmethionine decarboxylase. Plant Mol Biol 70:253–264

Perez-Amador MA, Leon J, Green PJ, Carbonel lJ. (2002) Induction of the arginine decarboxylase ADC2 gene provides evidence for the involvement of polyamines in the wound response in *Arabidopsis*. Plant Physiol 130:1454–1463

Peter GJ (2011) Regulation of starch biosynthesis in response to a fluctuating environment. Plant Physiol 155:1566–1577

Pillai MA, Akiyama T (2004) Differential expression of an S-adenosyl-L-methionine decarboxylase gene involved in polyamine biosynthesis under low temperature stress in japonica and indica rice genotypes. Mol Genet Genomics 271:141–149

Pohjanpelto P, Höltta E (1996) Phosphorylation of Okazaki-like DNA fragments in mammalian cells and role of polyamines in the processing of this DNA. EMBO J 15:1193–1200

Potters G, Horemans N, Jansen MAK (2010) The cellular redox state in plant stress biology – a charging concept. Plant Physiol Biochem 48:292–300

Prakash L, Prathapasenan G (1988) Effect of NaCl salinity and putrescine on shoot growth, tissue ion concentration and yield of rice (*Oryza sativa* L. GR3). J. Agric Crop Sci 160:325–334

Prasad M, Rengel Z (1998) Plant Acclimation and adaptation to natural and anthropogenic stress. Ann N Y Acad Sci 851(1):216–223

Renaut J, Hoffmann L, Hausman JF (2005) Biochemical and physiological mechanisms related to cold acclimation and enhanced freezing tolerance in poplar plantlets. Physiol Plant 125:82–94

Richards FJ, Coleman RG (1952) Occurrence of putrescine in potassium-deficient barley. Nature 170:460

Rossini Oliva S, Mingorance MD, Valdes B, Leidi EO (2010) Uptake, localisation and physiological changes in response to copper excess in *Erica andevalensis*. Plant and Soil 328:411–420

Roy P, Niyogi K, Sengupta DN, Ghosh B (2005) Spermidine treatment to rice seedlings recovers salinity stress-induced damage of plasma membrane and PM-bound H + -ATPase in salt-tolerant and salt-sensitive rice cultivars. Plant Sci 168:583–591

Roychoudhury A, Basu S, Sarkar SN, Sengupta DN (2008) Comparative physiological and molecular responses of a common aromatic indica rice cultivar to high salinity with non-aromatic indica rice cultivars. Plant Cell Rep 27:1395–1410

Roychoudhury A, Basu S, Sengupta DN (2011) Amelioration of salinity stress by exogenously applied spermidine or spermine in three varieties of Indica rice differing in their level of salt tolerance. J Plant Physiol 168:317–328

Saha J, Giri K (2017) Molecular phylogenomic study and the role of exogenous spermidine in the metabolic adjustment of endogenous polyamine in two rice cultivars under salt stress. Gene 609: 88–103

Sang QQ, Shan X, An YH, Shu S, Sun J, Guo SR (2017) Proteomic analysis reveals the positive effect of exogenous spermidine in tomato seedlings' response to high-temperature stress. Front Plant Sci 8:120

Santa-Cruz A, Acosta M, Perez-Alfocea F, Bolarin MC (1997) Changes in free polyamine levels induced by salt stress in leaves of cultivated and wild tomato species. Physiol Plant **101**:341–346

Sarjala T, Kaunisto S (2002) Potassium nutrition and free polyamines of *Betula pendula* Roth and *Betula pubescens* Ehrh. Plant and Soil 238:141–149

Schraudner M, Trost M, Kerner K, Heller W, Leonardi S, Langebartels C, Sanderman H Jr (1990) Ozone induction and function of polyamines in ozone-tolerant and ozone-sensitive tobacco cultivars. In: Flores HE, Arteca RN, Shannon JC (eds) Polyamines and ethylene: biochemistry, physiology and interactions. American Society of Plant Physiologists, Rockville, pp 394–396

Šebela M, Radová A, Angelini R, Tavladoraki P, Frébort I, Pec P (2001) FAD-containing polyamine oxidases: a timely challenge for researchers in biochemistry and physiology of plants. Plant Sci 160:197–207

Serafini-Fracassini D, Sandro AD, Duca SD (2010) Spermine delays leaf senescence in *Lactuca sativa* and prevents the decay of chloroplast photosystems. Plant Physiol Biochem 48:602–611

Shen W, Nada K, Tachibana S (2000) Involvement of polyamines in the chilling tolerance of cucumber cultivars. Plant Physiol 124:431

Shi H, Chan Z (2014) Improvement of plant abiotic stress tolerance through modulation of the polyamine pathway. J Integr Plant Biol 56:114–121

Simões ADN, Diniz NB, Vieira MRDS, Al E (2018) Impact of GA3 and spermine on postharvest quality of anthurium cut flowers (*Anthurium andraeanum*) cv. Arizona Sci Horticult 241:178–186

Slocum RD (1991) Tissue and subcellular localisation of polyamines and enzymes of polyamine metabolism. In: Slocum RD, Flores HE (eds) Biochemistry and physiology of polyamines in plants. CRC Press, Boca Raton, pp 93–105

Sobieszczuk-Nowicka E (2017) Polyamine catabolism adds fuel to leaf senescence. Amino Acids 49:49–56

Szafranska K, Cvikrova M, Kowalska U, Gorecka K, Gorecki R, Martincova O, Janas KM (2011) Influence of copper ions on growth, lipid peroxidation, and proline and polyamines content in carrot rosettes obtained from anther culture. Acta Physiologiae Plant 33:851–859

Sziderics AH, Oufir M, Trognitz F, Kopecky D, Matušikova I, Hausman JF, Wilhelm E (2010) Organ-specific defence strategies of pepper (*Capsicum annuum* L.) during early phase of water deficit. Plant Cell Rep 29:295–305

Tabor CW, Tabor H (1984) Polyamines. Annu Rev Biochem 53:749–790

Takahashi H, Imamura T, Miyagi A, Uchimiya H (2012) Comparative metabolomics of developmental alterations caused by mineral deficiency during in vitro culture of *Gentiana triflora*. Metabolomics 8:154–163

Takahashi T, Kakehi J-I (2010) Polyamines: ubiquitous polycations with unique roles in growth and stress responses. Ann Bot 105(1):1–6

Tanaka N et al (2010) The structure of starch can be manipulated by changing the expression levels of starch branching enzyme IIb in rice endosperm. J Plant Biol 2:507–516

Tassoni A, Antognoni F, Bagni N (1996) Polyamine binding to plasma membrane vesicles from zucchini hypocotyls. Plant Physiol 110:817–824

Tiburcio AF, Besford RT, Borrell A, Mace M (1995) Metabolism and function of polyamines during osmotically induced senescence in oat leaves and protoplasts. In: Wallsgrove RM (ed) Amino acids and their derivatives in higher plants. Cambridge University Press, Cambridge, pp 205–225

Tiburcio AF, Kaur-Sawhney R, Galston AW (1990) Polyamine metabolism. In: Miflin BJ, Lea PJ (eds) The biochemistry of plants, intermediary nitrogen fixation. Academic Press, New York, pp 283–325

Todorova D, Moskova I, Sergiev I, Alexieva V, Mapelli S (2008) Changes in endogenous polyamines and some stress markers content induced by drought, 4PU-30 and abscisic acid in wheat plants. In: Khan N, Singh S (eds) Abiotic stress and plant responses. International Publishing House, New Delhi/Bangalore/Mumbai, pp 205–215

Toumi I, Moschou PN, Paschalidis KA, Bouamama B, Salem-Fnayou AB, Ghorbel AW, Mliki A, Roubelakis-Angelakis KA (2010) Abscisic acid signals reorientation of polyamine metabolism to orchestrate stress response via the polyamine exodus pathway in grapevine. J Plant Physiol 167:519–525

Uemura T, Tachihara K, Tomitori H, Kashiwagi K, Igarashi K (2005) Characteristics of the polyamine transporter TPO1 and regulation of its activity and cellular localization by phosphorylation. J Biol Chem 280:9646–9652

Urano K, Hobo T, Shinozaki K (2005) *Arabidopsis* ADC genes involved in polyamine biosynthesis are essential for seed development. FEBS Lett 579:1557–1564

Urano K, Maruyama K, Ogata Y, Morishita Y, Takeda M, Sakurai N et al (2009) Characterization of the ABA-regulated global responses to dehydration in *Arabidopsis* by metabolomics. Plant J 57:1065–1078

Urano K, Yoshiba Y, Nanjo T, Igarashi Y, Seki M, Sekiguchi F, Yamaguchi-Shinozaki K, Shinozaki K (2003) Characterization of *Arabidopsis* genes involved in biosynthesis of polyamines in abiotic stress responses and developmental stages. Plant Cell Environ 26:1917–1926

Vladimir V, Shevyakova N (2007) Polyamines and stress tolerance of plants. Plant Stress 1(1): 50–71

Wang B-Q, Zhang Q-F, Liu J-H, Li G-H (2011) Overexpression of PtADC confers enhanced dehydration and drought tolerance in transgenic tobacco and tomato: effect on ROS elimination. Biochem Biophys Res Commun 413:10–16

Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218:1–14

Wen XP, Ban Y, Inoue H, Matsuda N, Moriguchi T (2010) Spermidine levels are implicated in enhanced heavy metal tolerance in a spermidine synthase –overexpressing transgenic European pear by exerting antioxidant activities. Transgenic Res 19:91–103

Wen X-P, Ban Y, Inoue H, Matsuda N, Moriguchi T (2009) Aluminum tolerance in a spermidine synthase-overexpressing transgenic European pear is correlated with the enhanced level of spermidine via alleviating oxidative status. Environ Exp Bot 66:471–478

Wen X-P, Pang X-M, Matsuda N, Kita M, Inoue H, Hao Y-J, Honda C, Moriguchi T (2008) Overexpression of the apple spermidine synthase gene in pear confers multiple abiotic stress tolerance by altering polyamine titers. Transgenic Res 17:251–263

Wimalasekera R, Tebartz F, Scherer GFE (2011) Polyamines, polyamine oxidases and nitric oxide in development, abiotic and biotic stresses. Plant Sci 181:593–603

Woo HR, Kim HJ, Nam HG, Lim PO (2013) Plant leaf senescence and death–regulation by multiple layers of control and implications for aging in general. J Cell Sci 126:4823–4833

Xu Y, Shi GX, Ding CX, Xu XY (2011) Polyamine metabolism and physiological responses of *Potamogeton crispus* leaves under lead stress. Russian J Plant Physiol 58(3):460–466

Yamaguchi K, Takahashi I, Berberich T, Imai A, Miyazaki A, Takahashi T, Michael A, Kusano T (2006) The polyamine spermine protect against high salt stress in *Arabidopsis thaliana*. FEBS Lett 580:6783–6788

Yamaguchi K, Takahashi Y, Berberich T, Imai A, Takahashi T, Michael AJ, Kusano T (2007) A protective role for the polyamine spermine against drought stress in *Arabidopsis*. Biochem Biophys Res Commun 352:486–490

Yang C, He S (2001) The relationship between polyamine and membrane lipid peroxidase during the senescence of cut rose flowers. Acta Botanica Boreali Occidentalia Sinica 21:1157–1161

Yang H, Shi G, Wang H, Xu Q (2010) Involvement of polyamines in adaptation of *Potamogeton crispus* L. to cadmium stress. Aquat Toxicol 100:282–288

Yang J, Zhang J, Liu K, Wang Z, Liu L (2007) Involvement of polyamines in the drought resistance of rice. J Exp Bot 58:1545–1555

Ye XS, Avdiushko SA, Kuc J (1994) Effect of polyamines on in vitro phosphorylation of soluble and plasma membrane proteins in tobacco, cucumber and *Arabidopsis thaliana*. Plant Sci 97: 109–118

Zacchini M, Iori V, Mugnozza GS, Pietrini F, Massacci A (2011) Cadmium accumulation and tolerance in *Populus nigra* and *Salix alba*. Biologia Plantarum 55(2):383–386

Zeid IM (2004) Response of bean (*Phaseolus vulgaris*) to exogenous putrescine treatment under salinity stress. Pak J Biol Sci 7(2):219–225

Zhang Z-K, Liu S-Q, Hao S-S, Liu S-H (2010) Grafting increases the copper tolerance of cucumber seedlings by improvement of polyamine contents and enhancement of antioxidant enzymes activity. Agric Sci China 9(7):985–994

Zhao J, Shi G, Qiuhong Y (2008) Polyamines content and physiological and biochemical responses to ladder concentration of nickel stress in *Hydrocharis dubia* (Bl.) Backer leaves. Biometals 21: 665–674

Zhou Q, Yu B (2010) Changes in content of free, conjugated and bound polyamines and osmotic adjustment in adaptation of vetiver grass to water deficit. Plant Physiol Biochem 48:417–425

Agriculture for Combating Global Starvation

20

Anil Kumar

Abstract

The paper deals with the issues of food insecurity, hunger, production, sustainable agriculture and environmental as well as regional issues. There are about 690 million people reported for chronic hunger at the end of the year 2020, and 135 million people were gone through the crisis levels, or alarming condition of food insecurity. As per global hunger index, about one-third countries in the world are facing serious or alarming situation. It is a positive sign that countries have overcome from extreme alarming situation since 2012, which were more than 17% in 2000. The outbreak of COVID-19 has increased risk of global poverty from 26% in 2019 (before pandemic) to 59% in 2020. Food system also faced the risk, particularly the jobs (about 35%) and livelihoods (about 34%). Overall agriculture sustainability index is improving but is required to reduce food loss and waste.

Keywords

Food habits · Food security · Hunger · Sustainable agriculture · Undernutrition

20.1 Introduction

This paper comes under interdisciplinary domain of the sociology of food, culture and environment. Several important works have been conducted by William Graham Sumner (1907), George Herbert Mead (1938/1972), Bronislaw Malinowski (1936, 1944), Marcel Mauss (1973), Pierre Bourdieu (1979/1984), Madhu Nagla (2020)

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and many more. The concept of food, culture and environment (in regional sense) differs from one society to another because of cultural world view of the people in different societies and geographical boundaries. However, in light of modernization and globalization, some concepts of food habits attracted the common people, academicians and scientists during COVID-19, which has played havoc in 2020–2021 and has made us learn more about the practices of food, nutrition, health and hygiene.

According to W. G. Sumner (1907), human beings had adopted and improved various means or ‘folkways’ to satisfy their four universal needs, i.e. hunger, love, vanity and fear (Weiler 2007). He explained how such conditions (hunger, love, vanity and fear) create needs and ideas to respond by using the path of habits, folkways, custom, mores and institutions (Sumner 1907). The need theory of Sumner was somehow supported by the cultural determinant theory given by Bronislaw Malinowski (1936, 1944), who explained that all (seven) fundamental needs of the human organism including food are responded/satisfied by the systems of organized activities in a cultural context. Such needs are not innate drives of human organism but reinforced by the cultural response to these innate urges.

As per George Herbert Mead (1938/1972), hunger may arise from some combination of dual factors, i.e. an inner state of the actor (human in society) and/or may be elicited by the availability of food in the environment. The hungry person must find a way of satisfying the immediate desire in the social environment. Non-fulfilment of such impulse (hunger) due to lack of plentiful or immediate food may create problem in the environment that must be overcome by the actor (Mead 1938/1972; Ritzer 2011).

Food is not only satiating the hungry stomach but also makes people feel the taste. Bourdieu (1979/84 c.f. Stewart 2013) worked in ‘Sociology of Taste’. He analysed views of 1217 respondents and said that most of the time expressions about the taste are determined by individuals’ social origin, enforced by their class and cultural settings (Stewart 2013). These jargons of taste are also expressing the existence of inequalities and powerlessness through exercise of social power, which are revived and maintained by the dominant cultural practices prevailing in the respective society (Stewart 2013).

Marcel Mauss (1973) analysed the approaches used in training and imitation, especially for those essential fashions that could be pronounced as four modes of life, i.e. the modes, the tonus, the ‘matter’, the ‘manners’, and the ‘way’. Such modes of life are being determined by the specific culture. It would be easier to understand the cultural influences on eating behaviour through an example (given by him): A pious Muslim can be easily recognized by his eating behaviour, because he will take food by using his hands and anyhow avoid using anything else, even when knife and fork are available, and will not have food by using the left hand. His certain gestures are neither driven by physiology nor psychology; it is tradition that enforces him to do it. He must apply such gesture, whenever he has a social choice (Mauss 1973). He explained the cultural (magical and religious) forces or holds over the recipient and sacred claim of the Anna/food[1] (Mauss 1966).

Overall, cultural context towards eating habits could not be ignored, and the influences raised by cultural diffusion, modernization, global markets and national/international policies could also be accepted. Such internal and external factors make change in cultural practices (rites and ritual) even food habits in human society and could be observed in the policy interventions before and during the pandemic of 2020–2021 on food security, population control and empowerment of the vulnerable sections in the society.

The increasing growth of the world population creates various challenges such as hunger, malnutrition, environmental degradation, climate change, etc., which provide scope for sustainable efforts and innovation to fulfil the need in order to increase agricultural production and proper storage and transportation, improve the system of global supply chain, decrease food losses and wastes due to mishandling, etc. It is also the need of the day to ensure the access of nutritious food to all who are suffering from hunger and malnutrition (SDG Knowledge Platform 2021). The future world population will increase between 8.1 and 9.6 billion by 2050 as per estimation made by the leading demographers. It will be visible in regions like sub-Saharan Africa, countries in the South Asia and Middle East of the world (Du Preez et al. 2020). Now, the farmers of the world are facing a critical challenge to produce more food for a large population within the available resources. Agriculture scientists are under pressure to diversify and develop improved varieties to avail the food and micronutrients, where policy makers make policies to protect the rights of the farmers as well as the consumers by minimising input cost. The social scientists should not deny their responsibilities in the development of new critical analysis towards the whole society in general and rural and agrarian society through specific multidisciplinary branch of sociology (Buttel et al. 1990) and paradigm shift in the sociology of agrarian society (Bjorkhaug 2012).

20.2 Hunger and Malnutrition

20.2.1 Global Trends of Hunger

The world is facing a serious situation of hunger, malnutrition and related problems that are increasing day by day. Generally, hunger is the distressed condition associated with poor absorption of calories and insufficiency in food; this may be the result of food deprivation and/or undernourishment and the habitualization of poor consumption of protein/calories that minimizes the dietary energy required for

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[1] Him who, without giving me to the gods or the
spirits, or to his servants or guests,
prepares and eats (me), and in
his folly thus eats poison, I eat him,
I am his death.

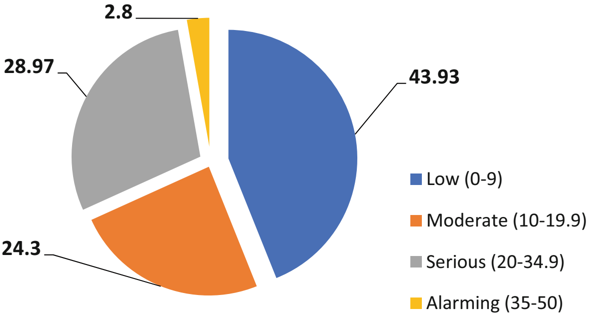

Fig. 20.1 GHI ranking of the countries (%) in the world. Source: von Grebmer et al. (2020)

human life to be healthy and productive. The requirement of protein/calories is not universal for all individuals; it has to be appropriate to the age, sex, body stature and level of physical activities (von Grebmer et al. 2020). There was 785 million hungry people in 2015 and increased up to 822 million in 2018 (von Grebmer et al. 2019). Findings suggest that about 690 million people of the world are suffering from the condition of chronic hunger, and 135 million human lives are facing severe food insecurity (von Grebmer et al. 2020).

