Plant Tolerance to Environmental Stress

Role of Phytoprotectants

EDITED BY

Mirza Hasanuzzaman • Masayuki Fujita
Hirosuke Oku • M. Tofazzal Islam

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Preface

The population of the world is estimated to increase from 7.3 to 9.7 billion by the year 2050. To keep up with the pace of population growth, it has recently been estimated that food production will need to be increased by 50% by 2030 and by 70–100% by 2050 for a well-fed world population. This situation will be exacerbated by a decrease in available arable land coupled with reduced crop yields, both of which are predicted to arise from climate change. Global climate change affects crop production not only through altered weather patterns, but also via increased environmental stresses such as soil salinity, drought, flooding, metal/metalloid toxicity, environmental pollution, low and high temperature, and the emergence of new diseases and insect-pests. It is estimated that these stresses will reduce the crop yield of staple food up to 70%. As sessile organisms, plants cannot avoid all these predicted abiotic stresses, but can evolve sophisticated mechanisms to adapt to the changing environment. Therefore, a better understanding of plant responses to abiotic stresses is fundamental in designing biorational strategies to improve crop plants and obtain a sustainable crop production. Over decades, agronomic, physiological, genetics, genomics and other molecular biological studies have generated a large body of knowledge on reactions of plants to various abiotic stresses. Considerable success has also been achieved in the improvement of plant tolerance to abiotic stresses through the utilization of new knowledge generated by research. The application of various omics approaches is shedding light on molecular crosstalks between plants and abiotic stresses; this should promote the development of stress-tolerant crop plants by the application of exogenous and endogenous regulators.

The application of various phytoprotectants has become one of the most effective and plausible approaches in enhancing plant tolerance to abiotic stresses. These phytoprotectants include but are not limited to osmoprotectants (compatible solutes), antioxidants, phytohormones, nitric oxide, polyamines, amino acids, and nutrient elements of plants. A large body of literature is available on how these protective agents exert beneficial effects on plants, helping them tolerate abiotic stresses. However, the actual dose, timing, and methods of practical application of phytoprotectants need to be finely tuned. Several lines of evidence suggest that exogenous osmolytes, phytohormones, signaling molecules and nutrient elements enhance the antioxidant defense system of plants. This, too, augments their tolerance to abiotic stresses. Additionally, the application of phytoprotectants activates reactive oxygen species (ROS) signaling in plants.

This book outlines the recent updates of our understanding of the effects that various abiotic and biotic agents (commonly known as phytoprotectants) have on plant tolerance to major abiotic stresses. It includes 26 chapters contributed by 127 leading experts, including diverse areas of life sciences such as agronomy, plant physiology, cell biology, environmental sciences, and biotechnology. Chapter 1 describes the morphological and physiological changes undergone by plants under various abiotic stresses. The roles of phytoprotectants on abiotic stress signaling in plants are discussed in Chapter 2. Chapter 3 focuses on the improvement of abiotic stress tolerance in plants brought by seed priming. The enhancement of abiotic stress tolerance in plants through the application of various osmolytes is discussed in Chapter 4. Proline is a small molecule biosynthesized in plants which plays a significant role in their tolerance to salinity and drought. Chapter 5 comprehensively reviews the functions of proline in conferring salinity and drought tolerance to plants. Phytohormones are involved in various physiological processes including plant adaptation to harsh environments. Chapter 6 discusses the role of phytohormones in improving abiotic stress tolerance in plants. The enhancement of drought tolerance in plants through the ROS-scavenging system of phytohormones is illustrated in Chapter 7.

Stigalactones are chemical compounds biosynthesized in roots and are known as branching-inhibition hormones in plants. Their molecules have profound roles in plant–fungi (e.g., mycorrhiza) interactions and signaling systems in plants. Chapter 8 describes the role of strigalactones as mediators of abiotic stress responses and parasitic attraction in plants. The effects of non-enzymatic antioxidants in improving the tolerance of plants to abiotic stresses are presented in Chapter 9. Nitric oxide is a signaling molecule involved in various physiological processes in plants and other organisms. It also plays an important role in plant tolerance to abiotic stresses through antioxidants and ROS responses. Chapter 10 updates the regulatory role of nitric oxides in plant tolerance to abiotic stresses. The improvement of abiotic stress tolerance in plants through exogenous hydrogen peroxide and nitric oxide is covered in Chapter 11. The application of amino acids, calcium, balanced sulfur nutrition, silicon, and selenium in the enhancement

of plants tolerance to abiotic stresses is described in Chapters 12, 13, 14, 15, and 16, respectively. The role of bioorganic fertilizers and biochar in the improvement of soil health and mitigation of stress-induced damages in plants is discussed in Chapters 17 and 18, respectively.

Plant-associated beneficial microorganisms (such as plant probiotic bacteria) play important roles in promoting abiotic stress tolerance in plants. Chapters 19–22 focus on the effects of various beneficial microorganisms in protecting plants from abiotic stresses and increasing the yield of crops. The long road to the development of novel priming products to increase crop yield under stressful environments is covered by Chapter 24. Finally, the alleviation of the adverse effects of abiotic stresses to plants through plant-derived smoke and magnetopriming is illustrated in Chapters 25 and 26, respectively.

This book represents a cooperative effort from editors and contributors representing many different countries. The editors gratefully acknowledge the authors who contributed to this book project. We are thankful for the enthusiasm and collegial spirit they demonstrated. Our profound thanks are also due to Lecturer Dr. Mahbub Alam of the Department of Agriculture of Noakhali Science and Technology University for his valuable support in formatting and incorporating all editorial changes in the manuscripts. We would like to thank Randy Brehm (Senior Editor) and Laura Piedrahita (Editorial Assistant) of CRC Press, who made suggestions on improving this book in view of our audience. Our thanks are also due to other editorial staffs for their precious help in formatting and incorporating editorial changes in the manuscripts. We believe researchers who work on plants tolerance to abiotic stress will find this book an essential reference.