GHI ranked global hunger score of the countries that is calculated from the world data on under five child mortality, child undernourishment, child stunting and child wasting. As per information available from GHI 2020 data, about 44% of the countries are at low (0–9.9) level in hunger index, 24.3% at moderate level (10–19.9), about 29% at its serious level (20–34.9) and only 2.8% at alarming situation (35–49.9). The situation is going to be under control that countries have been reported under extremely alarming situation (above 50) since 2012. On an average now, the global hunger level is at a moderate condition (von Grebmer et al. 2020; Fig. 20.1).

The situation of hunger is improving, but till now it is still reflecting the *serious* hunger condition among 31 countries of the world. There are additional 9 countries[2] also provisionally categorized as *serious* (score between 20 and 34.9). The situation of hunger is *alarming* in 3 countries, i.e. Chad (GHI score 44.7) an African country, Timor-Leste (GHI score 37.6) an island country of Southeast Asia and Madagascar (GHI score 36) the second largest island country of South Africa situated in the Indian Ocean. There are 8 more countries[3] also provisionally categorized to have *alarming* (score between 35 and 49.9) condition of hunger (von Grebmer et al. 2020; Fig. 20.2; Table 20.1).

The GHI report (von Grebmer et al. 2020) reflecting that global hunger score has declined to some extent between 2000 and 2020; within this period, Angola a Southwest African country was observed to have the highest absolute change in

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[2] Djibouti, Guinea, Guinea-Bissau, Lao PDR, Niger, Tajikistan, Uganda, Zambia, and Zimbabwe.

[3] Burundi, Central African Republic, Comoros, Democratic Republic of the Congo, Somalia, South Sudan, Syrian Arab Republic, and Yemen.

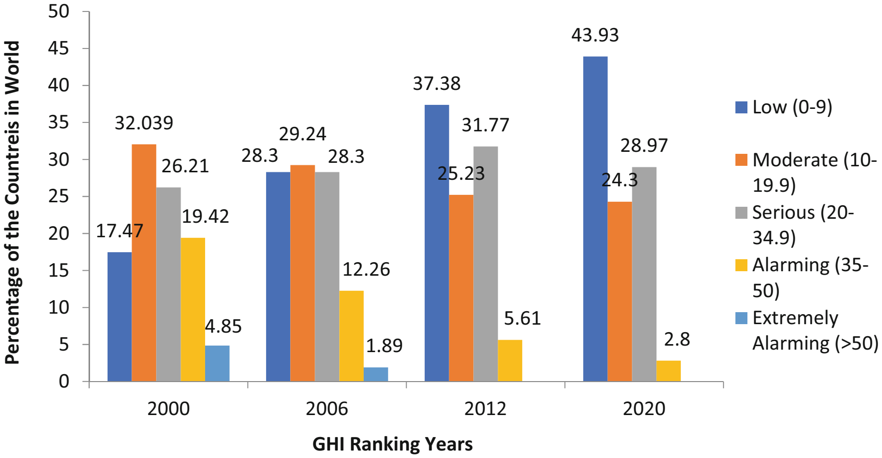

Fig. 20.2 Percentage of countries in GHI ranking in different years. Source: von Grebmer et al. (2020)

Table 20.1 Global Hunger Index of various countries

Ranking in GHI	Counties in the year 2000		Counties in the year 2006		Counties in the year 2012		Counties in the year 2020	
	No.	%	No.	%	No.	%	No.	%
Low (0–9)	18	17.47	30	28.30	40	37.38	47	43.93
Moderate (10–19.9)	33	32.039	31	29.24	27	25.23	26	24.3
Serious (20–34.9)	27	26.21	30	28.30	34	31.77	31	28.97
Alarming (35–50)	20	19.42	13	12.26	6	5.61	3	2.8
Extremely alarming (>50)	5	4.85	2	1.89	0	0	0	0
Total	103	100	106	100	107	100	107	100

Source: von Grebmer et al. (2020).

score, i.e. –38.1 (58.7%), but Albania a West European country has achieved the highest score percentage, i.e. –71.5% (von Grebmer et al. 2020). On the other hand, the progress of many countries is reflecting very slowly, and the situation of hunger remains severe. The places with the highest level of hunger and undernutrition in the world map are South Saharan region of Africa and South Asia, with GHI scores of 27.8 and 26.0, respectively, which have been considered as serious. Such areas were found highly vulnerable for the decline of food and nutrition insecurity that intensify the issues related to health, economy, environmental degradation and global crises of 2020–2021. As per estimation made by the GHI, the countries of the world failed on points of food security and sustainable agriculture; *that is why SDGs' target for achieving zero hunger will be partially achieved by 2030*. About 37 countries are going to fail to achieve it and even unable reach at low hunger level of the GHI severity scale (von Grebmer et al. 2020) (Table 20.2).

Table 20.2 The composition of Global Hunger Index

Dimensions of Global Hunger Index	Indicators linked with dimensions of Global Hunger Index
1. Child mortality	1. Under-five mortality rate • Death is the most serious consequence of hunger, and < 5 children are the most vulnerable in it • Wasting and stunting only partially capture the mortality risk of undernutrition • Improves the GHI's ability to reflect micronutrient deficiencies
2. Inadequate food supply	1. Undernourishment • Measures inadequate food supply (food insecurity) • Refers to the entire population, children and adults • Used as a lead indicator for international hunger targets
3. Child undernutrition	1. Wasting 2. Stunting • Goes beyond calorie availability, considers aspects of diet quality and utilization • Children are most vulnerable to nutritional deficiencies • Is sensitive to uneven distribution of food within the household • Stunting and wasting are nutrition indicators for the SDGs

Source: Wiesmann et al. (2015), von Grebmer et al. (2020).

Table 20.3 Prevalence of indicators adopted for the Global Hunger Index

		Prevalence	
S. no.	Indicators of global hunger index	Number (millions)	Percentage
1	Under 5 mortality rate (death/1000 live birth) in the world in 2019	5.189	38 (rate)
2	Prevalence of stunting among under 5 children in the world (%) in 2020	149.2	22
3	Prevalence of underweight among under 5 children in the world (%)	820	12.60
4	Prevalence of severe wasting among under 5 children in the world (%)	45.4	6.70

Source: UN IGME (2020), UNICEF et al. (2021), FAO et al. (2020).
There were 5.7% or 38.9 million children under 5 globally affected by overweight in 2020.

Hunger is directly associated with undernutrition that puts people in vulnerable condition, especially children and women in the society. The situation is also linked with the cultural practices and leadership skill among political leaders and bureaucrats. Many people in the world are facing the situation of hunger and undernourishment: about 690 million people are experiencing the situation of undernutrition; more than 149 million <5 children suffer from stunting (result of chronic undernutrition); more than 45 million <5 children suffer from severe wasting, a situation of acute undernutrition (Table 20.3). Studies suggest that about 5.3 million children of the world died a year before their fifth birthdays, and

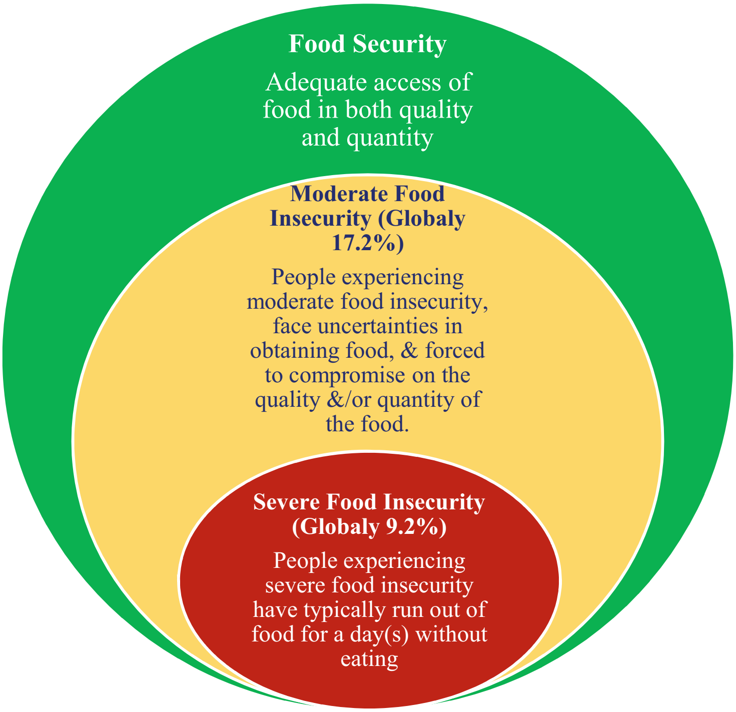

Fig. 20.3 Reasons behind food insecurity and its severity levels. Source: FIES, FAO et al. (2019)

many of those have lost their lives due to undernutrition (von Grebmer et al. 2020). Overall, 45% of deaths among under five children happen due to high prevalence of undernutrition (Black et al. 2013; von Grebmer et al. 2020).

Food security is one of the fundamental rights defined under universal declaration of human rights (Article 25) as well as in the Constitution of India (Article 21). It could be understood as ‘adequate access to food, both in quality and quantity’ without any discrimination for the whole population. Moderate food insecurity may be defined as ‘people’ experiencing and facing ‘uncertainties and inability’ to obtain food; they are forced to compromise to consume such food, i.e. not appropriate in quality and/or in quantity for their lives. Where in severe condition, people are experiencing severe condition of food insecurity and are typically fighting for their lives in search of food and expending the day(s) without getting food (FAO et al. 2019). As per the latest estimation made by FIES in the year 2018, slightly more than 700 million (9.2%) people of the world population have been exposed to severe condition of food insecurity (Fig. 20.3).

20.2.2 Severity of Food Insecurity Among Informal Workers in India

It can be observed at the labour markets (labour *adda*) in any metropolitan city in Indian subcontinent the crowd of skilled and unskilled labourers (male, female and sometimes adolescents also) with their instruments. Most of them have migrated from village areas of the nearby districts and states due to non-availability of employment, livelihoods and resources in their areas to survive. There is another problem faced by them is non-availability of regular work, shelter, potable water and toilet facility at work place as well as at the labour markets. Due to poor implementation of policies for migrant workers, they suffer from food insecurity and poor working condition. Due to irregularity/non-availability of work and denial of access to resources, they express their anger on most vulnerable members in the family, i.e. children and women, resulting in domestic violence and gender discrimination in food/nutrition, health and education, etc. Sometimes such type of pathetic conditions led to deviant behaviour or crime in society.

20.2.3 Factors Affecting Food Insecurity

The situation of insecurity in getting food may be called when individuals face crisis in getting safe, sufficient and nutritious food on regular basis for normal growth, development and active healthy life (FAO et al. 2020). The situation may occur due to unavailability of food with the people, and/or they are not able to get it. The severity level of food insecurity can be experienced by the people at different levels, i.e. influenced by the regional/geographical (soil condition and water availability), cultural (belief towards food and eating habits), social (ethnic/caste, gender) and overall economic condition (employment, buying capacity) or class. Food insecurity is not only responsible for hunger and undernutrition but also creates adverse condition for health and well-being as well as struggle in social relations (www.fao.org/hunger/en/). Such relations may result as domestic violence, community conflict (caste and religion) and class struggle. The food struggle is now touching the boundaries of the states and countries for owning the resources. The dynamics of food security and nutrition risks are serious concern of the society. It is an established fact that about 2 billion human beings have faced insecurity of food either at the moderate level or at severe level (FAO et al. 2020). The situation has been out of control due to spread of COVID-19 pandemic and its preventive measures.

20.2.4 COVID-19 and Food Insufficiency

The outbreak of the COVID-19 pandemic has created a major public health challenges and crisis related to appropriate and nutritional food for millions of people around the world. The children and poor developing countries were already suffering from hunger and malnutrition. The hit of corona virus has created a

Table 20.4 Jobs and livelihoods in the food systems at risk during COVID-19

Sectors	Food systems		Risk in food systems after COVID-19[a]			
	Jobs (millions)	Livelihoods (millions)	Jobs (millions)		Livelihoods (millions)	
			No.	%	No.	%
Food processing	716.77	2023.80	152.35	21.25	404.76	20.00
Food services	200.73	484.54	120.44	60.00	290.72	60.00
Distribution services	168.97	339.44	101.38	60.00	203.66	60.00
Transportation services	96.34	241.48	57.81	60.00	144.89	60.00
Machinery	41.61	101.05	16.64	40.00	40.42	40.00
Inputs	6.51	13.18	1.72	26.42	3.48	26.40
R&D	0.13	0.29	0.02	15.38	0.03	10.34
Total	1280.93	3214.84	451.64	35.26	1090.89	33.93

[a] Source: Unpublished FAO/IFPRI estimates, based on ILO (2020), UN (2020).

threatening condition as global food emergency and enlarged related consequences (UN 2020; FAO et al. 2020). In the future, the situation of hunger and vulnerabilities may increase due to socio-economic and political effects of COVID-19, which expended the economic challenges for the people residing in the developing nations including India. The assessment made by the World Bank (2021) to understand the impacts of COVID-19 is providing the facts that it influenced the severity and extensive increase in the global food insecurity and affected the most vulnerable households and people probably in almost every country. The World Food Programme (WFP) has estimated such impact and explored that people facing acute food insecurity have increased from 195 million to 296 million between April 2020 and April 2021 in 35 countries of the world. The situation is expected to continue through 2021 and up to 2022 (World Bank 2021) (Table 20.4).

The world is facing impending global food emergency (FAO 2020a) and massive social, psychological and economic losses during the pandemic of 2020–2021. The pandemic has caused a major destruction in the economic sector worldwide. The poor people and developing countries in the world are most affected. The large number of people engaged in food system is at risk of their jobs and livelihoods. As per estimation made by ILO (2020), UN (2020), about 35.26% workers of food system have lost their jobs, in which 21.25% in food processing, about 60% in food services, about 60% in distribution services, about 60% in transportation services, about 40% in machinery, 26.42% in inputs and 15.38% in research and design sectors are facing trouble either from losing their jobs or from likely being lost. There are more than 71% workers of the food system who engaged as informal workers for their livelihoods or survival. The proportion of the loss among the workers' engagement for livelihoods is nearer to those who have lost their jobs in the food system (Figs. 20.4, 20.5).

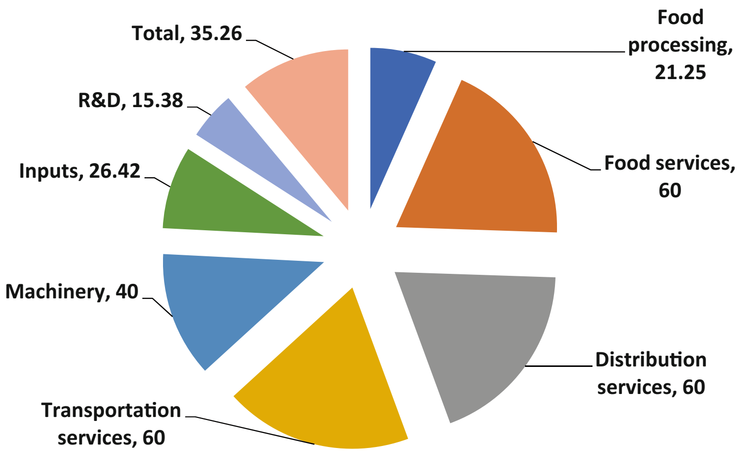

Fig. 20.4 Jobs at risk during pandemic in food systems (%). Source: ILO (2020), UN (2020)

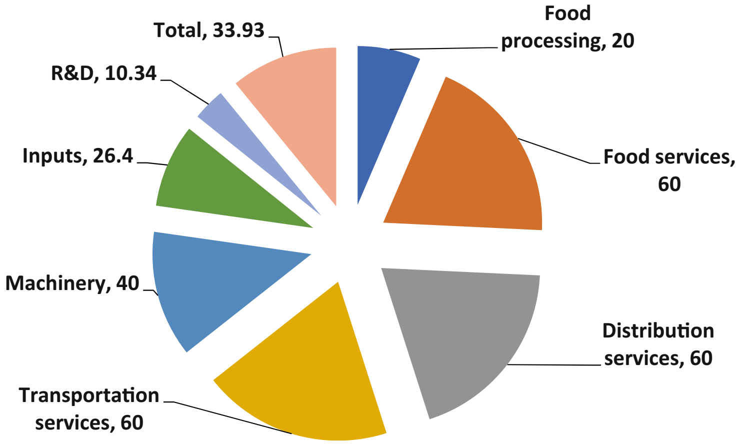

Fig. 20.5 Livelihoods at risk during pandemic in food systems (%). Source: ILO (2020)

There are links among food insufficiency, hunger, undernutrition and poverty. The workers of the informal sector are much vulnerable to food insufficiency, hunger and poverty because of unawareness about their rights and social security schemes/ programmes. COVID-19 has caused the worst hit to the poor and developing countries of the world. The pandemic has badly affected the lives of poor and informal workers. The International Labour Organisation (ILO) has estimated the possible impacts of the COVID-19 on informal workers by using poverty indicators. The data shows that the poverty level is going to increase from 26% to 59% during COVID-19. The increases in relative poverty rates are high among high-income countries (80%), lower-middle and low-income countries (74%), Africa (83%), America (84%) with highest and Europe and Central Asia (80%). The situation of

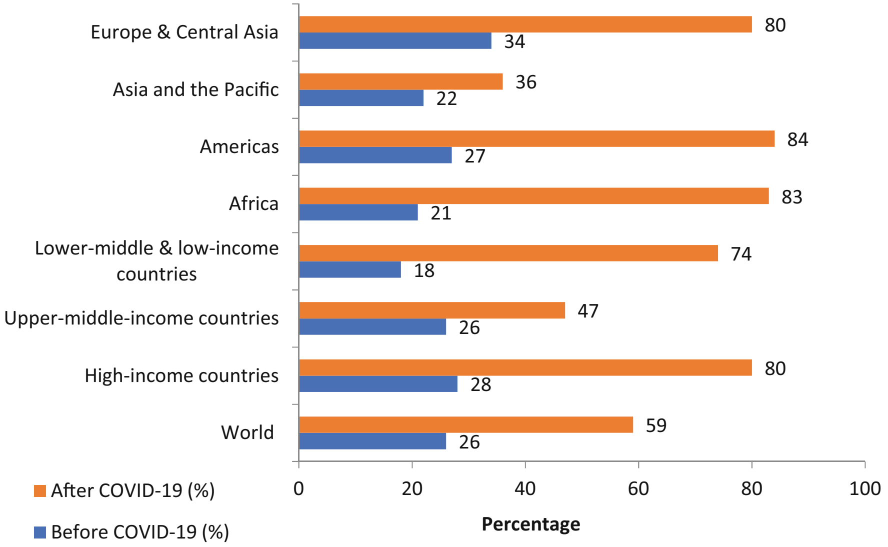

Fig. 20.6 Impacts of COVID-19 on poverty levels of informal workers. Source: FAOSTAT (2020)

increases in relative poverty rates is comparatively better in upper-middle income countries, i.e. 47%, and in the Asia and the Pacific, i.e. 36% (ILO 2020; Fig. 20.6).

The situation of lives in India is much more pathetic due to improper planning in development process, where economy and social infrastructure have been centralized in the specific metropolitan cities of the country like Delhi, Mumbai, Hyderabad, Bangalore, etc. This process has developed various features of inequality. People migrate towards such metropolitan cities for the livelihood, education, health and recreational facilities, but the poor and unskilled face various challenges there. There is positive correlation between metropolitan cities and crime against women, where more than 50% of crimes against women are happening in these four cities (NCRB 2018). Among the poor, this pandemic has most affected the lives of migrant workers and their family members in India. It has triggered massive reverse migration that has influenced the lives of people due to lack of adequate and delayed measures taken by the authorities to address the situation. India has observed the second largest people/workers' migration in history after 1947 that happened due to the partition of two countries, i.e. India and Pakistan, in which >14 million people migrated and displaced to India and Pakistan vice versa, depending on their religious belief (Mukhra et al. 2020). The current leadership is being criticized by the international media for their delayed and inappropriate decisions to minimize the effects of COVID-19. People with the world media are saying that politicians, policy makers and very few national media persons/houses believed that India has really mishandled the situation (Biswas 2021).

20.3 Food Sustainability and Response of Agriculture

20.3.1 The Context of Food Availability

There are 7.6 billion population of the world being fed by the resources available on the Earth with the support of agriculture and allied sectors. As per assumptions made by the United Nations, the world population is going to touch the number of 8.5 billion by the end of 2030, 9.7 billion by the end of 2050 and 10.9 billion by the end of twenty-first century. On an average, around 83 million people are being added in it every year, and even fertility rates may decline (UN 2019). The agriculture sector is now under pressure and expected to fulfil the global demand for food, feed and fibre, when the demand may be increased for bio-energy and other industrial purposes. This sector will be forced to face the decline in agriculture land and water resources due to unplanned urban settlements in developing countries. It will also be required to mitigate challenges of climate change, which will affect the natural resources, habitats and biodiversity on Earth. To feed the growing population on Earth, farmers have to adopt new technologies to produce more grains and food items from limited resources and their heard work.

As per statistical year book of ‘World Food and Agriculture-2020’, there is a positive sign observed in the total production of primary crops. The production level of primary crops was increased up to 9.2 billion tonnes during the year 2018; it was about 50% more in comparison to production level in 2000. There are four major crops[4] of the world measured for half of the global production of primary crops. In case of vegetable oils’ production, it had an increase that more than doubled between 2000 and 2017 due to an instant increase in the production of palm oil. There were 342 million tonnes (47% more than in 2000) of meat produced during the year 2018. America and Europe are the largest exporters, and Asia is the largest importer as well as consumer of the cereal crops in the world (FAOSTAT 2020; Fig. 20.7).

The agricultural sector is also being affected with the new liberal policies and looks for opportunities of industrial benefits in it. Globally, it is being promoted and industrialized to end hunger and to achieve the second goal of SDG. The increase in global productivity has been observed in many commodity crops but failed to achieve SDG2, even it has negatively affected the environment and crop diversity and biodiversity. The process has ignored the social consequences of this system and has adopted an assignment that is playing role as an anti-farmer agent. India is witness of the farmers’ agitation 2020–2021 against three bills passed by the Indian Parliament, without giving attention on the social consequences and farmers’ interest.

20.3.1.1 Farmers’ Agitation in India (2021–2021)

The farmers’ protest 2020–2021 is the largest ongoing protest in India. It is against the agriculture bills passed by the Indian Parliament in 2020. The protest was started

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[4] Sugar Cane, Maize, Wheat and Rice.

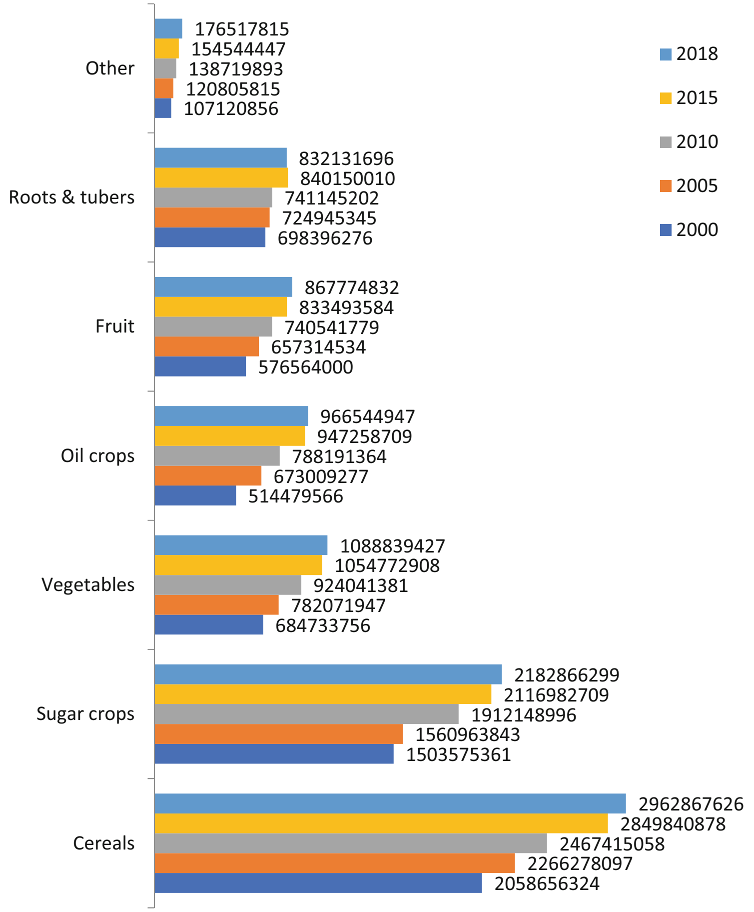

Fig. 20.7 Global crop production (metric tonnes) (FAOSTAT 2020)

on ninth August 2020 in Punjab, when these bills were made public. The Parliament of India passed two new Acts and made amendment of older one (in September 2020); all of these are dealing with agriculture in Indian subcontinent. These Acts are:

1. Farmers' Produce Trade and Commerce (Promotion and Facilitation) Act 2020 that prohibits the state governments from their levying, control, etc. and opens the sale of farm produces outside the *Kisan Mandis*/Agricultural Produce Market Committees (APMCs). In simple words these *Mandis*/markets have been thrown in the hands of private players to invest in the agricultural sector and also deal directly with the farmers.

2. Farmers (Empowerment and Protection) Agreement on Price Assurance and Farm Services Act 2020 has created framework for contract farming through an agreement between ‘a farmer’ and ‘a buyer’.
3. Essential Commodities (Amendment) Act 2020 that takes away the most essential commodities (cereals, pulses, oilseeds, potatoes, onions and edible oil) from the list of essential commodities (Ashmita and Barkataki 2021).

The decision of the government is against the farmers and the constitutional will because Indian agriculture is the state subject and the agriculture markets are being regulated by the state through its APMC (Act of 1939). It is the duty of the state and also the recommendations made by the National Commission on Farmers (NCF) of 2004, such Mandis /markets must be established within the radius of 5 kms to sale the farm-produces in 80 km^2. Further, to reach the standard coverage area India has need of 41,000 markets/*Mandis* (Manjula 2021).

Some people have questioned why farmers from Punjab, Hariyana and Western Uttar Pradesh have participated more and not from Eastern Uttar Pradesh. The answer is that people experiencing and practicing the culture of poverty could not assess their right and could not do movement. Findings suggest that in Uttar Pradesh, 92.5% of all farmers belong to the marginal (<1 ha) and small (1–2 ha) categories and hold 64.8% of the total area cultivated (Verma et al. 2017; Kumar 2018). It is essential to focus on regenerative farming systems such as agroecology and food sovereignty; it deserves more attention for their significant, potential, social and environmental benefits (Anderson and Rivera-Ferre 2021) in combating the global starvation and related challenges being faced by the world’s population.

20.3.2 Investment in the Agricultural Sectors

Investment in the agricultural sectors may be one of the key interventions for eradicating poverty, hunger and malnutrition, especially from the rural areas, where most poor population of the world live and survive with minimum facilities. The public sector investment is a key agent for eradicating absolute and relative poverty, hunger and malnutrition because it generates/develop public facilities like agricultural research institutions and extension services and social infrastructures such as education, health, transportation and recreation, which are usually not in reach of poor people if being provided by a private players. The public sector also plays a crucial role in regulating the sustainable management of natural resources through policy intervention and incentives (FAO 2017).

Private partners could play a strong role in agriculture sector, but their motive in such investments must fulfil the needs of the people through:

1. Creating roads and markets for the poor.
2. Lowering the costs of farm technologies and services.

3. Increasing productivity and income among small-scale and marginal farmers.
4. Developing value chain system and value addition facilities for primary agricultural produces; it will help to diversify and increase the farmers' income.
5. Creating appropriate and large number of job opportunities for the rural poor.

20.3.3 Reducing Poverty from Rural Areas

Rural society needs to reduce poverty, not only through economic and materialistic interventions but also in bringing them out from 'culture of poverty' in which people feel alienated from their society due to the inability of success. Such inabilities bring them in a frustrated state of mind and transcend it to their family, which convert them into situation of poverty. The culture of poverty tends to perpetuate itself and makes them unready (poor state of mind may be developed in their lifetime) to take full advantage of changing conditions and/or improving opportunities (Lewis 1966) available in present scenario and express gratification with their conditions of poverty as 'normal'. In this context, it is one of the major duties of the government, policy makers and programme implementing agencies (public or private) that they have to invest for change in rural area through strengthening rural institutions/ organizations, developing non-farm economies and intensifying the coverage of social protection policies, social infrastructure facilities and quality of services from public institutions. The policies have to improve access of technologies, services, markets and participation in sustainable management of natural resources by the resource poor farmers, family farmers and poor people to boost their productivity and income and finally to achieve the goals of SDGs.

20.3.4 Improving Food Sustainability

Problems related to food insufficiency and hunger is being experienced by most of the world countries, but food sustainability challenges may be different for low-, middle- and high-income countries. The world is going to face an alarming situation due to the early effects of climate change than what was once thought. Now, we have to limit global warming and avoid its negative effects in all aspects of social ecology. Agricultural activities also account for emission of about 30% of the global greenhouse gas (BCFN 2018b). Countries of the world have to address the issues of climate change without affecting the sustainability of the global food system. It is the responsibility of policy makers, scientists, social scientists, non-governmental organizations (NGOs), private players, the media and other food-system stakeholders to consider a sustainable global food system. They have to innovate and identify the best practices for future generations (BCFN 2018b). Consumers and primary producers could not be left free from taking responsibility from the creation of a sustainable food system, environmental sustainability, reducing food loss and waste, health and nutrition, which are inter-linked. People have to change their food habits and shift away from dependency on livestock to plants, for positive impact on

Table 20.5 Global food sustainability score

Food sustainability score 2018	Overall score		Food loss and waste		Sustainable agriculture		Nutritional challenges	
	No.	%	No.	%	No.	%	No.	%
Very high score (71.2 to ≥76.1)	16	23.88	17	25.37	16	23.88	17	25.37
High score (66.5 to ≥71.1)	16	23.88	16	23.88	17	25.37	16	23.88
Medium score (62.7 to ≥66.4)	18	26.87	17	25.37	16	23.88	17	25.37
Low score (52.3 to ≥62.6)	17	25.37	17	25.37	18	26.86	17	25.37
Total	67	100	67	100	67	100	67	100

Source: BCFN (2018a) Food Sustainability Index 2018.

global health. Scientific findings are also suggesting the use of plant-based protein that could protect human lives from cardiovascular disease (BCFN 2018a).

A major responsibility with the stakeholders is to improve the global food sustainability score of their countries. As per food sustainability index, about 24% countries scored very high (71.2 to ≥76.1), about 24% high (66.5 to ≥71.1), about 27% medium (62.7 to ≥66.4) and about 25% low (52.3 to ≥62.6) in overall ranking. The situations of 'food loss and waste' score, 'sustainable agriculture' score and 'nutritional challenges' score are nearby similar and have positive correlative among each other (BCFN 2018a). There is a major challenge in the food system of the world that about 14% of food waste valued to have lost an estimated 400 billion USD every year in the process of harvest and distribution. It is crucial to reduce food losses to improve food security, because food loss and waste are affecting all factors along with food supply chains (marketing and value addition) and finally the end consumers. Food loss and waste is also linked with inefficient use of resources (human resources, water, energy and land) as well as social and environmental burden (FAO 2021; Table 20.5).

Malthus' idea is still relevant for population growth and planning: 'human population increases geometrically, while food production increases arithmetically', is influencing policy makers and social scientists in taking scientific decision towards food security and mankind (Weir 1991). The growing population is creating pressure on Earth and natural resources to provide more primary products to fulfil the needs of food and nutrition, fodder for the livestock and wild life and raw material for various industries. There is a need to adopt sustainable agriculture practices to feed 9.7 billion people of the world, which will demand 70 percent more food in 2050 (FAO et al. 2019). Ensuring food security, reducing global hunger and malnutrition and substantial improvements in global food system are required.

As per report prepared by the Barilla Centre for Food and Nutrition (BCFN), Italy's overall score of the sustainable agriculture among all countries is 66.4%, food loss and waste score is about 69%, sustainable agriculture score is 67.7%, and nutritional challenge score is 62.6%. Food loss and waste score is richest among low-income countries, but nutritional challenge score is poor in such countries (Fig. 20.8).

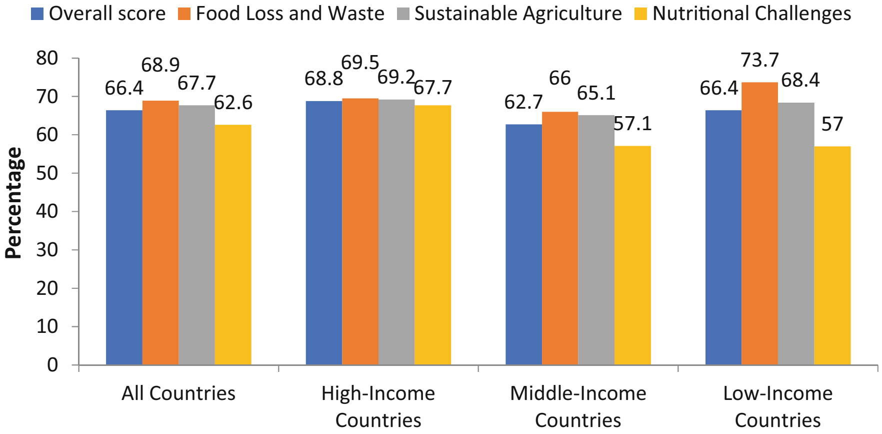

Fig. 20.8 Agricultural sustainability in various income group of countries. Source: BCFN (2018a). Agriculture Sustainability Index 2018 (regional compare)

20.3.5 Improving the Agriculture Sector

The agricultural sector needs effective intervention policies and programmes that have to provide input subsidies, knowledge dissemination and extension services, value chain system and its enhancement, etc. In case of small and marginal holder farmers in developing countries like India, such interventions will not be able to strengthen food security, and it may even mislead them and boost the inequities in the farming sector and deteriorate the food sufficiency with the poorest households. To address such issues of food insecurity and not just production of primary crops (Bizikova et al. 2020), there are some corrective measures to be considered:

1. The targeted of the intervention in agriculture is to be supportive for poor, small and marginal farmers, especially women; these groups of marginal section are facing the lack of assets (land and farm equipment, irrigation facilities, etc.), unable to get updated by the scientific knowledge and extension services and access to markets. As per recent report of the FAO (2020b), women comprise about 43% of the labour force in the agricultural sector of developing countries as well as two-thirds of poor livestock keepers (600 million) of the world. There are 79% economically active women from the least developed countries, and it was reported that the agricultural sector is the primary source of livelihoods for them; share of such women is about 48% worldwide among economically active women (FAO 2020b).
2. There is need of intervention with the features of equality in wage of farm workers, price of agriculture produces and equity in facilities for women workers and resource poor farmers. That should be a combination of multi-layered and multitasking complementary interventions that have to be appropriate small and marginal farmers.

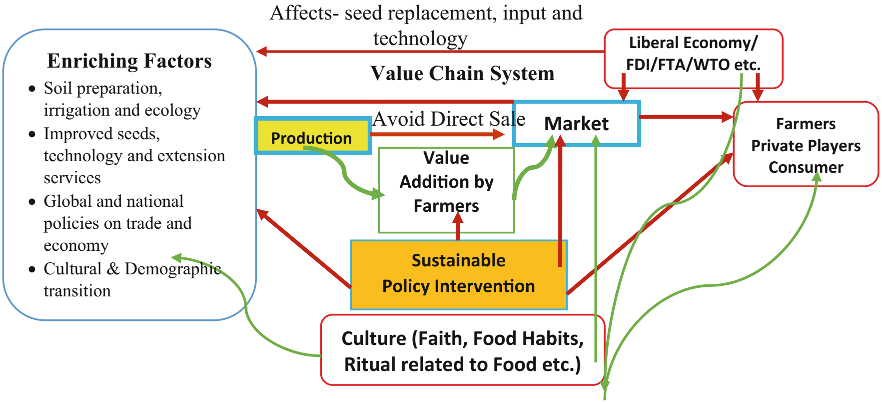

Fig. 20.9 Accessible, affordable and sustainable food system

3. Intervention programs must be focused on the production of crops that has to be relevant to local culture and climatic condition.
4. Adopt eco-friendly farming practices for sustainable resources on Earth.
5. Prevention and Reduction of Food Loss and Waste: now investments must be focused on prevention of yields from insects and environmental effects; such measure will be more effective. Management of food loss and waste will solve issues of poverty, starvation and malnutrition as well as the issue of climate change and social security (Fig. 20.9).

20.4 Conclusion and Suggestions

It is an important issue in front of the global society to give attention for sustainable agriculture and start safeguarding the natural resources; without that severity of hunger, food insecurity and undernutrition will not be solved. Our investment patterns must be supportive for the vulnerable population and sustainable development. The inclusive policies have to be adopted for developing social infrastructure accessible to the poor, and it must end hunger, food insecurity and all forms of malnutrition while ‘leaving no one behind’ (FAO et al. 2019).

We have to focus on four key dimensions of food security, which are the following:

1. Ensure supply of food at all levels, i.e. national, regional and local, to maintain price and food availability to reduce food insecurity and hunger. Some other services also required, i.e. potable water, sanitation and health services, for proper absorption of the food by the people.
2. Ensure accessibility of food to all individuals by making them able to produce their food or purchase it. This is to ensure complete removal of hunger and malnutrition from the world. It is the responsibility of the countries to give

emphasis on improvements in the productivity and quality production of food material. In this process, farmer's income and their interest should not be denied.

3. We could not ignore the cultural practices and belief that suggest people what they have to take or not, in which form that food item will be processed and served for people. Policy makers and intervention agencies have to consider the context for better use of food items and maintaining the nutritional quality that has to be obtained through its consumption.
4. It has to be kept in the minds of the policy makers as well as the implementing authorities to ensure food stability and accessibility at all times for the population in stabile price and securing incomes for the marginalized section of the society.