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Mirza Hasanuzzaman is a Professor of Agronomy at Sher-e-Bangla Agricultural University, Dhaka, Bangladesh. In 2012, he received his PhD on 'Plant Stress Physiology and Antioxidant Metabolism' from the United Graduate School of Agricultural Sciences, Ehime University, Japan with a Japanese Government (MEXT) Scholarship. Later, he completed his postdoctoral research in the Center of Molecular Biosciences (COMB), University of the Ryukyus, Okinawa, Japan with a 'Japan Society for the Promotion of Science (JSPS)' postdoctoral fellowship. Subsequently, he joined as Adjunct Senior Researcher at the University of Tasmania with an Australian Government's Endeavour Research Fellowship. He joined as a Lecturer in the Department of Agronomy, Sher-e-Bangla Agricultural University in June 2006. He was promoted to Assistant Professor, Associate Professor and Professor in June 2008, June 2013, and June 2017, respectively. Prof. Hasanuzzaman has been devoting himself to research in the field of Crop Science, especially focused on Environmental Stress Physiology, since 2004. He has been performing as team leader/principal investigator of different projects funded by World Bank, FAO, University Grants Commission of Bangladesh, Ministry of Science and Technology (Bangladesh), and so on.

Prof. Hasanuzzaman published over 100 articles in peer-reviewed journals and books. He has edited 2 books and written 35 book chapters on important aspects of plant physiology, plant stress responses, and environmental problems in relation to plant species. These books were published by internationally renowned publishers (Springer, Elsevier, CRC Press, Wiley, etc.). His publications received over 2,000 citations with h-index: 23 (according to Scopus). Prof. Mirza Hasanuzzaman is a research supervisor of undergraduate and graduate students and has supervised 20 M.S. students so far. He is an editor and reviewer of more than 50 peer-reviewed international journals and a recipient of the Publons Peer Review Award 2017. Dr. Hasanuzzaman is an active member of about 40 professional societies and acting as Publication Secretary of the Bangladesh Society of Agronomy. He has been honored by different authorities due to his outstanding performance in different fields, such as research and education. He received the World Academy of Science (TWAS) Young Scientist Award 2014. He attended and presented 25 papers and posters at national and international conferences in several countries (United States, United Kingdom, Germany, Australia, Japan, Austria, Sweden, Russia, etc.).

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Hirosuke Oku is a Professor in the Center of Molecular Biosciences at the Tropical Biosphere Research Center in the University of the Ryukyus, Okinawa, Japan. He obtained his Bachelor of Science in Agriculture from the University of the Ryukyus in 1980. He received his PhD in Biochemistry from Kyushu University, Japan in 1985. In the same year he started his career as Assistant Professor in the Faculty of Agriculture, University of the Ryukyus. He became a professor in 2009. He received several prestigious awards and medals including the Encouragement Award of Okinawa Research (1993) and the Encouragement Award of the Japanese Society of Nutrition and Food Science (1996). Prof. Oku is the group leader of the Molecular

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M. Tofazzal Islam is a Professor of the Department of Biotechnology of Bangabandhu Sheikh Mujibur Rahman Agricultural University in Bangladesh. He received his MS and PhD in Applied Biosciences from Hokkaido University in Japan. Dr. Islam attended postdoctoral research experiences at Hokkaido University, University of Goettingen, University of Nottingham and West Virginia University under the JSPS, Alexander von Humboldt, Commonwealth, and Fulbright Fellowships, respectively. He has published articles in many international journals and book series (over 200 peer-reviewed articles, total citation 1,664, h-index 22, i10-index 48; RG score 39.06). Dr. Islam was awarded many prizes and medals including the Bangladesh Academy of Science Gold Medal in 2011, University Grants Commission Bangladesh Awards in 2004 and 2008, and Best Young Scientist Award 2003 from the JSBBA. Prof. Islam is the chief editor of a book series, Bacillus and Agrobiotechnology, published by Springer. His research interests include genomics, genome editing, plant probiotics and novel biologicals, and bioactive natural products.

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1 Impacts of Abiotic Stresses on Growth and Development of Plants

Muhammad Fasih Khalid, Sajjad Hussain, Shakeel Ahmad, Shaghef Ejaz, Iqra Zakir, Muhammad Arif Ali, Niaz Ahmed, and Muhammad Akbar Anjum

CONTENTS

1.1 INTRODUCTION

Plants are frequently subjected to unfavorable conditions such as abiotic stresses, which play a major part in determining their yields (Boyer, 1982) as well as in the distribution of different plants species in distinctive environments (Chaves et al., 2003). Plants can face several kinds of abiotic stresses, such as low amounts of available water, extreme temperatures, insufficient availability of soil supplements and/or increase in toxic ions, abundance of light and soil hardness, which restrict plant growth and development (Versulues et al., 2006). A plant's ability to acclimate to diverse atmospheres is related to its adaptability and strength of photosynthetic process, in combination with other types of metabolism involved in its growth and development (Chaves et al., 2011). When plants are adapted to abiotic stresses, they activate different enzymes, complex gene interactions and crosstalk with molecular pathways (Basu, 2012; Umezawa et al., 2006).

The major abiotic stresses (cold, heat, drought and salinity) negatively affect survival, yield and biomass production of crops by as much as 70% and threaten food safety around the world. Desiccation is the major factor in plant growth, development and productivity, mainly occurring due to salt, drought and heat stress (Thakur et al., 2010). When a plant is exposed to abiotic stresses, it can face a number of problems (Figure 1.1).

Since resistance and tolerance to this problem in plants is of great importance in nature (Collins et al., 2008), breeders face an enormous challenge in attempting to manipulate genetic modification in plants to overcome the issue. Conventional plant breeding approaches have had limited effectiveness in improving resistance and tolerance to these stresses (Flowers et al., 2000).
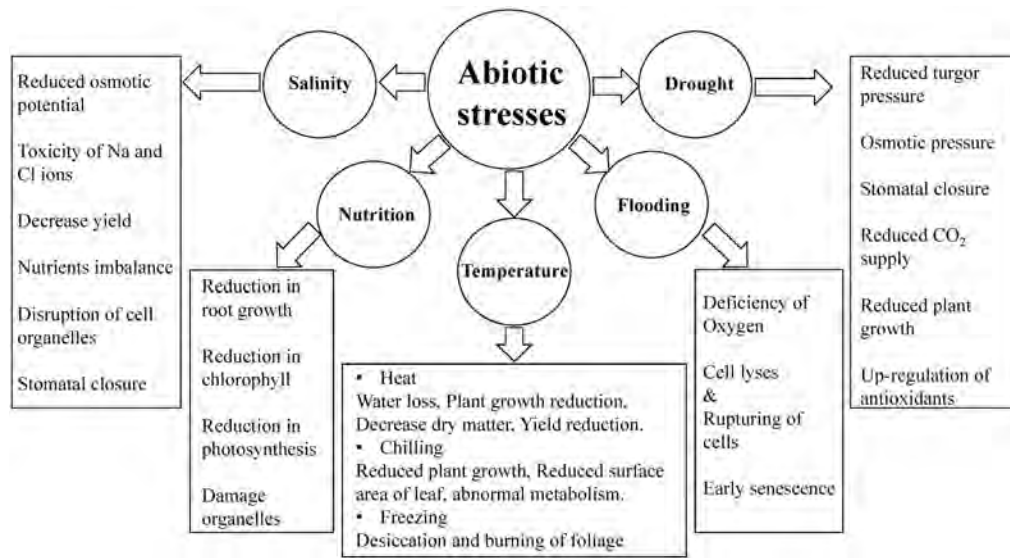
FIGURE 1.1 Effect of different abiotic stresses (salinity, nutrition, temperature, flooding and drought) on plant.

1.2 ABIOTIC STRESS AND PLANT DEVELOPMENT

1.2.1 TEMPERATURE

1.2.1.1 Chilling

Chilling injury in plants depends on the sensitivity of their different components to low temperatures. Cellular membrane integrity is the basic component that directly relates to the plants that are sensitive to chilling stress (Levitt, 1980). Lipids present in cell membranes change their state from liquid to solid when plants are brought into light at low temperatures, which mainly depends upon the amount of unsaturated fatty acids they contain (Quinn, 1988). In order for plants to tolerate frost or chilling stress, there must be some alterations in the classes of these unsaturated fatty acids, since plants that have more fatty acids in their cell membranes can tolerate more chilling or frost stress. Different enzyme contents and activities also increase or decrease under extremely low temperatures (Figure 1.2). In plant cell membranes, several changes in physicochemical states occur that compensate for the effect of chilling or frost by increasing cell membrane permeability and also cause ionic and pH imbalance, ultimately decreasing ATP (Levitt, 1980).

1.2.1.2 Freezing

Plants significantly vary in their capacities to manage freezing temperatures. Plants grown under tropical and subtropical conditions (i.e., maize, cotton, soybean, rice, mango, tomato, etc.) are more sensitive to freezing. Plants grown in a temperate climate can tolerate low temperatures, although the degree of tolerance varies from species to species. Moreover, the extreme freezing resistance of these plants is not inherent, as at low temperatures plants activate different physiological and biochemical processes to cope with freezing in a process known as 'cold acclimation'. For example, in one study, rye plants exposed to -5°C without prior acclimation to cold were not able to survive, but when cold acclimatized at 2°C for 7–14 days, they were able to survive temperatures as low as -30°C (Fowler et al., 1977).

Previous research on cold acclimation of plants was designed to examine what happens at low temperatures, helping improve resistance under these conditions. In earlier studies, it was shown that plants activate their enzymatic and non-enzymatic antioxidant defense mechanism to cope with freezing temperatures (Levitt, 1980; Sakai & Larcher, 1987). To prevent freezing injury (cellular membrane damage) under low-temperature conditions, plants produce different osmolytes and osmoprotectants, such as lipids, proline, glycine betaine, and sugars, which help in decreasing membrane damage. Along with solutes and polypeptides, studies have shown that many genes are involved in the activation of cold acclimation processes, ultimately improving freezing resistance. For example, all the chromosomes are involved in coping with freezing injury in hexaploid wheat.

Cold acclimatization is a combination of physiological, biochemical and hereditary processes. Changes do occur in plants exposed to freezing temperatures, but it is not yet clear which changes are involved in the cold acclimation process and which are involved in other resistance processes. However, freezing-tolerance mechanisms are not related to any individual gene that copes with the freezing injury. Many efforts have been
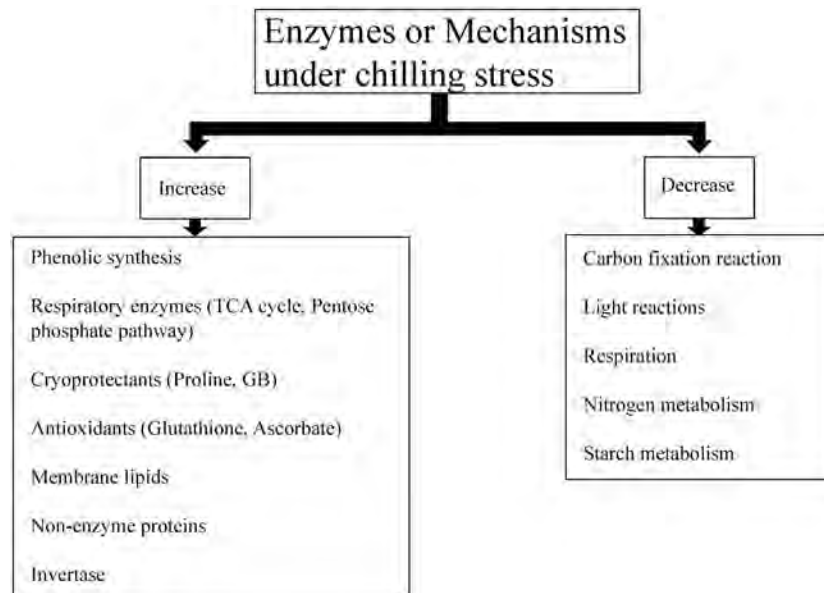
FIGURE 1.2 Enzymes and mechanisms which increase or decrease under chilling stress.

made to isolate and evaluate the genes that are induced under extremely low temperature. The latest studies confirm that *ICE2* is involved in the acclimation process in *Arabidopsis*, ultimately increasing the tolerance of plants to low-temperature stress. The recent discovery of the CBF cold-response pathway describes the involvement of clod acclimation in resistance to low temperatures.