References

Anderson Molly D, Rivera-Ferre M (2021) Food system narratives to end hunger: extractive versus regenerative. Curr Opin Environ Sustain 49:18–25

Ashmita S, Barkataki BD (2021) 'Dilli Chalo': the pulse of those that feed the nation, EPW Engage https://www.epw.in/engage/article/dilli-chalo-pulse-those-feed-nation

BCFN (2018a) Sustainable agriculture index 2018. Barilla Centre for Food and Nutrition (BCFN), Rome

BCFN (2018b) Fixing food 2018: best practices towards the sustainable development goals. Barilla Centre for Food and Nutrition (BCFN), Rome

Biswas S (2021) Covid-19: how India failed to prevent a deadly second wave, BBC, April 14. https://www.bbc.com/news/world-asia-india-56771766

Bizikova L, Jungcurt S, McDougal K, Tyler S (2020) How can agricultural interventions enhance contribution to food security and SDG 2.1? Glob Food Sec 26:1–8

Bjorkhaug H (2012) Exploring the sociology of agriculture: family farmers in Norway—future or past food producers? In: Sociological landscape—theories, realities and trends. In Tech, Sanghai

Black RE, Victora CG, Walker SP, Bhutta ZA, Christian P, de Onis M, Ezzati M et al (2013) Maternal and child undernutrition and overweight in low-income and middle-income countries. Lancet 832(9890):427–451

Bourdieu P (1979/1984) Distinction: a social critique of the judgement of taste. (Translated by Richard Nice). Howard University Press, Cambridge

Bronislaw M (1936) Culture as a determinant of behavior. Sci Mon 43(5):440–449

Bronislaw M (1944) A scientific theory of culture. A galaxy book. Oxford University Press, New York

Buttel FH, Larson OF, Gillespie GW (1990) The sociology of agriculture. Greenwood Press, New York

Du Preez CC, van Huyssteen CW, Kotze E, van Tol JJ (2020) Ecosystem services in sustainable food systems: operational definition, concepts, and applications. In: The role of ecosystem services in sustainable food systems. Academic Press, Cambridge

FAO (2017) Ending poverty and hunger by investing in agriculture and rural areas. Food and Agriculture Organization of the United Nations, Rome

FAO (2020a) Impacts of corona virus on food security and nutrition in Asia and the Pacific: building more resilient food systems. Bangkok, Food and Agriculture Organisation of United Nations

FAO (2020b) The female face of farming, reduce rural poverty. Food and Agriculture Organization of the United Nations, Rome. http://www.fao.org/reduce-rural-poverty/resources/resources-detail/en/c/468431/

FAO (2021) Food loss and waste. Food and Agriculture Organization of the United Nations, Rome. http://www.fao.org/policy-support/policy-themes/food-loss-food-waste/en/

FAO, IFAD, UNICEF, WFP, WHO (2019) The state of food security and nutrition in the world 2019: safeguarding against economic slowdowns and downturns. FAO, Rome

FAO, IFAD, UNICEF, WFP, WHO (2020) The state of food security and nutrition in the world 2020: transforming food systems for affordable healthy diets. Food and Agriculture Organization of the United Nations, Rome. https://doi.org/10.4060/ca9692en

FAOSTAT (2020) FAOSTAT 2020a stat yearbook 2020-fig20

GHI (2020) Global hunger index: one decade to zero hunger linking health and sustainable food systems (report). Chatham House

ILO (2020) ILO monitor: COVID-19 and the world of work. International Labour Organisation, Washington. https://www.ilo.org

Kumar A (2018) Challenges in adopting modern farming practices by resource poor farmers: a case of eastern Uttar Pradesh. East Anthropol 71(1–2):15–39

Lewis O (1966) The culture of poverty. Sci Am 215(4):19–25

Madhu N (2020) Sociology of food. Rawat Publication, Jaipur

Manjula M (2021) The smallholder in the agriculture market reforms in India. Econ Pol Wkly 56(15):22–26

Mauss M (1966) The gift, translated by Ian Gunnison with Introduction by E.E. Evans-Pritchard. Cohen & West Ltd., London

Mauss M (1973) Techniques of the body. Econ Soc 2(1):70–88

Mead GH (1938/1972) The philosophy of the act. University of Chicago Press, Chicago

Mukhra R, Krishan K, Kanchan T (2020) COVID-19 sets off mass migration in India. Arch Med Res 51(7):736–738

NCRB (2018) Crime in India 2018. National Crime Record Bureau, Government of India, Ministry of Home Affairs, New Delhi

Ritzer G (2011) Sociological theories. McGraw-Hill, New York

SDG Knowledge Platform (2021) Food security and nutrition and sustainable agriculture. https://sustainabledevelopment.un.org/topics/foodagriculture. Accessed 10 May 2021

Stewart S (2013) Why do we like what we like? In: A sociology of culture, taste and value. Palgrave Macmillan, London, pp 56–74

Sumner WG (1907) Folkways: a study of the sociological importance of usages, manners, customs, mores, and morals. Ginn and Company, Boston

UN (2019) World population prospects 2019: highlights. Department of Economic and Social Affairs Population Division, United Nations, New York

UN (2020) Policy brief: the impact of COVID-19 on food security and nutrition. United Nations, New York. https://www.un.org/sites/un2.un.org/files/sg_policy_brief_on_covid_impact_on_food_security.pdf

UN IGME (2020) United nations inter-agency group for child mortality estimation. https://data.unicef.org/topic/child-survival/under-five-mortality/

UNICEF, WHO, International Bank for Reconstruction and Development/The World Bank (2021) Levels and trends in child malnutrition: key findings of the 2020 edition of the joint child malnutrition estimates. World Health Organization, Geneva

Verma S, Gulati A, Hussain S (2017) Doubling agricultural growth in Uttar Pradesh: sources and drivers of agricultural growth and policy lessons. Working paper 335, Indian Council for Research on International Economic Relations, New Delhi

von Grebmer K, Bernstein J, Alders R, Dar O, Kock R, Rampa F, Wiemers M, Acheampong K, Hanano A, Higgins B, Ni Cheilleachair R, Foley C, Gitter S, Ekstrom K, Fritschel H (2020) 2020 global hunger index: one decade to zero hunger: linking health and sustainable food systems. Welthungerhilfe Bonn and Concern Worldwide, Dublin

von Grebmer K, Bernstein J, Mukerji R, Patterson F, Wiemers M, Ni Cheilleachair R, Foley C, Gitter S, Ekstrom K, Fritschel H (2019) 2019 global hunger index: the challenge of hunger and climate change. Welthungerhilfe Bonn and Concern Worldwide, Dublin

Weiler B (2007) Sumner, William Graham (1840–1910). In: Blackwell encyclopedia of sociology. Blackwell Publications, p 4893

Weir DR (1991) Malthus's theory of population. In the world of economics. The New Palgrave, London

Wiesmann D, Biesalski HK, von Grebmer K, Bernstein J (2015) Methodological review and revision of the global hunger index. ZEF working paper series no. 139 University of Bonn, Center for Development Research (ZEF), Bonn

World Bank (2021) Food security and COVID-19. https://www.worldbank.org/en/topic/agriculture/brief/food-security-and-covid-19. Accessed 11 May 2021

Land Use and Biodiversity Conservation Through Agroforestry

21

Salil Tewari, Pallavi Bhatt, Harshita Negi, Ashutosh Dubey, S. B. Chavan, Akash Chichaghare, and Rajesh Kaushal

Abstract

Perennials plants are vital for existence of human race since time immemorial. Agroforestry, i.e., agriculture with trees, is an age-old practice that had evolved with human society which is ecologically sound and economically viable and is made up of sustainable farming systems that help in tackling various issues including low income to climate change. Traditionally, in every part of the world, several tree species have been planted in and around the habitat to not only fulfil the requirements of food, fodder, fuel, fertilizer, fruits, and fiber but also provide many benefits like soil and water conservation, enhancing soil health, improving microclimate, sequestrating atmospheric carbon dioxide and many more ecological benefits. Among various systems, homegardens are the most biodiverse sites of the tropic and present an excellent example of "biomimics of nature" by manmade efforts. This paper focuses on various documented agroforestry types and the role of tree-based systems in biodiversity conservation and enhancement.

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Keywords

Agroforestry systems · Biodiversity conservation · Environment enrichment · Land use · Poverty alleviation

21.1 Introduction

Since the ancient times, Indian civilization had developed culture and wisdom of farming by the enlightened sages who interacted with the elements of nature and got acquainted with the rhythms of nature. This knowledge is cultivated in the form of historic Vedic scriptures describing the art and science of cultivation and production with agricultural techniques. Maharishi Kashyap in scripture titled “Krishishukti” classified land into several categories, thereby identifying suitable areas for planting merited trees. In Bhagwad Gita Chap. 10, shlok 26 conveys that Lord Vishnu identified himself as the tree of Ashawatha (Pipal). This well-known fact that the pipal tree has CAM-type photosynthetic machinery that can release oxygen even during the night profoundly proves that processes of photosynthesis and respiration were known to Indian scholars. “Atharva Veda” enlisted 300 varieties of trees, and “Krishi Parashar” is the first treatise on agriculture defining rain as “adhaka” with in-depth analysis of rain forecasting, rain measurement, etc. Vrukshaurved described tree plantation, its types, raising nursery, transplanting, grafting, etc. The role of many common trees such as Khejri or sami (*Prosopis cineraria*), aswattha (*Ficus religiosa*), Palasa (*Butea monosperma*), and varana (*Crataeva roxburghii*) in Indian folklife has been mentioned in Rigveda and Atharvaveda (Mann and Saxena 1980). Further domestication of useful trees from the forest instituted “agroforestry,” and further evolution of mankind agroforestry systems also thrived.

Henceforth Agroforestry is an age-old agricultural system as the process of human evolution when man learnt the means of domesticating plants/trees and animals and left hunting and gathering habit. Shifting cultivation is form of most primitive traditional agroforestry practice of prehistoric India by virtue of agro-ecological conditions in the region. Horticulture as co-existent with agriculture is found to have been prevalent in India from the early historic period (500 B.C. to 1st century AD). Raychaudhuri and Roy (1993) had reported that cultivation of date palm, banana, pomegranate, coconut, jujube, aonla (*Emblica officinalis*), bael (*Aegle marmelos*), lemon and many varieties of other fruits and requirement of livestock in agriculture and a mixed economy of agriculture and cattle breeding may be traced in proto-history chalcolithic periods of Indian civilization.

Agroforestry is an ancient land-use system that has ecological and economic benefits by deliberate inception of mixed trees or woody perennials in crops/animal production (Nair 1993). Agroforestry has been reported to serve as a potential source to conserve important indigenous tree species (Worku and Bantihun 2017). Integration of trees with agricultural systems may result in more efficient use of sunlight, moisture, and plant nutrients thereby reducing the risk and increasing the total productivity (Chavan et al. 2015, 2016; Newaj et al. 2016). The practice has been

Table 21.1 Primitive agroforestry systems in India

Systems/practices	Agroecological adaptations
A. Agrisilvicultural systems	(Woody perennials + crops)
1. Shifting cultivation	In tropical forest areas
2. Taungya	In all regions
3.Homegardens	Mainly tropical regions
4. Plantation-based cropping	Mainly humid tropical regions
system	In all regions specially semi-arid and arid regions
5. Scattered trees on	In wind-prone areas, all regions, viz., coastal,
farmlands	Arid, alpine areas
6. Shelter belts and wind	In all regions
breaks	In hilly areas, along the sea coast and ravine lands
7. Boundary plantation and	In all regions
live hedges	Mostly humid and sub-humid regions of Southeast Asia with
8.Woodlots for soil	less grazing pressure on plantation lands
conservation	Intensively cropped areas in northern India
9. Trees on rangelands	(trees + crops + animals/pasture)
10. Plantation crop with	Semi-arid and mountainous ecosystem
pastures and animals	Low lands
11. Industrial plantation with	In all regions
crops	All through subtropics and tropics with bioedaphic
B. Agro-silvopastoral	Sub-climaxes
systems	In hilly orchards
12. Seasonal forest grazing	
13. Aquaforestry	
14. Apiculture with trees	
C. Silvopastoral	
15. Silvopastures	
16. Horti-pastoral	

Adapted from Dagar et al. (2014)

utilized for many years, particularly in developing countries, and is now widely promoted as a land-use approach that includes a combination of agriculture, forestry, horticulture, husbandry etc.

In India different agroforestry systems had existed (Table 21.1). Although denouncement being put forward by the foresters and agriculturists, who have been concerned only on monoculture production of their respective preferred commodities of crops, animals and trees thereby ignoring socio-economic significance of such combined integrated ecological systems.

Therefore, it can be summarized that agroforestry can be used as a dynamic, ecologically based natural resource management practice which diversify production for increased social, economic, and environmental benefits (Newaj et al. 2015; Chavan et al. 2020).

Biodiversity, the variety of life forms, the genes they contain, and the ecosystems they form, consists of several layers of biological organization from gene to species and ecosystem, across multiple spatial scales. Since agroforestry is an integrated land-use system, its tree component may open new provisions for both floral and faunal biodiversity conservation, ecosystem services, and climate resilience. There are three hypotheses on agroforestry-based conservation of tropical biodiversity, viz.: (1) the agroforestry-deforestation hypothesis, agroforestry curb pressure of unsustainable deforestation by replacing it with protected agroforestry parks to cope with limited availability of forestland and resources, (2) agroforestry that provides suitable habitat for forest-dependent plant and animal species thereby preserving sensitive floral and faunal germplasm of area, and (3) continuous monocultures of one or two crops on the same land accompanied with crop domestication from the wild relatives that has contributed to the reducing biodiversity worldwide. This can be restrained by establishing a biodiversity-friendly corridor between existing natural habitats and buffering them against less sustainable land use patterns, e.g., modern agricultural farming methods focus on providing just one ecosystem service: food production. Agroforestry practices also provide ecosystem services for sustainable agriculture such as soil erosion prevention and water recharge, thereby preventing the degradation and loss of surrounding habitat (Newaj et al. 2020).

21.2 Agroforestry Systems in India

Globally, agroforestry, the intentional integration of trees on farmland, is practiced by 1.2 billion people (World Bank 2004) on 43% area of total agricultural lands having more at least 10% cover; i.e., >1 billion ha (Zomer et al. 2016). Tree-incorporated agriculture systems in India are integral part of agriculture for support of livelihood and environment security (Chavan et al. 2021). The meticulous growth of trees on bunds as well as in agricultural fields as scattered trees, besides use of open interspaces in the newly planted orchards for cultivating field crops, is a widespread activity in the Indian subcontinent. Homegardens in coastal states not only provide food security and diversity but also provide basic needs of fuelwood, fodder, plant-derived medicines, and income from small land holdings of individual farmer. Different agroforestry systems had been recommended for different regions of India as per the need of the location as *Morus* and *Grewia-based* system had been recommended for the western Himalayas, alder-based for the North Eastern Hill (NEH) region, poplar-based agroforestry system for the Indo-Gangetic region, aonla and khejri-based for the semi-arid and arid regions, teak-based for the tropical region, and *Gmelina* and *Acacia*-based system for humid and sub-humid regions (Handa et al. 2016; Keerthika et al. 2015; Newaj et al. 2016; Chavan et al. 2020). Agroforestry practices have been further associated with the various ecological services like watershed development, soil rehabilitation, and treatments of degraded and other wastelands (Chavan et al. 2015). It is estimated that, currently, agroforestry has a greater number of trees than the respective “state forests.” The prominent agroforestry systems from different regions of the country are enumerated and presented in Table 21.2 and Fig. 21.1 (ICAR-CAFRI, Jhansi).

Table 21.2 Prominent agroforestry systems in different regions of India

Agro-climatic zone	Agroforestry systems	Tree component	Crop/grass
Western Himalayas	Silvopasture (RF)	*Grewia optiva*	*Setaria* spp.
		Morus alba	*Setaria* spp.
	Agrihorticulture	*Malus pumila*	Millets, wheat
	Agrihorticulture	*Prunus persica*	Maize, soybean
Eastern Himalayas	Agrisilviculture	*Anthocephalus cadamba*	Rice
	Agrihorticulture	*Alnus nepalensis*	Large cardamom/coffee
	Silvopasture	Bamboos, *Parkia roxburghii, Morus alba*	–
	Silvopasture	*Bauhinia variegata, Ficus, Morus alba*	Napier
Lower Gangetic Plains	Agrisilviculture (Irri)	*Eucalyptus, Albizia lebbeck*	Rice
	Agrihorticulture (Irri)	Mango/Banana/litchi	Wheat, paddy, maize
	Silvopasture	*Morus alba, Albizia lebbeck*	*Dichanthium, Pennisetum*
Middle Gangetic Plains	Agrisilviculture (Irri)	*Populus deltoides*	Sugarcane-wheat
	Agrisilviculture (Irri)	*Eucalyptus* spp.	Rice-wheat
	Agrisilviculture	*Dalbergia sissoo*	Sesamum
	Agrihorticulture (Irri)	Mango/citrus	Rice-wheat
	Silvopasture	*Albizia lebbeck*	*Chrysopogan, Dicanthium*
Trans Gangetic Plains	Agrihorticulture (Irri)	*Emblica officinalis*	Black gram/green gram
	Agrisilviculture	*Azadirachta indica*	Black gram/wheat/mustard
	Silvopasture	*Bauhinia variegata, Albizia lebbeck*	*Cenchrus, Pennisetum*
Upper Gangetic Plains	Agrisilviculture (Irri)	*Populus deltoides*	Wheat, bajra fodder
	Agrisilviculture (Irri)	*Eucalyptus*	Rice-wheat
	Silvopasture	*Bauhinia variegata, Albizia lebbeck*	*Chrysopogon, Poa*
Eastern plateau & hills	Agrisilviculture	*Gmelina arborea*	Rice, linseed
	Agrisilviculture	*Acacia nilotica*	Rice
	Silvopasture	*Acacia mangium, A. nilotica, bamboos*	–
	Silvopasture	*Leucaena leucocephala*	*Chrysopogon, Pennisetum, Dichanthium*

(continued)

Table 21.2 (continued)

Agro-climatic zone	Agroforestry systems	Tree component	Crop/grass
Central plateau & hills	Agrihorticulture (Irri)	*Psidium guajava*	Bengal gram/ groundnut
	Agrihorticulture (RF)	*Emblica officinalis*	Black gram/green gram
	Agrisilviculture	*Acacia nilotica/Leucaena leucocephala/Azadirachta indica/Albizia lebbeck*	Soybean, black gram-mustard/ wheat
	Silvopasture (RF- and degraded lands)	*Albizia Amara, Leucaena leucocephala, Dichrostachys cinerea*	*Chrysopogon, Stylosanthes hamata, S. scabra*
	TBOs (RF)	*Jatropha curcas*	–
Western plateau and hills	Agrihortisilviculture (Irri)	*Tectona grandis, Achrus zapota*	Rice, maize
	Agrihorticulture	*Areca catechu*	Black pepper, cardamom
	Silviculture	*Prosopis juliflora, Ailanthus excelsa*	–
	Silvopasture	*Acacia mangium, Albizia Amara*	*Cenchrus*
Southern plateau and hills	Agrisilviculture (RF)	*Eucalyptus, Casuarina equisetifolia, Ailanthus excelsa*	Cotton, groundnut
	Agrisilviculture (Irri)	*Eucalyptus tereticornis, Melia dubia*	Chilli
	Silviculture (RF)	*Leucaena leucocephala, Acacia leucophloea*	–
		Eucalyptus	–
	Agrihorticulture	*Tamarindus indica*	Chilli
	TBOs	*Pongamia pinnata*	–
East Coast Plains & Hills	Agrisilviculture (RF)	*Ailanthus excelsa, Acacia leucophloea*	Cow pea
	Silviculture	*Casuarina equisetifolia, Leucaena leucocephala*	–
	TBOs	*Pongamia pinnata*	–
	Silvopasture	*Artocarpus* spp.	*Chrysopogon, Napier, Cenchrus*
West coast plains & hills	Agrisilviculture (RF)	*Acacia auriculiformis*	Black pepper
	Agrihorticulture (RF)	*Artocarpus heterophyllus*	Black pepper
	Agrisilviculture (RF)	*Acacia auriculiformis*	Rice
	Agrihorticulture	*Cocos nucifera/Areca catechu*	Rice
	Agrisilviculture	*Casuarina equisetifolia*	Rice
	Silvopasture	*Hardwickia binata, Albizia lebbeck*	*Cenchrus*
	Agrisilviculture	*Azadirachta indica, Ailanthus excelsa*	Cow pea, green gram

(continued)

Table 21.2 (continued)

Agro-climatic zone	Agroforestry systems	Tree component	Crop/grass
Gujarat coast plains & hills	Silviculture	*Prosopis juliflora, Acacia nilotica*	–
	Silvopasture	*Leucaena leucocephala*	*Cenchrus, Setaria*
Western dry region	Agrisilviculture	*Prosopis cineraria, Tecomella indica, Acacia nilotica, Azadirachta indica*	Pearl millet
	TBOs	*Jatropha curcas*	–
	Silvopasture	*Albizia lebbeck, Hardwickia binata*	*Cenchrus*
All islands	Agrihorticulture	*Cocos nucifera*	Rice
	Silvopasture	*Bauhinia* spp., *Erythrina indica, Leucaena leucocephala*	*Cenchrus, Pennisetum*

Irri irrigated, *RF* rainfed, *TBOs* tree-borne oil seed (Source: Dhyani et al. 2009)

21.3 Importance of Biodiversity in Agroforestry

Agroforestry denotes sustainable development, and its commercial viability had made these systems popular among farmers (Kaushal et al. 2016a, b) as agroforestry systems enhance inter-species diversity land-use systems to combine crops, shrubs, trees, and in some cases livestock on the same piece of land (Atta-Krah et al. 2004a, b). By integrating trees on farms, agroforestry has the potential to contribute to biodiversity conservation by creating habitat for species that are tolerant to some level of disturbance (Harvey and Villalobos 2007). Agroforestry systems mimic nature or forest and additionally enhance floral diversity by integrating various trees, herbs, shrubs, and arable crops; enhance faunal diversity by attracting important pollinators, herbivores, and even many bird species; and improve rhizospheric biological activity through providing amiable environment conditions at micro and micro levels. The food security, health care, and ecosystem resilience of indigenous plants and trees are robustly dependent on prevailing biodiversity (Garí 2001). Biodiversity supports prevention of climate change, acquires ecological balance, and attains food security (Claverías and Quispe 2001). Upgraded carbon sequestration processes can be attributed to higher amounts of flora due to high biodiversity levels (Schroth et al. 2004). Principally, agroforestry has determined the use of land-use systems resulting in greater diversity for closely coupled nutrient cycling, soil retention, and increased biodiversity without compromising aspect of productivity, making agroforestry a valuable land-use system in rural planning. The meta-analysis studies had revealed overall positive effect of agroforestry on biodiversity in contrast to conventional monocropping (Torralba et al. 2016).