1.2.1.3 Heat

Plants subjected to high temperatures undergo numerous distinctive changes and adjustments. Adaptation to high temperatures occurs on diverse time scales and levels of plant organization. Exposure of plants to extremely high temperatures for long periods of time may cause severe injury, leading to death. Under such temperatures, different plant parts are affected in different ways. The nature of the injury depends on the growth stage of the plant, its susceptibility and cellular processes taking place at that time. However, in extremely high temperatures, heat not only damages the plant at a cellular level but also affects many complex processes and structures that ultimately cause death of the plant. When plants are exposed to high temperatures, several changes occur at the cellular level, including modification of lipids (which become more fluid and develop osmotic pressure) and production of reactive oxygen species (ROS) that disturb the cell membrane metabolism. Proteins work efficiently at a specific temperature, but when temperatures exceed their optimal zone, they are deactivated, causing changes in the activity of enzymes and increasing the production of active oxygen species

(AOS) and ROS. Several enzymatic (e.g., SOD, POD, CAT) and non-enzymatic antioxidants (e.g., proline, GB) are produced to cope with ROS, but antioxidants have very little effect on the activity of AOS, which are prevalent under extremely high temperatures. The effects of AOS, including reduced photosynthesis, increased oxidative stress, and changes in movement of assimilates, significantly damage the plant and ultimately cause its death (Hall, 2001). However, many processes and genes are involved in plant tolerance under heat stress. Commonly, under field conditions, plants are exposed to heat with a combination of other stresses, such as heat and drought stress or heat and radiation stress. Similar damage may occur via other stresses when combined with heat stress. Plants respond to different stresses in similar ways. Under heat stress, plants produce proteins to cope with the effects of high temperatures at a cellular level. These are called heat-shock proteins (HSPs; Boston et al., 1996). Different pathways are involved in mitigating heat stress in which HSPs are the only component of heat tolerance. When a plant is exposed to extremely high temperatures, different signaling genes become involved in resistance mechanisms by signaling and activating several metabolic processes. More effort is required to identify and characterize the genes that play a vital role in plant tolerance to extremely high temperatures. When the pathways involved in the resistance and tolerance of plants to heat stress are clearer, it will be easier to recognize the interaction between high-temperature stress and other stresses, which in turn will aid in devising strategies to make plants more tolerant (Nobel, 1991). The main challenge here is to recognize

the cellular and metabolic pathways affected by heat stress in order to devise strategies to reduce adverse effects on crop yield.

1.2.2 SALINITY

Salt stress is the major problem in arid and semiarid regions, limiting agricultural production and crop yields worldwide. About 20% of cultivated and 50% of irrigated land is directly affected by salinity, which reduces crop yield and productivity (Flowers, 2004; Munns, 2002). At present, improvement in plant growth and yield in salt-affected soils is the basic research priority. Salt tolerance in crop plants can be enhanced by conventional breeding methods as well as molecular breeding techniques (Flowers, 2004). Crop-yield stability under salt-stress conditions is also an important factor. There is only limited understanding about how the different cellular metabolisms of cell division and differentiation are directly affected under salt-stress conditions. This ultimately leads to reduced plant growth and yield (Zhu, 2001). In the past, it was proposed that plant adjustment to salinity most likely includes phenological reactions that are imperative for plant-health management in a saline environment but may negatively affect yield (Bressan et al., 1990). Yet, in some cases, high crop yield can be attained under saline conditions by following proper crop management practices (Flowers, 2004).

Some species of tomatoes, mainly wild species and primitive cultivars, possess genes for salt tolerance (Cuartero et al., 1992; Jones, 1986). Cases where adequate hereditary diversity for salt resistance exists or is available in cultivars ordinarily used in programs of breeding are risky (Flowers, 2004; Yeo & Flowers, 1986). The varieties chosen against the capacity for resistance to salt have a limited gene pool in which negative linkages exist between loci mindful for tall abdicate and those which are important for salt resistance. Recent studies on distinguishing proof of salt-resistance determinants and separation of the integration between salt resistance, plant growth and development offer some considerations for plant breeding and biotechnological strategies to enhance yield. Molecular marker-based breeding techniques will distinguish loci dependable for salt resistance and encourage the division of physically connected loci that adversely impact the yield (Flowers et al., 2000; Foolad et al., 2001; Foolad & Lin, 1997). Monogenic introgression of salt-resistance determinants can be done directly into high-yielding recent crop genotypes to improve yield. Seed germination is the basic phase in seedling establishment, determining effective crop generation (Almansouri et al., 2001). The

establishment of crops relies on the interaction between seed quality and seedbed environment (Khajeh-Hosseini et al., 2003). Factors unfavorably affecting seed germination include susceptibility to water-deficit conditions and salt resilience. Earlier development stages are more susceptible to salinity than advanced ones, and the growth development and yield of plants are adversely affected when humidity is reduced. Due to constrained precipitation at sowing time, poor and unsynchronized seedlings are produced if soil moisture is low in seedbeds at the time of sowing (Mwale et al., 2003), influencing the consistency of the plant population with a negative impact on crop productivity.

Additionally, salt stress delays seed germination and reduces the rate and speed of germination, resulting in decreased plant growth, improper development and reduced final-crop productivity. Seeds are powerless to cope with stress, especially stress experienced between sowing and seedling foundation, while plant salt resistance usually increases with plant ontogeny. Soil salinity may influence the germination of seeds either by increasing osmotic potential outside the seeds avoiding water uptake, or through the toxic effects of Na^+ and Cl^- ions on germinating seeds (Khajeh-Hosseini et al., 2003).

1.2.3 WATER STRESS

1.2.3.1 Drought

Living creatures have two distinctive features: a cellular organization and a need for water. In spite of the fact that the cellular origin of life can be discussed, especially due to evolutionary science developments, the necessity for water reigns supreme. Life forms are able to exploit any biological specialty, no matter how extraordinary, if free water is accessible. Water is very important for plants, as it performs many vital functions. According to Kramer and Boyer (1995), herbaceous plants contain 90% of water in their fresh weight. Water maintains plant cell turgor, thus facilitating the respiration process. Water also has several biophysical characteristics (i.e., high-temperature vaporization, increased surface tension) that make it a good solvent. These characteristics allow water to remain in liquid form even in extreme temperature ranges and to act as a solvent for many molecules, minerals, ions and elements. In addition, water plays a critical role in many biochemical processes, such as serving as primary electron donor in photosynthesis. According to Boyer (1982), scarcity of water is one of the major issues in plant production, decreasing plant health, productivity and distribution of plant species. On Earth, about 35% of land is arid or semi-arid. Here, the only source of water is rainfall. Areas having sufficient amounts of

rainfall but uneven distribution throughout the year still face water-deficit conditions that decrease crop yields. Drought causes approximately 50% of global yield loss. Almost all cultivated regions in the world are facing water-deficit conditions. Drought stress or water-deficit conditions are mostly unpredictable, but in some areas 'dry seasons' are expected. In the 21st century, developing plants that can resist drought stress or withstand water-deficit conditions for a long time and maintain their health and yield constitute one of the main research areas in agriculture. Thus, more studies are required to understand the cell physiology of plants under drought stress. Such studies will help us to increase plant growth and yield under water-deficit conditions.