Agroforestry systems can support up to 50–80% of biodiversity of similar natural system (Noble and Dirzo 1997). It is assessed that in developing countries about

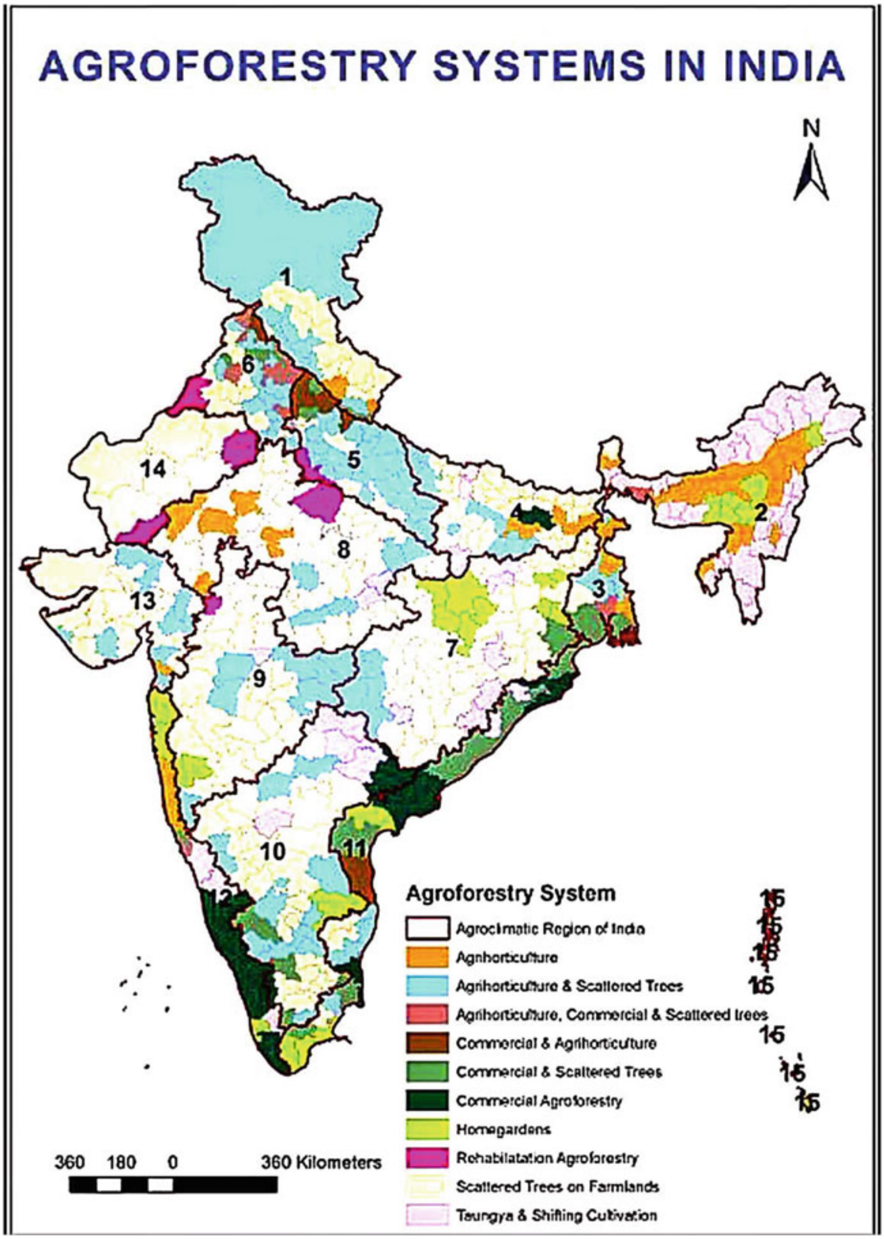

Fig. 21.1 Different agroforestry systems present on farmer's field in different parts of India (Source: ICAR-CAFRI, Jhansi www.cafri.res.in)

20% of world population (approximately 1.2 billion people) depends directly on agroforestry products and services which can provide goods and services and also offset 5–20% of deforestation (Leakey and Sanchez 1997; Dixon 1995). Due to climate change, invasive species, deforestation, and disruption of migration paths by urbanization, there is threat to biodiversity. Bucheli and Bokelmann (2017) supported the need to maintain agroforestry systems and their biodiversity to ensure the ecosystem services, food security, and livelihoods. Soil fauna decides soil health, and agroforestry facilitates to maintain faunal biodiversity and soil health (Kibblewhite et al. 2008). Macro-fauna such as earthworms, ants, and termites play a crucial role in maintenance of soil structure and also complement the saprotrophic activity of microorganisms for carbon transformations in the soil (Bucheli and Bokelmann 2017). Jose (2012) had compiled following major roles of agroforestry systems in biodiversity conservation:

- Availability of habitat for species that can tolerate a certain level of disturbance
- Germplasm preservation of sensitive species
- Reduction in conversion rates of natural habitat by providing a more productive and sustainable alternative to traditional agricultural systems that may involve clearing natural habitats
- Provides connectivity by creating corridors between fragmented habitat remnants which may support the integrity of these remnants and conserve area-sensitive floral and faunal species
- Conserves biological diversity by providing other ecosystem services such as erosion control and water recharge, thereby preventing the degradation and loss of surrounding habitat

To design, develop, and manage an agroforestry system with conservation goals, the overall landscape context and adopting less-intensive cultural practices are considered to achieve the maximum benefits (Table 21.3).

21.4 Agroforestry Systems and Floral Biodiversity

Prevailing monoculture cropping systems leads to lowering in species diversity and lower functional range, which ultimately results in reduction in efficiency of ecosystem functioning. A strong correlation between spread of invasive species and abandonment of agricultural land allowing limitations of natural resources to access the under storey vegetation (Guillerme et al., 2020) makes agroforestry an effective land use strategy to prohibit biological invasion of exotic species on biodiversity (Ramos et al., 2015). Potentially, agroforestry practices upkeep higher species richness and diversity; their role in the biodiversity conservation extend along with natural habitat within agricultural landscapes. The well documented susceptibility of plant biodiversity to intensive agricultural practices leading to dry and fragmented land conditions encourage farmers to adopt different agroforestry systems (Guyassa and Raj 2013) and intensive management activities leads to different levels of

Table 21.3 Designing of agroforestry through appropriate variable and desirable characteristics of various components for biodiversity conservation

Activity	Variable	Desirable characteristics
Design of agroforestry system	Species composition	Diverse species composition, mixtures of early, mid- and late-successional species, preferably native species
	Tree/shrub density	Higher tree/shrub density (and greater areas) leads to greater biodiversity
	Type of agroforestry system	Any system as long as it is floristically and structurally diverse
	Duration of agroforestry system	Long rotation is desirable to provide stability
Management of agroforestry system	Management regime	Minimal management is preferable Management strategies should maximize habitat heterogeneity and availability of diverse resources for wildlife
	Soil management	Minimal
	Harvesting of products	Minimal harvesting or harvesting that emulates natural disturbance regimes
	Fire management	Fire regimes should follow natural fire regimes to the extent possible
	Management of snags and coarse woody debris	Maintain snags and coarse woody debris as habitat for certain species
Spatial configuration	Location within the broader landscape	Position the agroforestry practices strategically to enhance landscape connectivity by functionally linking habitat fragments Position adjacent to protected areas, riparian corridors, and remnant native habitat, to buffer these areas from agricultural impacts
	Types of land	Degraded sites, where vegetation through agroforestry will have a beneficial impact on biodiversity

Adapted from Harvey and Villalobos (2007) and Jose (2012)

negative response. The agroforest landscapes support similar species diversity and richness to unmanaged secondary forests (Sistla et al., 2016) encouraging tribal communities living around forest reserves to reduce their dependency on forest resources by diversifying their sources of income (Masozera and Alavalapati, 2004). The biodiversity in different agroforestry systems/practices is given in Table 21.4.

Despite the fact that agroforestry systems are an insufficient alternative for natural forests, these can be exploited as heterogeneous buffers between protected and actively managed landscapes, thereby maximizing the benefits of both sustainable crop production and plant diversity conservation (Asase and Tetteh 2010). The widespread loss of species due to forest fragmentation can be combated by buffering existing protected forest reserves allowing species movement across landscapes (Bhagwat et al., 2005), connecting nature reserves and alleviating resource-use

Table 21.4 Biodiversity dimensions in different agroforestry systems/practices

Agroforestry system	Biodiversity issues
Shifting cultivation or slash-and-burn	Fallows consist of multiple species, and biological diversity, in both inter- and intraspecies, is intense. Long fallow periods of 15–20 years preserve wild species diversity
Homegardens and compound farms	High inter- and intraspecies diversity involving a number of fruit, fodder and timber trees and shrubs, food crops, medicinal, and other plants of economic value
Forest garden/agroforests	High species diversity similar to natural forests but dominated by a few carefully managed economically valuable tree species
Parkland systems	A variety of crops grown in association with naturally propagated trees ensure wide species diversity (Takeuchi et al. 2005). Parks range from monospecific to multispecific with up to 20 tree species
Trees on farmlands (boundary plantings scattered trees)	Diversity is more at the landscape level rather than at field level in terms of both inter- and intraspecies
Alley cropping/hedgerow intercropping	Diversity limited to intraspecies, e.g., selection within oil palm plantations improved microclimatic conditions (Ashraf at al. 2019). Emphasis on a few tree species has raised concerns on pests and diseases
Improved fallows or planted fallows	Mostly based on mono-tree species
Fodder banks	Sole stands of either leguminous trees or shrubs or high yielding fodder grasses makes the system less diverse
Rotational woodlots	Planted using sole stands of fast growing species for short-cycle harvest
Tree-based intercropping systems	Less diverse due to planting of single species

Atta-Krah et al. (2004a, b)

pressure on conservation areas (Bhagwat et al., 2008). Vegetative buffer strips (VBSs) of multiple species in various designs have been found to significantly reduce dissolution and transport of herbicides and antibiotic surface runoff (Lin et al., 2011) thereby assisting in management of soil properties (Chu et al., 2010). Heterogeneity among plant species provide variable ecological niches thereby supporting variety of biodiversity assets, e.g., thorny plants such as prickly paperback provide protection for small birds such as fairy wrens, casuarinas fixing atmospheric nitrogen etc. (Yunusa et al. 2003). Shelterbelts, relative to the prevailing winds not only prevent spread of wind transmitted aphids, pests and viruses by reducing the wind speed (Szigeti et al. 2020) but also reduce evapotranspiration by acting as vegetative buffers (Svoma et al. 2016). The loss of biodiversity of forest reserves can be prevented by planting and protecting trees outside forests (Thaman 2002). A suitable agroforestry can naturally draw and maintain better biodiversity. Homegardens with high canopy cover, high species richness, and lesser management have been recognized to be an intermediary for biodiversity conservation (Bardhan et al. 2012). Kumar and Nair (2004) reported that species richness of tropical homegardens vary from 27 (Sri Lanka) to 602 (West Java). A study in Bangladesh had concluded that in composition of tree species in homegardens and natural forests, 30% similarity had showed up, and the species richness increased as the size of homegardens increased (Kabir and Webb 2009). In different states of India, varying floral diversity had been reported as 127 species in Kerala (Kumar et al. 1994), 68 species in Karnataka (Shastri et al. 2002), and 122 species in Barak valley of Assam (Das and Das 2005). Similarly, 74 species of different plants had been reported in the homegardens of North Bengal along with milch animals, meat animals, and poultry which are linked to the owner socially and economically (Panwar and Chakravarty 2010). Though coffee-based agroforests, e.g., coffee–banana plantations in Mount Kilimanjaro have shown to maintain a high level of biodiversity with 520 plant species similar to tropical montane forests (Hemp 2006), multistrata agroforests were emphasized to maintain relatively higher woody species diversity as in circa situm biodiversity conservation (Negash et al. 2012).

Forest farming has been adopted by many nations including few Indian states; also according to the forests rights act (2006), respective forest departments can de-notify fringe areas of forests as forest land allowing the tribal people to get the rights of cultivation. It is different from shifting cultivation, as these are permanent cultivation with trees of forest. In India, this type farming support organic production unlike wild collection form forests as non-timber forest products (NTFPs). Under traditional agroforestry systems maintained by Nyishi tribe of Arunachal Pradesh, India cultivates a total of 45 culturally important tree species. Among these, about 88.89% of these tree species are used as fuelwood, followed by food (66.67%), field use (46.67%), tool (37.78%), construction (31.11%), and other uses (80%) (Pangging et al. 2017).

21.5 Agroforestry and Faunal Biodiversity

Agroforestry systems with their integrated land-use approach are capable of creating a multipurpose ecosystem with higher floristic and structural diversity to support greater faunal diversity compared to monoculture systems. Tree-based intercropping (TBI) systems contribute access to food sources and breeding territory and provide connectivity, nesting sites, protection against predators, low risk areas, breeding areas, food sources, landscape complexity, and heterogeneity, thereby integrating aquatic systems, pollinators, and beneficial species into the landscape. Agroforestry encourages beneficial species such as pollinators and thus is used to increase pollinator diversity, which is essential for food production as well as maintenance of population levels of wild plants. The pollinator service is invaluable as ~90% of flowering plants are pollinated by insects and over 75% of world's most important crops and 35% of food production depend on animal pollination. Bentrup et al. (2019) suggested that agroforestry systems provide three main benefits to insect pollinators and influence their pollination services by: (1) providing habitat including foraging resources and nesting or egg-laying sites, (2) enhancing site and landscape connectivity, and (3) mitigating pesticide exposure. Agroforests provide pollen and nesting resources for honey and wild bees that positively translate into taxonomic and functional diversity of pollinator fauna and maintain stable pollinator visitation networks (Hass et al. 2018; Varah et al. 2013). This ensures continued pollination services and biodiversity conservation. Wild bee diversity and abundance is negatively linked to plantation forests. Thus, the intensity of the management in agroforestry systems also affects bee diversity as maintaining or restoring wild bee communities in agricultural landscapes requires restoration measures such as forest planting (Wu et al. 2019). Chandler et al. (2013) found that shaded coffee had 66 higher species richness of Nearctic migrant birds than forest. Cocoa agroforest covers have been confirmed to be natural biodiversity reserves for some rainforest insect species (Perry et al. 2016) and birds (Cabral et al. 2021). The integration of trees in agricultural areas provides connectivity, protection against predators, nesting sites, breeding areas, low risk areas, food sources, landscape complexity, and heterogeneity, thereby integrating aquatic systems, pollinators, and beneficial species into the landscape. The silvopastoral systems can contribute in maintaining bird diversity, cattle yield, and conservation of forest phylodiversity (Mastrangelo and Gavin 2012). The scattered trees within these silvopastures coexist as mosaics of habitats with each habitat contributing to uphold high level of total species diversity (Moreno et al. 2016). The abundance of diversity for beneficial insects and natural enemies in silvopastoral environments are also capable of providing microhabitats, greater protection from predators (Auad et al. 2012), and sustainable crop production (Begg et al. 2017; Boinot et al. 2020). The warmer temperatures under agroforests have potential to increase predation over crop pests such as aphids (Martin-Chave et al. 2019) while simultaneously increasing abundance of spiders and beetles (Guenat et al. 2019). Neita and Escobar (2012) suggested the potential role of *Borojoa patinoi* agroforestry systems in diversity of dung beetle populations. Rahman et al. (2012) reported the abundance of ants, beetles, termites, crickets, centipedes, and spiders in forest ecosystems. *Cabrucas,* an agroforestry system, provides alternative habitat for several forest species, such as ferns, bromeliads, birds, bats, invertebrates, mammals, leaf-litter *Herpetofauna, nymphalid,* butterflies, and other insects, increasing the connectivity between forest fragments and reducing the edge effects to which fragments are exposed (Sagastuy and Krause 2019). Shelterbelts can play a significant role in domestic honey production in addition to providing pollens and nectars for bees (Donkersley 2019). Interactions between ants and bees for inflorescences of *Syzygium jambolanum* in an agroforestry system in Brazilian Meridional Amazonian showed that bees and ants avoid agonistic encounters by generating a pattern of vertical stratification on its competitive effort, i.e., competition for inflorescences was stratum specific to each group (Dáttilo et al. 2012). Shade coffee and multi-strata cocoa agroforestry systems provide habitat for avian, mammalian, and other species and thereby enhance faunal diversity. For example, in Makalu Barun National Park and Conservation Area of Nepal, agroforestry with *Alnus nepalensis* and cardamom (*Elettaria cardamomum*) contributed to the integrity of riparian corridors for wildlife conservation. Ashraf et al. (2018) found alley cropping to significantly improve arthropod biodiversity and ecosystem functions within oil palm plantations.

Thus, understory vegetation can be maintained in oil palm landscapes to improve ground forage ant-mediated ecosystem services (Hood et al. 2020). Tree species diversity and avian richness in agroforests were higher or similar to secondary forests (Quazi and Ticktin 2016). Similarly, structurally diverse rubber-based agroforest in Sumatra supports frugivorous birds that were absent from monocultures, 7 to 13 additional threatened species, and 8 additional forest specialists (Prabowo et al. 2016). Many agroforestry systems act as a corridor between the forest and remnant land fragments, thereby serving as a habitat for the protection of species outside of formally protected forest areas. Shaded coffee agroforest in Nicaragua were observed to be alternative wildlife habitats and act as corridors between forest fragments for mantled howling monkeys (Williams-Guillén et al. 2006). Rubber agroforestry system supported four additional butterfly species that were more similar in composition to forest fragments than intensive rubber in Brazil (Barbosa Cambui et al. 2017).

21.6 Agroforestry and Soil Microbial Biodiversity

Major part of Earth's biodiversity resides within the soil that contains fungi, bacteria, virus, protozoa, nematodes, and many other species. Soil microbial communities play a vital role in most biogeochemical processes, viz., mineralization, nutrient cycling, nutrient supply, biodegradation of xenobiotics, soil formation, and soil health besides affecting the aboveground biodiversity. These soil microbial communities live within the soil, rhizosphere, and other materials to carry out various useful as well deleterious processes. Their functions also help improve the quality of water and soil ultimately impacting climate regulation. Trees and soil biota interact through facilitation and synergies. Guillot et al. (2019) observed soil microbial response to drought and heat stress induced by spatial heterogeneity in agroforestry systems. A major contribution of agroforestry trees to soil-based ecosystem services occurs as a result of aboveground and belowground organic inputs that provide food and nutrients needed for the soil organisms involved in carbon transformations and nutrient cycling (Fig. 21.3).

The tree cover protects soil from erosion and further degradation. Trees have the potential of reducing soil erosion through five processes, viz., interception of rainfall impact by tree canopy, surface runoff impediment by tree stems, soil surface cover by litter mulch, promotion of water infiltration, and formation of erosion-resistant blocky soil structure. The soil's physical properties are maintained through the addition of organic matter and effects of the roots. The soil's biological properties are improved due to the addition of different qualities of plant litter through the supply of a mixture of woody and herbaceous material, including root residues. Multistrata successional agroforestry have the potential to self regulate ecosystem functions thereby promoting positive changes in the abundance, diversity, and function of soil organisms through their impact on the soil as a habitat for soil biota (Cezar et al., 2015). The soil biodiversity reserves of micro-arthropods (Lakshmi and Joseph, 2017) and macro-arthropods (Villanueva-López et al., 2019)

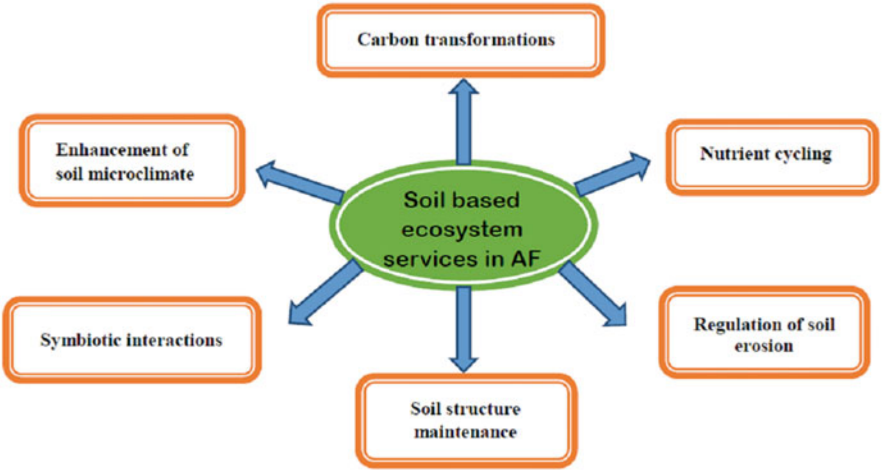

Fig. 21.3 Soil-based ecosystem services provided by agroforestry systems (Uthappa et al. 2015)

have been found to be effective indicators for soil quality assessment, maintenance and soil nutrient recycling. AF buffers show better soil thermal and microclimate properties against extreme temperature conditions as compared to monocrop areas. AF buffer areas show favorable soil temperature, humidity, and wind speeds since the removal of shade trees increase the surface soil temperature and thereby affect humidity-moisture conditions, decomposition rates, nutrient status, and soil communities (Adhikari et al. 2014). The permanent tree cover helps in maintaining and improving soil health through various functions as depicted in Fig. 21.4.

The modified environment under tree-based systems enhances many soil process and soil biota (Paudel et al., 2011) as well as minimize the application of inorganic synthetic fertilizers (Thiele-Bruhn et al. 2012). Prober et al. (2015) established a significant correlation between plant beta diversity (compositional dissimilarity between sites) and beta diversity of soil microbial communities even under controlled environmental conditions. Because of the high density of roots of multiple vegetation including trees, shrubs, grass, and crops as well as contributions from livestock, inevitable belowground interactions occur within the soil. Researchers have found a higher level of root colonization and greater spore densities in the rhizosphere of crops growing near the trees than away from trees. Differences in fungal densities and community structures have been found between agroforestry and monocropping practices for temperate and tropical regions. The comparative analysis of soil fungal biodiversity under different agricultural management systems revealed that the types of land-use system affect the filamentous fungal populations (Costa et al. 2012; Arévalo-Gardini et al. 2020). Arbuscular mycorrhizal fungi (AMF) mycorrhization is beneficial for soil health as it can increase soil structure, nutrient status, and microbial community structure and suppress weed populations but human interferences have borne negative impact on AMF diversity suggesting a need to promote subsistence farming (Muchane et al. 2012). Various

Fig. 21.4 Agroforestry soil basket for maintaining soil health (Adapted from Uthappa et al. 2015)

studies have shown greater AMF richness in a tree-based cropping system and several taxa that were not present in a monocrop system (Bainard et al. 2012). Thus, increasing plant diversity have been shown to have a positive influence on AM fungal diversity (Bainard et al. 2011). The phospholipid fatty acid (PLFA) profiling studies have shown significantly greater microbial biomass and altered microbial community structure in long-term no-till soil (Helgason et al. 2010) suggesting a tree-based AF system to harbour AMF diversity much better when compared to an adjacent conventional monocropping system. The AMF communities growing on rhizosphere of annual crop were influenced by the tree root exudates, and also these communities differ for different tree species. Differences in abundance of soil organisms can be even greater when contrasting the impact of agroforestry systems to that of continuous cropping without trees (Table 21.5).

21.7 Biological Nitrogen Fixation

Biological nitrogen fixation (BNF) constitutes a key nutrient input to agroecosystems. The contribution of leguminous trees to building up N in degraded soils through BNF is well recognized as an important component of the ecosystem service of nutrient cycling (Uthappa et al. 2015). Leguminous trees and shrubs can

Table 21.5 Comparison of mean densities (individuals per m^2) of different soil biota in soils under agroforestry and continuous cultivation without trees

Soil biota	Agroforestry	Monocropping	Response ratio*
Soil macrofauna			
Earthworm	54.4	17.6	3.1
Beetles	20.9	9.6	2.2
Centipedes	2.7	0.5	5.6
Millipedes	8.1	1.3	6.1
Termites	90.7	81.0	1.1
Ants	23.2	8.6	2.7
Soil mesofauna			
Collembola	3890	2000.7	1.9
Mites	5100	1860.1	2.7
Soil microfauna			
Non-parasitic nematodes	2922	1288	***2.3***
Parasitic nematodes	203.7	211.5	1

The response ratio (RR) is the ratio of the mean value of the agroforestry practice to that of the control (continuous cropping). In this Table RR quantifies both the direction and magnitude of changes in soil biota abundance: if trees do not have any effect on abundance, RR = 1. If agroforestry trees favor soil biota, the value of RR will be larger than unity and vice versa if trees do not favor soil biota

Adapted from Barrios et al. (2012)

affect the biodiversity in agroforestry systems in unique ways although the number of species is limited to the temperate regions relative to the tropics. Banarjee et al. (2015) observed the importance of composition of leguminous trees of agroforestry systems in controlling soil microbial communities. The correct composition of leguminous trees at strategic locations ascertains a degree of predictability in the control of microbial communities in agroforestry systems, thereby promoting biodiversity, soil fertility, and water quality. Soil pH and carbon contents have been proven to be principal drivers of bacterial community characteristics. In agroforestry system, BNF trees contribute toward complementary interaction, which makes agroforestry system sustainable for nutrient requirements. The agroforestry systems in tropical countries are designed based on BNF in trees which can act as fertilizers to annual components. Figure 21.5 illustrates the BNF trees with their potential to fix atmospheric nitrogen in the soil.

Henceforth, despite the importance and benefits of agroforestry systems, the fundamental understanding of the patterns and determinants of soil microbial communities should be thoroughly examined. Land-use type exerts strong effects on bacterial abundance and community composition, and this impact mediates through change in edaphic factors.

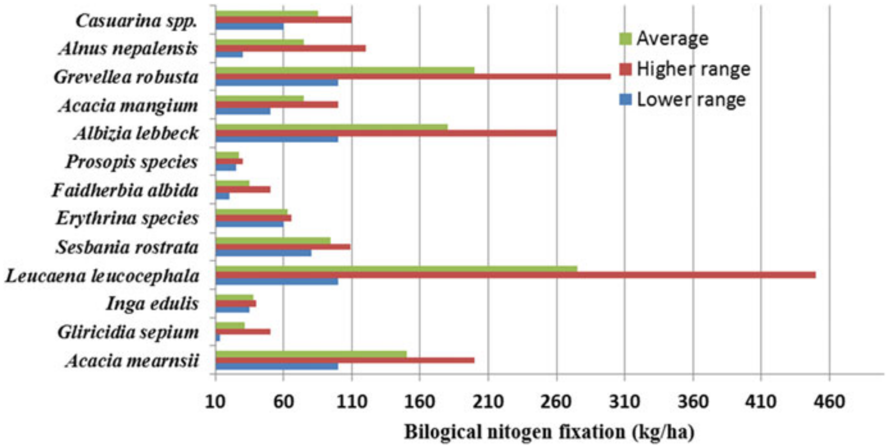

Fig. 21.5 Biological nitrogen fixing (kg ha^{-1}) in different agroforestry trees and shrubs (Modified from Young 1997)

21.8 Diversity Enhancing Processes of Agroforestry

Newly developed agroforestry systems are generally developed using only few selected tree species often in mono-tree species systems, usually with preferred characteristic such as high yielding, fast grown species. Such an approach results in low diversity on farms and makes the system vulnerable to insect/or diseases. These systems thus need to be modified so as to increase the diversity. Some of the diversity increasing measures are given in Table 21.6.

While there is a growing literature on biodiversity within agroforestry systems, the important questions still remain about the long-term viability of animal and plant population in agroforestry systems. Most studies so far have monitored or inventoried biodiversity within landscapes that still retain some forest cover or have focused on few taxa and have been conducted on small spatial and temporal scales. The future agroforestry research in biodiversity should include:

- Development of economically and socially acceptable land-use systems that function like undisturbed ecosystem and maintain diversity.
- Controlled experiments to determine the relationship between agriculture intensification and floral and faunal biodiversity.
- Determine the floral and faunal diversity in different agroforestry systems and their implications for ecological functioning at different scales.
- Improving the diversity of the agroforestry systems by integrating the trees/shrubs/grasses and/or animals in different combinations.
- Develop resilient and diversity enhancing agroforestry systems in climate change scenario.

Table 21.6 Diversity enhancing measures in modern agroforestry

Agroforestry systems	Ways of enhancing diversity
Alley cropping/hedgerow intercropping	Tree diversity can be increased through multispecies hedgerows and crop diversity increased by adopting intercropping in the alleys to increase efficiency of nutrient cycling
Improved fallows or planted fallows	Multi-species fallows combining coppicing and non-coppicing species or species differing in leaf litter characteristics are likely to enhance fallow function as well as reduce risk from pests
Fodder banks	Combining trees and fodder grasses in different diversity increasing manner
Rotational woodlots	Mixing of N2-fixing species with non-N2-fixing species will improve diversity, nutrient cycling, and site enrichment compared with non-N2-fixing species alone
Tree-based intercropping	Adopting new agroforestry systems such as agrisystems horti-silviculture, Agri-silvipastoral, apiculture with trees, aquaculture with trees, etc.

21.9 Conclusion

The correlation between loss of biodiversity and intensive human-mediated management and development activities has been a well-known fact through centuries. This has attracted the idea of multifunctional ecosystems to manage, conserve, and enhance biodiversity along with fulfilling the rest of the economic requirements for livelihood. Agroforestry, sustaining a high floristic and faunal diversity, is a critical ecological tool for biodiversity conservation in human-dominated landscapes that can act as a multifunctional ecosystem. Thus, identification of appropriate agroforestry tree species, designing agroforestry, and devising sound management approaches should be acknowledged to further understand the role of agroforestry in biodiversity conservation and climate-resilient agriculture.

References

Adhikari K, Hartemink AE, Minasny B, BouKheir R, Greve MB, Greve MH (2014) Digital mapping of soil organic carbon contents and stocks in Denmark. PLoS One 9:e105519

Arévalo-Gardini E, Canto M, Alegre J, Arévalo-Hernández CO, Loli O, Julca A, Baligar V (2020) Cacao agroforestry management systems effects on soil fungi diversity in the Peruvian Amazon. Ecol Indic 115:106404

Asase A, Tetteh DA (2010) The role of complex agroforestry systems in the conservation of forest tree diversity and structure in southeastern Ghana. Agr Syst 79(3):355–368

Ashraf M, Sanusi R, Zulkifli R, Tohiran KA, Moslim R, Ashton-Butt A, Azhar B (2019) Alley-cropping system increases vegetation heterogeneity and moderates extreme microclimates in oil palm plantations. Agric For Meteorol 276:107632

Ashraf M, Zulkifli R, Sanusi R, Tohiran KA, Terhem R, Moslim R, Azhar B (2018) Alley-cropping system can boost arthropod biodiversity and ecosystem functions in oil palm plantations. Agric Ecosyst Environ 260:19–26

Atta-Krah K, Kindt R, Skilton JN, Amaral W (2004a) Managing biological and genetic diversity in tropical agroforestry. Agr Syst 61:183–194

Atta-Krah K, Kindt R, Skilton JN, Amaral W (2004b) Managing biological and genetic diversity in tropical agroforestry. In: New vistas in agroforestry. Springer, Dordrecht, pp 183–194

Auad AM, Resende TT, Da Silva DM, das Graças Fonseca, M. (2012) Hymenoptera (Insecta: Hymenoptera) associated with silvopastoral systems. Agr Syst 85(1):113–119

Bainard LD, Koch AM, Gordon AM, Klironomos JN (2012) Temporal and compositional differences of arbuscular mycorrhizal fungal communities in conventional monocropping and tree-based intercropping systems. Soil Biol Biochem 45:172–180

Bainard LD, Kochb AM, Gordon AM, Newmaster SG, Thevathasan NV, Klironomosb JN (2011) Influence of trees on the spatial structure of arbuscular mycorrhizal communities in a temperate tree-based intercropping system. Agric Ecosyst Environ 144:13–20

Banarjee S, Baah-Acheamfour M, Carlyle CM, Bissett A, Richardon AE, Siddique T, Bork EW, Chang SX (2015) Determinants of bacterial communities in Canadian agroforestry systems. Environ Microbiol 18:1805–1816

Barbosa Cambui EC, Nogueira de Vasconcelos R, Mariano-Neto E, Felipe Viana B, Zikán Cardoso M (2017) Positive forestry: the effect of rubber tree plantations on fruit feeding butterfly assemblages in the Brazilian Atlantic forest. For Ecol Manage 397:150–156. https://doi.org/10.1016/j.foreco.2017.04.043

Bardhan S, Jose S, Biswas S, Kabir K, Rogers W (2012) Homegarden agroforestry systems: an intermediary for biodiversity conservation in Bangladesh. Agr Syst 85(1):29–34

Barrios E, Sileshi GW, Shepherd K, Sinclair F (2012) Agroforestry and soil health: linking trees, soil biota and ecosystem services. Soil Ecol Ecosyst Serv 14:315–330

Begg GS, Cook SM, Dye R, Ferrante M, Franck P, Lavigne C, Birch ANE (2017) A functional overview of conservation biological control. Crop Prot 97:145–158

Bentrup G, Hopwood J, Adamson NL, Vaughan M (2019) Temperate agroforestry systems and insect pollinators: a review. Forests 10(11):981

Bhagwat SA, Kushalappa CG, Williams PH, Brown ND (2005) The role of informal protected areas in maintaining biodiversity in the Western Ghats of India. Ecol Soc 10:1

Bhagwat SA, Willis KJ, Birks HJB, Whittaker RJ (2008) Agroforestry: a refuge for tropical biodiversity? Trends Ecol Evol 23(5):261–267

Boinot S, Mézière D, Poulmarc'h J, Saintilan A, Lauri PE, Sarthou JP (2020) Promoting generalist predators of crop pests in alley cropping agroforestry fields: farming system matters. Ecol Eng 158:106041

Bucheli VJ, Bokelmann W (2017) Agroforestry systems for biodiversity and ecosystem services: the case of the Sibundoy Valley in the Colombian province of Putumayo. Int J Biodiv Sci Ecosyst Serv Manage 13(1):380–397

Cabral JP, Faria D, Morante-Filho JC (2021) Landscape composition is more important than local vegetation structure for understory birds in cocoa agroforestry systems. For Ecol Manage 481:118704

Cezar RM, Vezzani FM, Schwiderke DK, Gaiad S, Brown GG, Seoane CES, Froufe LCM (2015) Soil biological properties in multistrata successional agroforestry systems and in natural regeneration. Agr Syst 89(6):1035–1047

Chandler RB, King DI, Raudales R, Trubey R, Chandler C, Chavez VJA (2013) A small-scale land-sparing approach to conserving biological diversity in tropical agricultural landscapes. Conserv Biol 27:785–795

Chavan SB, Keerthika A, Bhat SS, Handa AK, Rajarajan K, Ahmad S (2020) Poplar (*Populus deltoides*) in Jammu and Kashmir, India: facts and fiction. Curr Sci 119(6):910–911

Chavan SB, Keerthika A, Dhyani SK, Handa AK, Newaj R, Rajarajan K (2015) National agroforestry policy in India: a low hanging fruit. Curr Sci 108(10):1826–1834

Chavan SB, Newaj R, Rizvi RH (2021) Reduction of global warming potential Vis-à-Vis greenhouse gases through traditional agroforestry systems in Rajasthan, India. Environ Dev Sustain 23:4573–4593. https://doi.org/10.1007/s10668-020-00788-w

Chavan SB, Uthappa AR, Sridhar KB, Keerthika A, Handa AK, Newaj R, Kumar N, Kumar D, Chaturvedi OP (2016) Trees for life: creating sustainable livelihood in Bundelkhand region of Central India. Curr Sci 11(6):994–1002

Chu B, Goyne KW, Anderson SH, Lin CH, Udawatta RP (2010) Veterinary antibiotic sorption to agroforestry buffer, grass buffer, and cropland soils. Agr Syst 2010(79):67–80

Claverías R, Quispe C (2001) Biodiversidad cultivada: una estrategia campesina para supercar la pobreza y relacionarse con el Mercado [Agricultural biodiversity: a peasant strategy for overcoming poverty and entering the markets]. SEPIA, Lima, pp 180–204