1.2.3.2 Flooding

Flooding of land mainly occurs due to over-irrigation, poor drainage and heavy rainfall (Kozlowski & Pallardy, 1997). Waterlogging is currently a significant concern, not only in rainfall areas but also in areas where irrigation water is used. In some countries, about 0.7 million acres are affected by flooding, and 60 thousand acres are always waterlogged due to poor drainage and leakage of water through water channels. Sodium also causes waterlogging conditions in some soils, and sodicity can cause infiltration in various types of soil. When the amount of Na ion is increased in the soil, it restricts the soil pores, limiting the movement of air and water, leading to waterlogging. Fruit trees also vary in flood-resistance capacity, as found by multiple studies of citrus rootstocks under flood conditions. For example, 80% *Citrus jambhiri* plants can withstand waterlogging for two months,

whereas only 10% of *Citrus aurantium* plants can tolerate one month. Under flood stress, plants are affected in many ways (i.e., decreased photosynthesis, decrement in stomatal conductance, reduced chlorophyll and rubisco or RuBisCO; Vu & Yelenosky, 1991).

Under waterlogging conditions, plants act differently depending on their stages. When a plant is in the development stage, waterlogging conditions severely decrease its yield and productivity. However, when a plant is dormant, the effect is very small and seen only for a short time (Kozlowski & Pallardy, 1997). When plants are exposed to waterlogging stress, they are affected in many ways, such as reticence of seed germination, decrease in vegetative and reproductive growth, alteration in plant structure and accelerated senescence. Plant responses under waterlogging conditions also vary with plant age, genotype, duration of stress and properties of water (Kozlowski, 1984). Unfavorable impacts of flooding frequently lead to changes in forest dissemination and composition (Oliveira-Filho et al., 1994). Trees and herbs that can be grown in short- and long-term flooded soil are listed in Figure 1.3.

1.2.4 NUTRITION

The transport of metals into roots is increased in corrosive soils. Heavy metals (iron, manganese, copper and zinc) can damage the growth of plants at higher concentrations, affecting root development, reducing photosynthesis and inhibiting several enzymes which could also lead to cell damage. However, numerous plant species have created hereditary and physiological resistance to
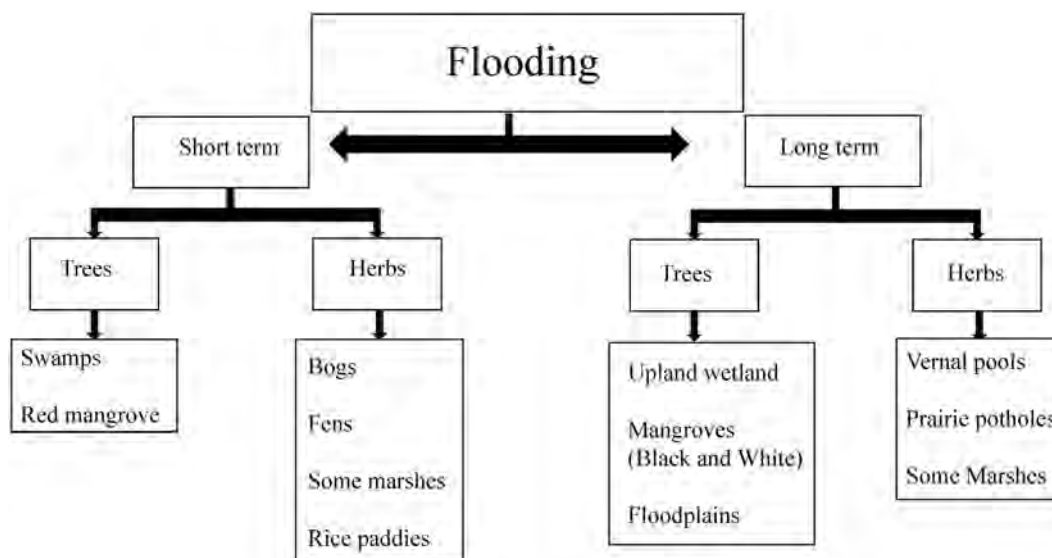

FIGURE 1.3 Trees and herbs grown in short- and long-term flooded areas.

survive in common metal-rich soils or in soils subjected to more heavy-metal contamination (Herrera-Estrella et al., 1999). The plants or crops possessing the ability to tolerate heavy metals can be divided into two distinct pathways: excluders or gatherers. In plants with an exclusion mechanism, the transport of heavy metals is controlled, leading to a relatively consistently low level of metallic particles in sprouts over an extensive period of outside concentrations. In contrast, gatherers take up the metals and store them in their non-food parts or apply a chemical transformation to metal salts, thus reducing their toxicity. In the excluder methodology, metals can be kept outside the root via root exudation of chelating substances or by the actuation of membrane transporters that drive metal particles back into the soil.

1.3 PLANT DEVELOPMENT AND MORPHOLOGY UNDER ABIOTIC FACTORS

1.3.1 GERMINATION AND SEEDLING EMERGENCE

The development of plants is a complex mechanism influenced by both biotic and abiotic factors. Among these, soil moisture is an important feature that influences the germination and development of seedlings. This feature is of more critical importance in species grown in riparian zones. In fact, the provision of oxygen could be an essential feature in the activation of physiological processes for seed germination. Soil moisture may confine oxygen accessibility to the embryo, thus accelerating or delaying seed germination (Martin et al., 2011). The germination rate and respiration rates are higher in some species that grow at a normal partial pressure of oxygen comparable with that of air. A decreased partial pressure of oxygen could result in failure of the seeds to germinate and marked decline in growth (Bradford et al., 2007; Finch-Savage et al., 2005).

1.3.2 VEGETATIVE GROWTH

1.3.2.1 Leaves

Plant responses to various stresses are multilateral in nature; however, leaves are thought to respond early. Although roots are most susceptible to abiotic stresses, they are also responsible for poor growth of leaves, shoots and other parts. Abiotic stress unfavorably influences shoot development in numerous woody plants by suppressing extension of leaves, internodes and leaf initiation, causing untimely leaf senescence that could further lead to dieback (Vinocur & Altman, 2005).

1.3.2.2 Shoots

As previously mentioned, abiotic stress unfavorably influences shoot development. Scientists around the globe have presented various hypotheses for this, many of which have been given serious consideration.

Salinity diminishes shoot development by halting leaf formation and development of internodes and by quickening leaf abscission (de Lacerda et al., 2003; Kozlowski & Pallardy, 2002). Reduced development could be linked to accumulation of chlorides that might result in shedding of leaves in all types of plants, including gymnosperms and angiosperms (de Lacerda et al., 2003; Hatfield & Prueger, 2015).