Costa PMO, Souza-Motta CM, Malosso E (2012) Diversity of filamentous fungi in different systems of land use. Agr Syst 85(1):195–203

Dagar JC, Singh AK, Arunachalam A (2014) Introduction. In: Dagar J, Singh A, Arunachalam A, Agroforestry systems in India: livelihood security & ecosystem services. Advances in agroforestry, Springer, New Delhi

Das T, Das AK (2005) Inventorying plant biodiversity in home gardens: a case study in Barak valley, Assam, Northeast India. Curr Sci 89(1):155–163

Dáttilo W, Martins RL, Uhde V, Noronha JC, Florêncio FP, Izzo TJ (2012) Floral resource partitioning by ants and bees in a jambolan *Syzygium jambolanum* (Myrtaceae) agroforestry system in Brazilian meridional Amazon. Agr Syst 85(1):105–111

Dhyani SK, Kareemulla K, Handa AK (2009) Agroforestry potential and scope for development across agro-climatic zones in India. Indian J For 32:181–190

Dixon RK (1995) Agroforestry systems: sources or sinks of greenhouse gases? Agr Syst 31(2): 99–116

Donkersley P (2019) Trees for bees. Agric Ecosyst Environ 270:79–83

Garí J (2001) Biodiversity and indigenous agroecology in Amazonia: the indigenous peoples of Pastaza. Etnoecológica 5(7):21–37

Guenat S, Kaartinen R, Jonsson M (2019) Shade trees decrease pest abundances on *Brassica* crops in Kenya. Agr Syst 93(2):641–652

Guillerme S, Barcet H, de Munnik N, Maire E, Marais-Sicre C (2020) Evolution of traditional agroforestry landscapes and development of invasive species: lessons from the Pyrenees (France). Sustain Sci 15(5):1285–1299

Guillot E, Hinsinger P, Dufour L, Roy J, Bertrand I (2019) With or without trees: resistance and resilience of soil microbial communities to drought and heat stress in a Mediterranean agroforestry system. Soil Biol Biochem 129:122–135

Guyassa E, Raj AJ (2013) Assessment of biodiversity in cropland agroforestry and its role in livelihood development in dryland areas: a case study from Tigray region, Ethiopia. J Agric Technol 9(4):829–844

Handa AK, Toky OP, Dhyani SK, Chavan SB (2016) Innovative agroforestry for livelihood security in India. World Agric 5:7–11

Harvey CA, Villalobos GJA (2007) Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodivers Conserv 16:2257–2292

Hass AL, Liese B, Heong KL, Settele J, Tscharntke T, Westphal C (2018) Plant-pollinator interactions and bee functional diversity are driven by agroforests in rice-dominated landscapes. Agric Ecosyst Environ 253:140–147

Helgason BL, Walley FL, Germida JJ (2010) No-till and soil management increases microbial biomass and alters community profiles in soil aggregates. App Soil Ecol 46:390–397

Hemp A (2006) The banana forests of Kilimanjaro: biodiversity and conservation of the Chagga homegardens. Biodivers Conserv 15(4):1193–1217

Hood AS, Advento AD, Stone J, Fayle TM, Fairnie AL, Waters HS, Turner EC (2020) Removing understory vegetation in oil palm agroforestry reduces ground-foraging ant abundance but not species richness. Basic Appl Ecol 48:26–36

Jose S (2012) Agroforestry for conserving and enhancing biodiversity. Agr Syst 85:1–8

Kabir EM, Webb EL (2009) Can homegardens conserve biodiversity in Bangladesh? Biotropica 40: 95–103

Kaushal R, Panwar P, Sarvade S, Tomar JMS, Chaturvedi OP (2016a) Agroforestry for biodiversity conservation. In: Kumar S, Panwar P, Kaushal R (eds) Agroforestry for increased production and livelihood security. New India Publishing Agency, New Delhi, pp 363–377

Kaushal R, Verma A, Mehta H, Mandal D, Tomar JMS, Jana C, Jayparkash J, Chaturvedi OP (2016b) Soil quality under *Grewia optiva* based agroforestry systems in western sub-Himalaya. Range Manage Agrofor 37(1):50–55

Keerthika A, Chavan SB, Shukla M (2015) Khejri agroforestry for addressing issues of soil health. Lifesci Leaf 64(06):102–108

Kibblewhite MG, Ritz K, Swift MJ (2008) Soil health in agricultural systems. Philos Trans R Soc B: Biol Sci 363(1492):685–701

Kumar BM, George SJ, Chinnamani S (1994) Diversity, structure and standing stock of wood in the home gardens of Kerala in peninsular India. Agr Syst 25:243–262

Kumar BM, Nair PKR (2004) Tropical homegardens: a time-tested example of sustainable agroforestry. In: Advances in agroforestry. Springer, Dordrecht

Lakshmi G, Joseph A (2017) Soil microarthropods as indicators of soil quality of tropical home gardens in a village in Kerala, India. Agr Syst 91(3):439–450

Leakey RRB, Sanchez PA (1997) How many people use agroforestry products? Agrofor Today 9(3):4–5

Lin CH, Lerch RN, Goyne KW, Garrett HE (2011) Reducing herbicides and veterinary antibiotic losses from agroecosystems using vegetative buffers. J Environ Qual 40:791–799

Mann HS, Saxena SK (1980) Khejri (*Prosopis cineraria*) in the Indian desert: its role in agroforestry. CAZRI, Jodhpur

Martin-Chave A, Béral C, Capowiez Y (2019) Agroforestry has an impact on nocturnal predation by ground beetles and Opiliones in a temperate organic alley cropping system. Biol Control 129: 128–135

Masozera MK, Alavalapati JR (2004) Forest dependency and its implications for protected areas management: a case study from the Nyungwe Forest reserve, Rwanda. Scand J For Res 19(S4): 85–92

Mastrangelo ME, Gavin MC (2012) Trade-offs between cattle production and bird conservation in an agricultural frontier of the Gran Chaco of Argentina. Conserv Biol 26(6):1040–1051

Moreno G, Gonzalez-Bornay G, Pulido F, Lopez-Diaz ML, Bertomeu M, Juárez E, Diaz M (2016) Exploring the causes of high biodiversity of Iberian dehesas: the importance of wood pastures and marginal habitats. Agr Syst 90(1):87–105

Muchane MN, Muchane M, Mugoya C, Clet W (2012) Effect of land use system on arbuscular mycorrhiza fungi in Maasai Mara ecosystem, Kenya. Afr J Microbiol Res 6(17):3904–3916

Nair PKR (1993) An introduction to agroforestry. Kluwer Academic, Amsterdam, p 491

Negash M, Yirdaw E, Luukkanen O (2012) Potential of indigenous multistrata agroforests for maintaining native floristic diversity in the south-eastern Rift Valley escarpment, Ethiopia. Agr Syst 85(1):9–28

Neita JC, Escobar F (2012) The potential value of agroforestry to dung beetle diversity in the wet tropical forests of the Pacific lowlands of Colombia. Agr Syst 85(1):121–131

Newaj R, Chaturvedi OP, Kumar D, Chavan SB, Rajawat BS, Yadav DK (2020) Carbon sequestration potential of agroforestry systems for rehabilitating degraded lands of India. In: Agroforestry for degraded landscapes. Springer, Singapore, pp 319–348

Newaj R, Chavan SB, Kumar D, Uthappa AR, Singh M, Sridhar KB (2016) Agroforestry research in India: relevance in livelihood and climate change. In: Dagar JC, Tewari JC (eds) Agroforestry research developments. Nova Science Publishers, New York

Newaj R, Chavan SB, Prasad R (2015) Climate-smart agriculture with special reference to agroforestry. Indian J Agroforest 17(1):96–108

Noble IR, Dirzo R (1997) Forests as human-dominated ecosystems. Science 277:522–525

Pangging G, Sangma SJ, Sharma CL, Sharma M (2017) Documentation and valuation of tree species used in traditional agroforestry systems by nyishi tribe of Arunachal Pradesh, eastern himalaya. Int J Res Appl Sci Eng Technol 5(9):1489–1496

Panwar P, Chakravarty S (2010) Floristic structure and ecological function of homegardens in humid tropics of West Bengal, India. Indian J Agrofor 12(2)

Paudel B, Udawatta RP, Kremer RJ, Anderson SH (2011) Agroforestry and grass buffer effects on soil quality parameters for grazed pasture and row-crop systems. Appl Soil Ecol 48:125–132

Perry J, Lojka B, Quinones Ruiz LG, Van Damme P, Houška J, Fernandez Cusimamani E (2016) How natural forest conversion affects insect biodiversity in the Peruvian Amazon: can agroforestry help? Forests 7(4):82

Prabowo WE, Darras K, Clough Y, Toledo-Hernandez M, Arlettaz R, Mulyani YA, Tscharntke T (2016) Bird responses to lowland rainforest conversion in Sumatran smallholder landscapes, Indonesia. PLoS One 11(5):1–17

Prober SM, Left JW, Bates ST, Borer ET, Firn J, Harpole WS, Lind EM, Seabloom EW, Adler PB, Bakker JD (2015) Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. Ecol Lett 18:85–95

Quazi SA, Ticktin T (2016) Understanding drivers of forest diversity and structure in managed landscapes: secondary forests, plantations, and agroforests in Bangladesh. For Ecol Manage 366:118–134

Rahman PM, Varma RV, Sileshi GW (2012) Abundance and diversity of soil invertebrates in annual crops, agroforestry and forest ecosystems in the Nilgiri biosphere reserve of Western Ghats, India. Agr Syst 85(1):165–177

Ramos NC, Gastauer M, Cordeiro ADAC, Meira-Neto JAA (2015) Environmental filtering of agroforestry systems reduces the risk of biological invasion. Agr Syst 89(2):279–289

Raychaudhuri SP, Roy M (1993) Agriculture in ancient India. ICAR, New Delhi

Sagastuy M, Krause T (2019) Agroforestry as a biodiversity conservation tool in the Atlantic Forest? Motivations and limitations for small-scale farmers to implement agroforestry systems in North-Eastern Brazil. Sustainability 11(24):6932

Schroth G, da Fonseca GAB, Harvey CA (2004) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington, p 523

Shastri CM, Bhat DM, Nagaraja BC, Murali KS, Ravindranath NH (2002) Tree species diversity in a village ecosystem in Uttara Kannada district in Western Ghats, Karnataka. Curr Sci 82(9): 1080–1084

Sistla SA, Roddy AB, Williams NE, Kramer DB, Stevens K, Allison SD (2016) Agroforestry practices promote biodiversity and natural resource diversity in Atlantic Nicaragua. PLoS One 11:e0162529

Svoma BM, Fox NI, Pallardy Q, Udawatta RP (2016) Evapotranspiration deference between agroforestry and grass buffer systems. Agric Water Manag 176:214–221

Szigeti N, Frank N, Vityi A (2020) The multifunctional role of shelterbelts in intensively managed agricultural land–Silvoarable agroforestry in Hungary. ACTA Silvatica et Lignaria Hungarica 16(1):19–38

Takeuchi K, Tsunekawa A, Abdoellah OS (2005) Kebon tatangkalan: a disappearing agroforest in the Upper Citarum Watershed, West Java, Indonesia. Agr Syst 63(2):171–182

Thaman RR (2002) Trees outside forests as a foundation for sustainable development in the Small Island developing states of the Pacific Ocean. Int For Rev 4(4):268–276

Thiele-Bruhn S, Bloem J, De Vries FT, Kalbitz K, Wagg C (2012) Linking soil biodiversity and agricultural soil management. Curr Opin Environ Sustain 4:523–528

Torralba M, Fagerholm N, Burgess PJ, Moreno G, Plieninger T (2016) Do European agroforestry systems enhance biodiversity and ecosystem services? A meta-analysis. Agric Ecosyst Environ 230:150–161

Uthappa AR, Chavan SB, Dhyani SK, Handa AK, Newaj R (2015) Trees for soil health and sustainable agriculture. Indian Farming 65(3):2–5

Varah A, Jones H, Smith J, Potts SG (2013) Enhanced biodiversity and pollination in UK agroforestry systems. J Sci Food Agric 93:2073–2075

Villanueva-López G, Lara-Pérez LA, Oros-Ortega I, Ramírez-Barajas PJ, Casanova-Lugo F, Ramos-Reyes R, Aryal DR (2019) Diversity of soil macro-arthropods correlates to the richness of plant species in traditional agroforestry systems in the humid tropics of Mexico. Agric Ecosyst Environ 286:106658

Williams-Guillén K, McCann C, Martínez Sánchez JC, Koontz F (2006) Resource availability and habitat use by mantled howling monkeys in a Nicaraguan coffee plantation: can agroforests serve as core habitat for a forest mammal? Anim Conserv 9(3):331–338

Worku M, Bantihun A (2017) Review on woody species and socio-economic roles of traditional agroforestry practices in Ethiopia. J Fundam Renew Energy 7(6):5

World Bank (2004) Sustaining forest: a development strategy. World Bank, Washington

Wu P, Axmacher JC, Li X, Song X, Yu Z, Xu H, Liu Y (2019) Contrasting effects of natural shrubland and plantation forests on bee assemblages at neighboring apple orchards in Beijing, China. Biol Conserv 237:456–462

Young A (1997) Agroforestry for soil management, 2nd edn. CAB International, Wallingford

Yunusa IA, Brown GW, Kwong RM, Ronnfeldt GR, Slater T, Crouch A, Unkovich M (2003) Integrating biodiversity and productivity on intensive farms: a potential role for shelterbelts in the Victorian Riverina. In: agriculture for the Australian environment. In Proceedings of the 2002 Australian Academy of Science Fenner conference on the environment. The Johnstone Centre, Charles Sturt University, Albury, NSW, pp 255–277

Zomer RJ, Neufeldt H, Xu J, Ahrends A, Bossio D, Trabucco A, Wang M (2016) Global tree cover and biomass carbon on agricultural land: the contribution of agroforestry to global and national carbon budgets. Sci Rep 6:29987

Challenges of Stressed Soil: A Case Study of Acid Soil

22

Arvind Kumar, Manas Denre, B. K. Agarwal, and D. K. Shahi

Abstract

Sustainable agriculture has a significant role in the national economy and food security of many developing countries in world. Growth of agriculture over the years is therefore critical to eradicate poverty, hunger, and malnutrition from the same region. Natural resource constraints, climate change, small land holding, and low farm profits are major challenges in this sector. In India, agriculture is the primary industry, source of livelihood, and way of life for more than 70% of the population. With high population growth, per capita availability of land is decreasing fast. We have about 120 Mha degraded and wastelands in India, which include area affected by salinity, alkalinity, acidity, water or wind erosion, water logging, etc. Most of these areas are inhabited by marginal or landless farmers, poor people with food, nutrition, and livelihood insecurity. Rejuvenating such areas through scientific and farmer-friendly technologies can help in poverty alleviation and help conserve natural resources.

The present chapter has been specifically designed to provide scientific inputs on the basic as well as applied aspects on "acid soil management—a challenge and opportunity." Some of these are current status of acid soil, cause of soil acidity, impact of acid soil on crop productions, amelioration of acid soil adopting new technology for sustainable soil health, crop productivity, and for higher farm profit.

Keywords

Acid soil · Amelioration of acid soil · Sustainable soil health · Higher farm profit

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22.1 Introduction

The present-day management of agricultural soils must protect them against erosion and leaching losses, if their productivity, even at high input, is to be sustained. The fact that the most acid upland soils are not used for agriculture is an indication that it is very difficult to practice sustainable agriculture on them. Soil acidity means an addition of acidity to the soil. Acidification occurs naturally, but faulty agricultural practices also enhance this process. Soil pH is a measure of the soil solution's acidity or alkalinity. By definition, pH is the negative logarithm of the hydrogen ion activity of the soil solution. Soils of humid regions and soils derived from the acidic parent materials have poor base saturation and, therefore, low pH. These soils are widely distributed across the globe including India. Acid soil are less productive because of some soil-related constrains. These are toxicity of Al or Mn; deficiency of some plant nutrients, such as P, Ca, Mg, B, and Mo; and poor biological activity. It is possible to ameliorate soil acidity by application of lime at the time of sowing of crops. Another option to manage soil acidity is to grow crops, which are relatively tolerant and grow well under acidic environments.

Sustainable agriculture has a significant role in the national economy and food security situation of many developing countries. Growth of agriculture over the years is, therefore, critical to eradicate poverty, hunger, and malnutrition from the region (Fan 2013). Natural resource constraints, climate change, small land holding, and low farm profits are major challenges in this sector. In India, agriculture is the primary industry, source of livelihood, and way of life for more than 70% of the population.

With high population growth, per capita availability of land is decreasing fast. We have about 120 Mha degraded and wastelands in India, which include area affected by salinity, alkalinity, acidity, water or wind erosion, water logging, etc. (NAAS 2010). Most of these areas are inhabited by marginal or landless farmers, poor people with food, nutrition, and livelihood insecurity. Rejuvenating such areas through scientific and farmer-friendly technologies can help in poverty alleviation and help conserve natural resources.

The present charter has been specifically designed to provide scientific inputs on the basic as well as applied aspects on "acid soil management—a challenge and opportunity." Some of these are current status of acid soil, cause of soil acidity, impact of acid soil on crop productions, amelioration of acid soil for sustainable soil health, and crop productivity.

22.2 Extend of Soil Acidity

Acid soils are formed mainly due to leaching of bases. Weathering of acidic rocks and minerals (quartz, schist) also contributes in the formation of acid soils. The degree of acidity indicated by soil pH is determined by soil forming factors such as rainfall, temperature, vegetation, parent rock, and hydrological conditions. In India, acid soils comprise about 28% of the total geographical area (TGA), out of which

9.3% are strong to moderately acidic (pH <5.5), while 18.9% are slightly acidic (pH 5.5–6.5). Such soils occupy about 90 Mha (Table 22.1) of the TGA, out of which 50% is under cultivation, and the rest is under forestry and other uses. About 30 Mha of cultivated land with pH less than 5.5 is critically degraded with major soil-related constraints leading to poor crop production (Rattan et al. 2015).

22.3 Cause of Soil Acidity

Acid soils are formed mainly from acidic parent materials and leaching of bases caused by high rainfall. Acid granite rocks as parent material, for example, in the process of soil formation, render the soil acidic. Continuous use of acid-forming fertilizers, such as ammonium sulfate or urea in soils create soil acidity, as Ca^{2+} and other basic elements are displaced by NH^{4+} ion, leading to the formation of calcium sulfate, which is leachable. Movement of excess water through soil rapidly in sloppy terrain in high rainfall areas is an important factor in acid soil development. The regions with annual rainfall of 1350 mm have acid soils with pH value 5.0 or less. Microorganisms are responsible for the decomposition of organic residues. Organic acids, thus formed during the process, are neutralized by basic ions, such as Ca, Mg, etc. If base saturation is low, acids generated are not neutralized. In coastal and marshy areas, dense vegetation is accompanied by high rainfall and water logging. Under such situations, organic materials do not get enough oxygen to decompose completely. This gives rise to soil acidity. Topography also influences soil formation by moderating hydrological conditions. Oxidation of S-containing compounds present in soils also leads to acidity development, as in case of acid sulfate soils. Acid rains also cause soil acidity problems.

22.4 Impact on Soil Health and Crop Production

The indicators of health of acid soils in order of importance are soil pH, exchangeable Al^{3+}, available P, water holding capacity, CEC, exchangeable Ca^{2+}, soil texture and soil organic matter, and microbial population. In hilly terrain, extent of soil loss and nutrient loss are important (Sarkar 2013).