1.3.2.3 Roots

Soil moisture decreases root development in several timber crops through various mechanisms that might include hindering root establishment and branching along with stopping the growth of already mature roots. Moreover, such phenomena could result in enhanced susceptibility of the plant to various pathological diseases (Achuo et al., 2006). Shallow, spreading root frameworks are characteristic of areas with high water tables (Roering et al., 2003). Since root development regularly decreases more than stem development, the root/shoot proportion is reduced. It is interesting to observe that when floods subside, the overflowed plants tend to be more susceptible to abiotic stresses owing to their reduced root network.

1.3.2.4 Reproductive Growth

The effects of constant high temperatures are multifarious in nature, but grain development, yield and fertilization are more likely to be affected by heat stress. Unfortunately, diminished fertility and reduced grain filling have not been thoroughly researched, and many areas need to be explored owing to constant variations over time. Such problems include malfunctioning in male meiosis, pollen germination, pollen tube development, or mega gametophyte surrenders. Moreover, effects on bloom generation, grain set, endosperm division, source photosynthesis, and absorption transport and dividing can all contribute to extreme seed yield and weight. Indeed, attempts to characterize the heat-sensitive forms of distinctive plant species continue (Hatfield & Prueger, 2015; Liu et al., 2016). Drastic changes could be seen in the starch content of wheat. In spite of the fact that transcript levels of three isoforms of starch synthase were significantly reduced by the heat treatment, this effect was not reflected in the rate of starch accumulation. The general time to grain-fill was seriously shortened, and the starch granule type changed.

In this regard, Zahedi et al. (2003) research to study the influence of heat stress on the enzymes responsible for starch synthesis. They concluded that temperature could drastically reduce the activity of enzymes, thus leading to poor filling of grains and poor yield. Soil moisture frequently represses blossom bud start, anthesis, natural product set, and natural product extension in flood-intolerant species. It also actuates early abscission of blossoms and natural products. The degree of the changes in regenerative development varies as a function of plant genotype along with intensity of floods. Saltiness antagonistically affects several aspects of regenerative development, including blossoming, fertilization, natural product advancement, yield and quality, and seed generation. The regenerative development of *Citrus* is particularly sensitive to saline flooding (Arbona et al., 2017; Syvertsen & Garcia-Sanchez, 2014). As already discussed, when plants are exposed to environmental stress, they face numerous problems. When *Citrus scinensis* is exposed to salinity, the stress reduces flowering, which decreases the fruit set and number of fruits. Fruit trees exposed to salt-stress conditions display delays in fruiting and yield (Howie & Lloyd, 1989).

1.4 CONCLUSION

Plant growth and development are affected by various factors, including abiotic factors. Abiotic stresses include temperature extremities, nutritional imbalance, salinity, and water deficit and excess. These stresses alter physiological (reduction in photosynthesis, stomatal conductance, transpiration) and biochemical processes (denaturing of proteins, production of ROS, activation of antioxidants) in plants. The effects of these abiotic stresses overlap. When plants are exposed to high-temperature stress, eventually drought stress follows. Similarly, under drought or salinity stress, nutritional imbalance also occurs. Tolerant genotypes have been produced to cope with these abiotic stresses, but more efforts are required for genetic modification of plant genomes that can help us to maintain plant growth and ultimately increase yield to meet the food requirements of the increasing world population.

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2 Influence of Phytoprotectants on Abiotic Stress Signaling in Plants

Rabia Amir, Tooba Iqbal, Maryam Khan, Faiza Munir, and Rumana Keyani

CONTENTS

2.1 INTRODUCTION: ABIOTIC STRESS SIGNALING IN PLANTS

Plants as multicellular organisms communicate to bring coordination in their physiological and molecular responses. They have a complex cellular signaling network, as it involves various responses to stimuli from the outside and inside world after their reception and transduction (Gill et al., 2016). Being sessile organisms, plants have to face constant environmental harshness that interferes with their optimum growth. In case of defense signaling, plants react to stresses by regulating gene expression, which acts as a molecular control mechanism (Akpinar et al., 2012). Two major classes of genes are induced under stress conditions: 1) structural genes which confer tolerance to abiotic stress and 2) regulatory genes which control downstream processing and expression of stress-responsive genes (Hirayama and Shinozaki, 2010; Nakashima et al., 2012).

In plants, the perception of abiotic stress by receptors, for example receptor-like kinases (RLKs), hormones, G-protein-coupled receptors (GPCRs), phytochromes, etc., leads to signal transduction which generates secondary signaling molecules. Consequently, these secondary molecules, such as ROS, inositol phosphate and abscisic acid (ABA), facilitate Ca^{2+} flux for the initiation

of protein phosphorylation in order to generate a stress response via transcription factors (Boguszewska and Zagdańska, 2012). For example, the SOS protein kinase complex, through Ca^{2+} mediated cell signaling, maintains the homeostasis of Na^+ in the cytoplasm of plant cells during salt stress (Chinnusamy et al., 2004). In another example, ABA triggered by osmotic or cold stress reduces water loss by ROS and calcium-mediated signaling (Roychoudhury et al., 2013). Therefore, transcription factors (TFs), reactive oxygen species (ROS), phytohormones, calcium (Ca^{2+}) and protein kinases play vital roles in abiotic stress signaling in plants (Boursiac et al., 2008). Plants produce numerous chemicals such as polyamines, antioxidants, osmoprotectants, and trace elements that trigger adaptive immune responses. These molecules have also been reported to act as immunoboosters after their exogenous application on plants under stress conditions. Increased photosynthesis rate, yield and antioxidative capacities are some of the underlying mechanisms of phytoprotectants (Ahmad and Wani, 2013). Hormonal signaling, ROS signaling, Ca^{2+} mediated cell signaling and transcriptional networking, which form an integrative signaling network in abiotic stress, will be discussed in reference to phytochemicals in the following sub-sections. A concise overview of abiotic stress signaling is illustrated in Figure 2.1.
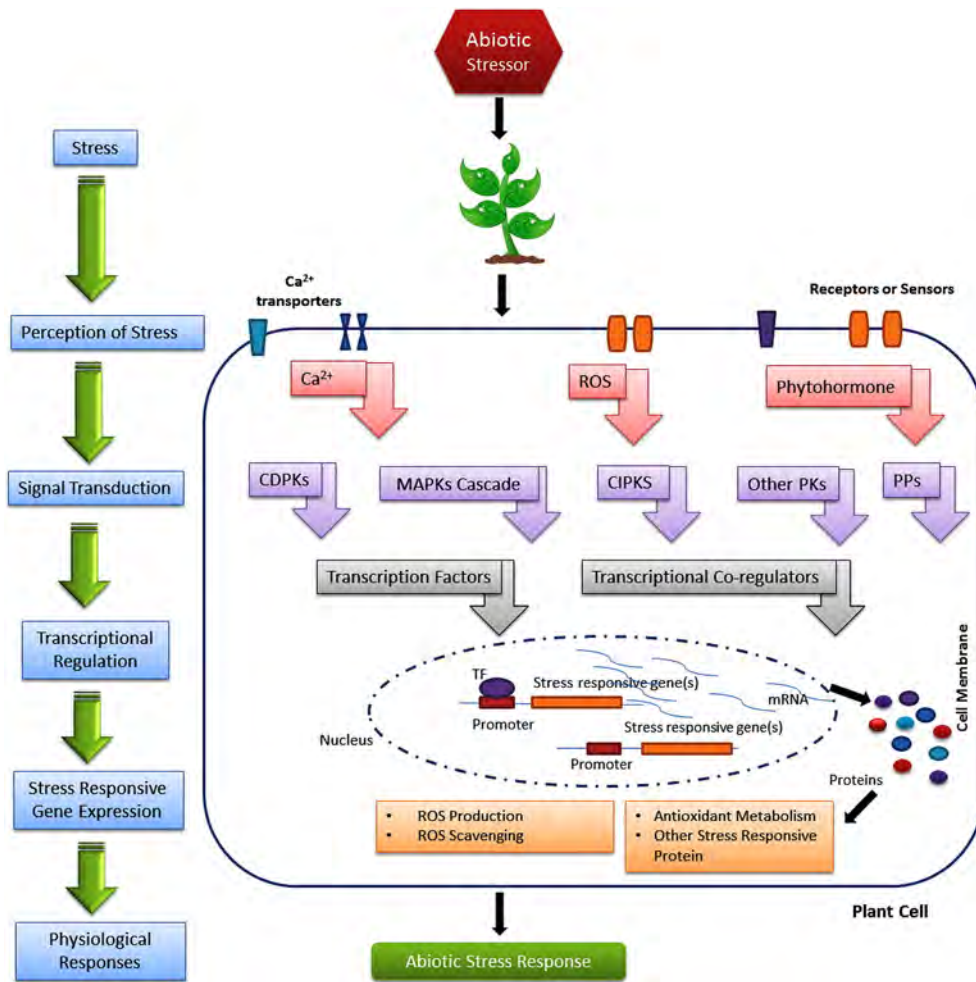
FIGURE 2.1 Overview of abiotic stress signaling components from stress perception to stress response. Where ROS−Reactive oxygen species; PK− Protein kinase; PP−Protein phosphatase; CBL−Calcineurin B-like proteins; CDPKs−Ca^{2+} dependent protein kinases; MAPK−mitogen-activated protein kinase and TF−Transcription factors (Wang et al., 2016; You and Chan, 2015).

2.2 PHYTOPROTECTANTS AFFECTING PHYTO-HORMONAL SIGNALING

Phytohormones are specialized chemicals produced through different pathways which help plants fine-tune their responses with respect to environmental conditions. They integrate numerous stress signals and control the transcription of stress-responsive genes. The interconnected mode of action of one hormonal signaling pathway with the other makes them an exceptionally important and useful resource for helping plants to cope with different abiotic stresses (Chapman and Estelle, 2009). There are several plant hormones, such as Gibberellins (GA), auxins, abscisic acid (ABA), jasmonates (JA), strigolactones (SLs), cytokinins (CK), ethylene (ET), salicylic acid (SA), brassinosteroids (BR). The list is getting longer with time. Plant hormones play an important role in growth, development, nutrient allocation and sink/source

transitions of plants. But our main focus here is on how they regulate various signal transduction pathways, and how a network of hormones correlate with each other to exchange information and produce a robust response to cope with environmental stresses.

Synthesis of ABA is one of the fastest responses of plants to various abiotic stresses. ABA significantly contributes to the regulation and stimulation of adaptive responses, e.g. in drought stress ABA triggers the expression of ABA-inducible genes, which cause stomatal closure leading to a reduced rate of transpiration and consequently a reduced growth rate of the plant (Schroeder et al., 2001). ABA signaling causes changes in gene expression at transcriptional and post-transcriptional level (Cutler et al., 2010). It has been observed that ABA functions as a connecting center for primary metabolism and environmental adaptation in plants. ABA elicits the transcriptional programming of different

cellular mechanisms underlying abiotic stresses and also changes the expression of genes which control lipid and carbohydrate metabolism. This indicates that ABA functions as an interface for abiotic stress regulation and also monitors primary metabolism in plants (Hey et al., 2010; Li et al., 2006; Seki et al., 2002).

Analysis of ABA-inducible genes revealed that the expression of these genes contains numerous cis-regulatory elements called ABA-responsive elements or ABREs (PyACGTGG/TC) (Giraudat et al., 1994; Umezawa et al., 2010). Proteins which bind to ABA-responsive elements are called ABRE binding factors. The expression of AREB1/ABF2 is up-regulated during different abiotic stresses such as salinity and dehydration. An overexpression of these binding factors resulted in increased tolerance to drought (Arasimowicz and Floryszak-Wieczorek, 2007; Fujita et al., 2005).

In the presence of ABA, hormonal signals are received by specific cellular receptors of the PYR/PYL/RCAR family (PYrabactin Resistance-Like/Regulatory component of ABA receptors). ABA binds these receptors and inactivates PP2Cs (type 2C protein phosphatases) such as ABI2 and ABI1. Upon inactivation of PP2C, another class of proteins called SnRK2 is activated (SNF1-related protein kinases) (Ma et al., 2009; Park et al., 2009). SnRK2 proteins regulate transcription factors such as binding factors (ABFs) and ABA-responsive promoter elements (ABREs), which are involved in the activation of ABA-responsive genes and ABA-dependent physiological processes (Umezawa et al., 2009; Vlad et al., 2009).

Another class of receptors involved in ABA signaling is GTGs (G-protein-coupled receptor-type G protein) localized in the plasma membrane (Pandey et al., 2009). The function of GTG proteins as ABA receptors was confirmed in *Arabidopsis* when the GTG1/GTG2 absent mutants were found hyposensitive to ABA (Pandey et al., 2009).