Soil reaction is the master variable controlling the availability of nutrients in acid soils (Malavolta 2006). Availability of nutrients is highest in soil pH range of 5.8 and 7.0 (Fig.22.1), as soils become acidic that adversely affects root activity and impacts negatively the water and nutrient absorption by growing plants.

Most acid soils are deficient in a number of plant nutrients, both macro and micro indicating poor soil health (Sarkar and Singh 2003; Sarkar et al. 2007). Population of bacteria and actinomycetes is low in most acid soils, while fungal population is high. This imbalance adversely affects the biological transformation of plant nutrients in soils. In general, yields of pulses, oilseeds, maize, and wheat are poor in low pH soils (Mandal et al. 1975). On the other hand, rice, minor millets, potato, mesta, niger, mustard, and plantation crops, such as tea and coffee, perform well under acidic soil

Table 22.1 State-wise distribution of acid soils in India (area in '000 ha)

S. no.	State	Strongly acidic (pH < 4.5)	Moderately acidic (pH 4.5–5.5)	Slightly acidic (pH 5.5–6.5)	Total	TGA	% in TGA
		(area in '000 ha)					
1.	Andhra Pradesh	0.0	0.0	2827.5	2827.5	27504.5	10.3
2.	Arunachal Pradesh	4775.9	1742.7	268.8	6787.4	8374.3	81.1
3.	Assam	23.5	2331.2	2332.7	4687.5	7843.8	59.8
4.	Bihar	0.0	36.7	2324.9	2361.6	9416.3	25.1
5.	Chhattisgarh	156.4	5930.1	4386.6	10473.0	13480.5	77.7
6.	Goa	3.6	113.7	191.1	308.3	370.2	83.3
7.	Himachal Pradesh	0.0	157.0	16.20.6	1777.6	5567.3	31.9
8.	Jammu and Kashmir	0.0	93.3	1480.1	1573.4	22223.6	7.1
9.	Jharkhand	0.0	999.6	5772.1	6771.7	7971.4	84.9
10.	Karnataka	0.0	61.4	3254.7	3316.1	19179.1	17.3
11.	Kerala	138.0	2789.6	753.2	3680.7	3886.3	94.7
12.	Madhya Pradesh	0.0	1124.7	10601.8	11726.5	30864.1	38.0
13.	Maharashtra	0.0	240.0	4332.6	4572.6	30771.3	14.9
14.	Manipur	426.9	1437.2	325.1	2189.2	2232.7	98.1
15.	Meghalaya	0.0	1186.3	1054.4	2240.7	2242.9	99.9
16.	Mizoram	0.0	1267.6	777.3	2044.9	2108.1	97.0
17.	Nagaland	118.9	1483.3	55.7	1657.9	1657.9	100.0
18.	Orissa	0.0	261.6	8409.7	8671.3	15570.7	55.7
19.	Sikkim	278.9	323.4	2.8	605.0	709.6	85.3
20.	Tamil Nadu	264.0	347.3	4294.5	4905.8	13005.8	37.7
21.	Tripura	56.6	749.0	237.2	1042.8	1048.6	99.5
22.	Uttar Pradesh	0.0	0.0	337.5	337.5	24104.6	1.4
23.	Uttarakhand	0.0	1183.6	2300.6	3484.2	5336.5	65.3

24.	West Bengal	0.0	556.6	4199.7	4755.3	8875.2	53.6
25.	Others[a]	0.0	0.0	0.0	0.0	64,381	0.0
26.	Total	6242.6	24414.6	62141.2	92798.4	328726.3	28.2
27.	Area (%)	1.9	7.4	18.9	28.2	100.0	

[a] Others: Delhi, Gujarat, Haryana, Punjab, Rajasthan, A&N Islands, D&N Haveli, Daman and Diu, Lakshadweep and Pondicherry.

Sources: Rattan et al. (2015).

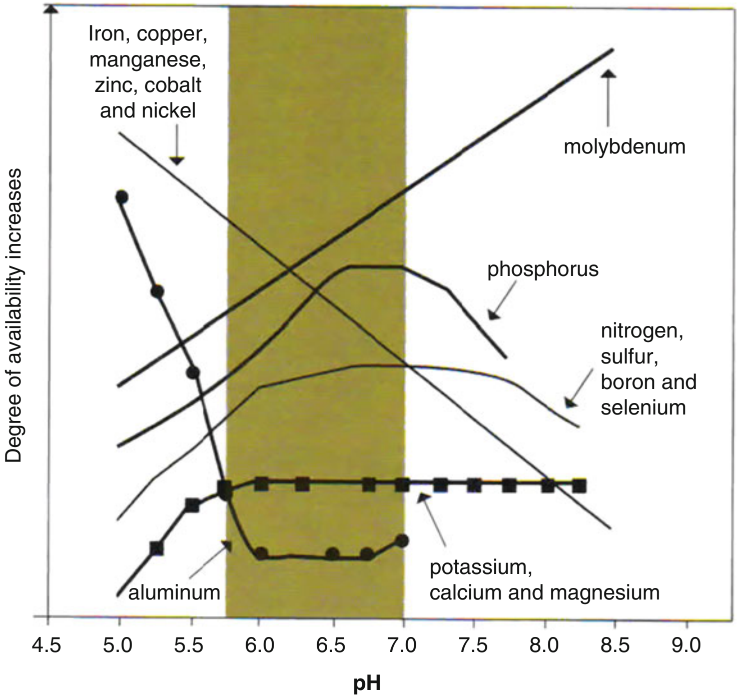

Fig. 22.1 Typical effect of change in soil pH on the availability of plant nutrients. Source: Malavolta (2006)

environments. Crops like soybean, pigeon pea, potato, cotton, and vegetables respond to liming, indicating their sensitivity to soil acidity.

22.5 Amelioration of Acid Soil for Sustainable Soil Health and Crop Production

Pioneering work by Professor S.C. Mandal and his coworkers paved the way for systematic research on acid soil management. These workers identified liming as the most important input for amelioration of soil acidity (Mandal et al. 1966, 1975; Mathur et al. 1985). The investigations were focused on (1) response of crops to liming, (2) lime requirement of acid soils, (3) quality of liming materials, (4) fineness of liming materials, (5) frequency of liming, (6) methods of lime application, (7) crop rotation in relation to liming, etc. It was found that all the liming materials, when added on equivalent lime basis, were more or less equally effective in increasing the yield of crops in acid soils. The minimum fineness of the liming material to be effective should be such that it passes through ten mesh sieve, but in the case of basic slag, passes through 30 or 40 mesh sieve are recommended for application as a soil amendment. Considering major soil-related constraints in acid soils of India, studies were undertaken on their correction by several workers. These have been well documented (Panda et al. 1991, 1996; Sarkar et al. 2007; Jena 2008; Pattanayak et al. 2008; Pattanayak and Sarkar 2016).

Subsequently, attempts were made to reduce the dose of lime to one-fourth from one-half of the lime requirement and apply in split doses. Lime provides Ca, which is in short supply in acidic soils due to removal by growing crops and leaching due to high rainfall. Mathur et al. (1985) reported that application of 3–4 q ha^{-1} of lime in furrows below the seed at sowing could increase the yield of groundnut, soybean, gram, and barley by 20–36%. Liming at this level increased the pH as well as calcium saturation of soils by 37–50% (Tables 22.2 and 22.3) in kaolinite-rich soils. Mathur et al. (1989) compared lime application at 1/10, 1/15, and 1/20th of lime requirement (LR) applied in rhizosphere at sowing for 6 years with LR dose applied as broadcast only once in the beginning. The mean yield of urd bean, soybean, groundnut, lentil, and other crops grown with 1/20 LR dose was at par with 1 LR dose. After 6 years, exchangeable calcium was found to be the highest in soils receiving 1/10 LR dose of lime and was more profitable than LR dose (Table 22.4). The uptake of phosphorus by crops was greatly enhanced by liming. The return per rupee investment not only increased with time at all split doses of lime, but also the gap between full dose and lower doses of lime narrowed down, showing thereby higher profitability at lower doses in most crop rotations. Further, application of FYM with 50% recommended NPK + lime increased the yield of crops from 6 to 82% over 100% NPK application. Results show that conjunctive use of lime and FYM even with 50% NPK application was superior because of higher crop yields with improved soil health (Tables 22.5 and 22.6).

22.6 Future Research Strategy

22.6.1 Support Services for Acid Soil Management

- Soil amendments must be available to farmers (PPP mode).
- A consolidated database on the availability of organics, nutrient input and removal by crops, available water sources, and pest and disease of crops at block level should be available.
- Based on farmer’s resources, investment capacity, and level of management, package of practices should be developed.
- Assistance from other rural development and livelihood security initiatives at state level is needed.

22.6.2 Research Prioritization

- Emphasis on productivity enhancement of acid soils.
- Chemistry of acid soils collected from benchmark sites.

Table 22.2 pH, exchangeable Ca saturation of soils as affected by lime application

Lime (Q/ha)	Groundnut			Soybean			Gram		
	pH	Exch. Ca[a]	Ca saturation%	pH	Exch. Ca	Ca saturation%	pH	Exch. Ca	Ca saturation%
Control	5.2	3.3	38.4	5.1	3.2	37.2	5.5	3.2	37.2
As per LR[b]	6.9	5.3	61.6	6.7	3.5	40.7	6.9	4.7	54.6
2	5.6	3.4	39.5	5.4	3.4	39.5	5.7	3.4	59.5
3	5.6	3.5	40.7	5.6	3.7	43.0	5.8	3.6	41.9
4	5.7	3.6	41.9	6.0	4.1	47.7	6.0	3.9	45.3
5	6.0	4.5	50.0	6.1	4.3	50.0	5.2	4.2	48.8

[a] Cmol(P+)kg^{-1}.

[b] Lime requirement.

Table 22.3 Grain yield (q ha^{-1}) of crops with lime application in acid soils

	Groundnut		Soybean		Gram		Barley	
Lime (q/ha)	Yield	% increase	Yield	% increase	Yield	% increase	Yield	% increase
Control	17.5		20.3		13.1		24.3	
As per LR[a]	22.7	29.9	28.1	38.4	18.4	40.1	35.6	46.2
2(furrow)	20.8	19.0	24.8	22.2	16.0	22.1	30.1	23.6
3(furrow)	20.8	19.0	27.3	34.6	16.4	25.4	32.0	31.6
4 (furrow)	20.7	18.5	26.3	29.3	17.2	31.5	33.8	38.8
5 (furrow)	21.3	21.9	26.1	28.6	16.7	27.2	33.7	38.6
C.D. at 5%	1.2		1.4		1.3		1.4	

[a] L.R. Lime requirement of soils growing groundnut, soybean, gram, and barley were 46.5, 55.0, 28.5, and 28.5 q ha^{-1}, respectively.

Table 22.4 Grain yield (q/ha) of crops due to liming in acidic soils of Jharkhand

	Crops						
Treatments	Moong	Groundnut	Urad	Soybean	Lentil	Pea	Gram
No lime	2.8	12.0	5.8	13.3	11.4	11.3	2.2
1 LR (broadcast)	6.1	16.7	12.1	22.0	17.7	17.6	5.1
1/10 LR (furrow)	6.0	17.2	11.5	22.0	17.6	16.6	6.1
1/15 LR (furrow)	5.8	16.0	11.3	21.7	17.1	16.2	5.9
1/20 LR (furrow)	5.3	15.2	11.1	20.4	15.8	15.6	5.7
CD (P = 0.05)	0.03	1.6	1.8	19.8	1.8	1.7	1.8

- Steps to improve use efficiency of lime and plant nutrient sources (4R Nutrient Stewardship).
- Soil and water pollution assessment in acid soils.
- Integration of water resources management with lime + nutrient application in crops under rainfed uplands/medium lands.
- Al tolerance mechanism in crops/varieties in acid soils.
- Nutrient cycles in agroforestry/horticulture-based systems in hilly areas with strongly acid soils.

22.6.3 Policy Issues

- Availability of cheap and efficient liming materials at block level.
- Soil health cards will act as tool to help farmers on lime use.
- Village level, block level, and district level soil nutrient mapping required for management with reassessment of the after 5 years gap.

Table 22.5 Effect of lime, fertilizer, and FYM application on crop yield (q ha^{-1}) in acid soils

States	Crop	100% NPK	50% NPK + Lime	50% NPK + Lime + FYM
Assam	Rape seed	9.7	10.1 (4.1)	11.9 (22.68)
	Summer green gram	4.4	5.2 (18.2)	6.8 (54.5)
Himachal	Maize	34.0	33.1 (−2.7)	36.1 (6.2)
	Wheat	27.9	23.7 (−15.0)	29.8 (6.8)
Jharkhand	Maize + pigeon pea (maize equivalent yield)	69.0	65.0 (−5.8)	82.5 (19.6)
	Pea (pod)	38.4	50.8 (32.3)	69.7 (81.5)
Kerala	Cow pea	8.6	10.6 (23.3)	11.3 (31.4)
	Black gram	6.4	8.1 (26.6)	9.2 (43.7)
Meghalaya	Maize	30.5	30.3 (−0.7)	36.4 (19.3)
	Groundnut	14.2	21.3 (50.0)	25.4 (78.9)
Odisha	Groundnut	22.5	23.6 (4.9)	26.6 (18.2)
	Pigeon pea	12.0	12.2 (1.7)	14.6 (21.7)
West Bengal	Mustard	8.2	8.4 (2.4)	11.2 (36.6)
	Wheat	16.7	17.1 (2.4)	22.1 (32.3)
All state	Average of all crops	27.1	22.8 (−15.9)	28.1 (3.7)

() % yield increase/decrease over 100% NPK.

Table 22.6 Grain yield, nutrient uptake, and apparent nutrient recovery after 40 years of long-term fertilizer expt. at Ranchi with soybean and wheat

	Grain yield (kg ha^{-1})		Nutrient uptake (kg ha^{-1})[a]			Apparent nutrient recovery (%)		
Treatment	Soybean	Wheat	N	P	K	N	P	K
100% NPK	1550	2806	224	16.4	87.6	150	21	88
150% NPK	1529	2888	242	18.0	100.6	113	16	68
Lime+100% NPK	1807	3159	277	21	110.6	207	30	127
FYM + 100% NPK	1888	3354	296	24	128	229	34	147
No fertilizer	571	716	63	3.6	23.6	–	–	–

Source: Personal Communication, LTFE, Ranchi Centre Report, 2016.
[a] Nutrient uptake for Soybean-wheat system.

- Location-specific problems, such as soil erosion, hilly terrain, and water scarcity, need to be solved.

22.6.4 Science-Led Development

- Increase production without environmental problems.
- Value chain management for liming materials.
- Promote soil test-based balanced nutrient use.
- Include new products, processes in research.
- Encourage IT-led technology transfer modules.

22.7 Conclusion

Acidity is a major soil-related constraints affecting agricultural productivity in about 18 M ha of land in India. These soils are spread in the Himalayan region, eastern and north-eastern plains, peninsular India, and coastal plains under varying conditions of landscape, geology, climate, and vegetation. Acid soils have low pH (less than 5.5), poor base saturation, high exchangeable aluminum concentration, and inadequate supply of several essential plant nutrients, such as N, P, Ca, Mg, B, Mo, S, etc. Major growth-limiting factors of these soils are the direct and indirect effects of metal toxicities, nutrient deficiencies, and poor soil biological activities.

During the last five decades, excellent research work has been carried out on the characterization of acid soils, their chemistry, genesis and classification, and management. The present paper is an attempt to review the good work on acid soil management. Results show that, besides the use of amendments, such as lime, dolomite, paper mill sludges, basic slag, etc., there is need to look into the other complementary issues, which pose challenges for successful crop production and maintain soil health in the long run. Some such issues are managing the water availability in rain-fed uplands and medium lands for increasing cropping intensity through inter-cropping/sequence cropping systems, agro-forestry, horticulture in hilly areas, promoting organic matter application and bio-fertilizers to boost soil biological activity, use of lime with plant nutrients deficient in acid soils with emphasis on secondary and micronutrients, and checking soil degradation by different location specific measures. These measures along with soil amendments to raise the soil pH have the potential to arrest the degradation process in acid soil regions.

Finally, a long-term vision on soil acidity management has been provided. This comprises of work on a missionary mode on five priority areas: creation of a database of nutrients, amendments, irrigation, land holding, etc. at block, panchayat level, managing the supply and availability of soil amendments, linking soil health cards with use of amendments and nutrients in acid soil regions, promoting resource conservation technologies, and addressing the transfer of technology concerns. The indicated measures need to be debated with the stakeholders and implemented for bringing about perceptible changes in the livelihood security of farmers and their families in regions affected by soil acidity in the next 5–10 years.

References

Fan S (2013) Ensuring food and nutritional security in Asia: the role of Agricultural Innovation. In: 7th TAAS foundation day lecture. New Delhi, I.A.R.I

Jena D (2008) Management of acid soils for sustainable crop production, NAE-Acid soil Bulletin No.4, OUAT, Bhubaneshwar

Malavolta E (2006) Manual of mineral plant nutrition. Editora Agronomica Ceres Ltd, Sao Paulo, pp 1–631

Mandal SC, Sinha H, Prasad CR, Ali MA (1966) Studies on liming acidic red loam soils. J Indian Soc Soil Sci 14:127–131

Mandal SC, Sinha MK, Sinha H (1975) Acid soils of India and liming. ICAR Technical Bulletin no.75

Mathur BS, Rana NK, Sinha H, Lal S (1985) Lime as an effective source of fertiliser in acid red loam soil of Bihar. J Indian Soc Soil Sci 33:328–332

Mathur BS, Rana NK, Sinha KP, Lal S (1989) SSAC/BAU research bulletin no. 2/89, Birsa Agricultural University, Ranchi

NAAS (2010) Degraded and wastelands of India—status and spatial distribution. National Academy of Agricultural Science, ICAR report, pp 1–155

Panda N, Prasad RN, Mukhopadhaya AK, Sarkar AK (1991) Managing acid soils for optimum productivity in red, laterite and associated soils of eastern India. Bull Indian Soc Soil Sci 15:27–37

Panda N, Sarkar AK, Mathur BS (1996) Chemical degradation leading to soil acidity and its amelioration. Bull Indian Soc Soil Sci 17:82–88

Pattanayak SK, Mohanty S, Mishra KN, Nayak RK, Mohanty GP, Rao DLN (2008) Technical Bulletin on ‘Biofertilisers for tropical vegetables’. All India Network Project on Biofertilsers. O. U.A.T, Bhubaneshwar

Pattanayak SK, Sarkar AK (2016) Sustainable management of acid soils-technologies and their transfer. Indian J Fertil 12(7):16–24

Rattan RK, Katyal JC, Dwivedi BS, Sarkar AK, Tapas B, Tarafdar JC, Kukal SS (2015) Soil science: an international. Indian Society of Soil Science, New Delhi

Sahoo AK, Sarkar D (2013) Genesis and classification of acid soils of India. In: Sarkar AK (ed) Acid soils-their chemistry and management. New India Publishing Agency, New Delhi, pp 49–104

Sarkar AK (2013) Soil health management in acid soils. In: Tandon HLS (ed) Soil health management. Fertilizer Development and Consultative Organisation, New Delhi, pp 142–164

Sarkar AK, Mahapatra P, Kumar A (2007) Management of macronutrients in acid soils. Bull Indian Soc Soil Sci 25:10–26

Sarkar AK, Singh S (2003) Crop response to secondary and micronutrients in acidic soils of India. Fertilizer News 48(4):47–54