There is increasing evidence for the role of CHLH/ABAR (H subunit of Mg-chelatase) in ABA perception. Incorporation of CHLH/ABAR in the ABA signaling cascade at cellular level as a chloroplastic receptor and by plastid-to-nucleus regressive signaling via the ABA-responsive nucleo-cytoplasmic transcription repressor WRKY40 has been reported. This evidence suggests that chloroplast-mediated pathway also controls cellular ABA signaling (Shang et al., 2010; Shen et al., 2006).

Furthermore, studies indicate that ABA-mediated stress signaling is also modulated through interaction with other key hormone regulators (CK, SA, ET, and JA) associated with plant growth and development. The complex cascades of exogenous and endogenous signals which plants experience during environmental fluctuation and development are linked to each other through some convergence points between their signal transduction pathways, called crosstalk. This is predominant in modulating ABA signaling during stress and developmental transitions (Golldack et al., 2013). In *Arabidopsis*, GA signaling is modulated by the binding of GA to specific receptors called GID1a/b/c, which are orthologs of GA receptors in rice, *OsGID1 (GA-Insensitive Dwarf)* (Ueguchi-Tanaka et al., 2005). GA signals mediate the binding of DELLA proteins to GID1, which is followed by a conformational conversion of DELLA proteins. The modified DELLAs are recognized by the F-box protein SLEEPY1 (SLY1) in *Arabidopsis*. Subsequently, DELLAs are polyubiquitinated by the SCFSLY1/GID2 ubiquitin E3 ligase complex and degraded via the 26S proteasome pathway, thus activating GA-mediated responses (Dill et al., 2004; Silverstone et al., 2001). DELLA proteins, which consist of RGA-LIKE1 (RGL1), GA-insensitive repressor of GA1–3, RGL2, and RGL3, act as an interface linking GA-controlled developmental responses and ABA-mediated abiotic stress signaling (Achard et al., 2006). In addition, RING-H2 gene *XERICO* regulates tolerance to drought and ABA biosynthesis in *Arabidopsis*, as it is a transcriptional target of DELLAs downstream. This clearly indicates XERICO functions as an assembler of plant development and abiotic stress responses by linking ABA and GA signaling pathways.

Keeping the role of XERICO in mind, there is an increasing number of reports which suggest a crosstalk occurs between GA, ABA and jasmonate, another regulator in the response to drought stress. Jasmonates have signaling functions in biotic stress responses (Golldack et al., 2014); however, it was recently reported that JA receptor proteins such as *OsCOI1a* (Coronatineinsensi-Tive 1) and *JAZ* (jasmonic acid ZIM-domain proteins) are transcriptionally regulated in response to drought stress, which shows that JA signaling has a role in abiotic stress responses as well, as illustrated in Figure 2.2. Besides, the expression of the DELLA protein RGL3 responds to JA, and RGL3 interacts with JAZ proteins (Wild et al., 2012). These research advances indicate that DELLA functions as an interface between GA, JA and ABA signaling. There is also a pivotal functional involvement of lipid-related signaling in abiotic stress responses (Golldack et al., 2014).

2.3 ROLE OF PHYTOPROTECTANTS IN CALCIUM-MEDIATED CELL SIGNALING

Calcium is known as a strict spatiotemporal regulator for its critical role as a key player in the signaling network as well as in plant growth and development.
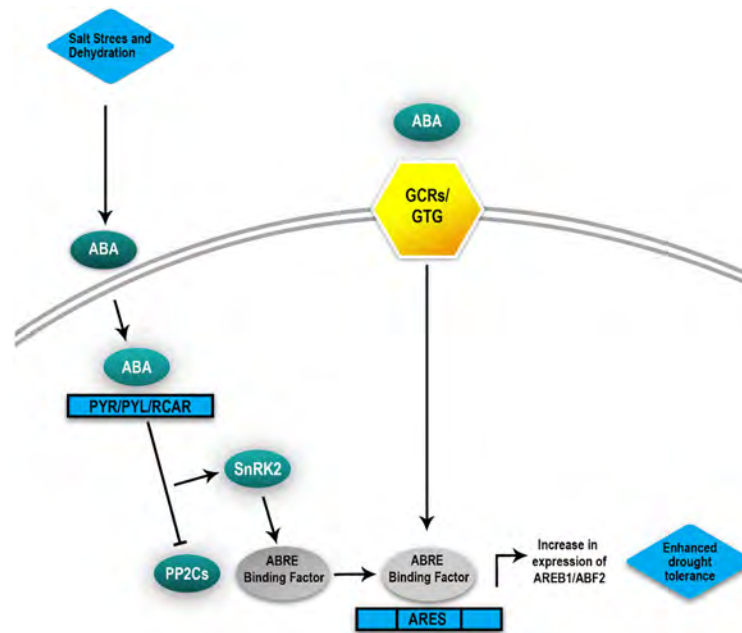
FIGURE 2.2   Schematic representation of ABA-mediated abiotic stress signaling. ABA accumulation induced by abiotic stresses cues cascade of signaling events which induce expression of stress-responsive genes.

Abiotic stresses are perceived by plants through calcium-mediated signaling which consecutively triggers stress-induced transcription factors, ROS signaling and lipid signaling. The specificity of the signaling response to abiotic stresses depends on the calcium level in a cell and its ability to metabolize hydroxyl radical signaling (Wilkins et al., 2016). Plants maintain their Ca^{2+} homeostasis through carriers, pumps and channels in their cellular membranes under the influences of various stimuli (Kudla et al., 2010). Furthermore, plants have an abundance of Ca^{2+} binding proteins termed as Ca^{2+} sensors, which have Ca^{2+} buffering capacity (Dodd et al., 2010). Such sensors include calcineurin B-like proteins (CBL) and calmodulins (CaMs) that transmit a signal to Ca^{2+} dependent protein kinases (CDPKs) or Ca^{2+} and calmodulin-dependent protein kinases (CCaMKs) through direct calcium binding. They decipher Ca^{2+} signals and encourage Ca^{2+} mediated modification of specific proteins (Huang et al., 2013; Tuteja and Mahajan, 2007). Various transcription factors, protein kinases, phosphatases, channels, antiporters, pumps, metabolic enzymes and other functional proteins are the target proteins for CBL and CaM, which one way or the other respond to environmental stresses (Zeng et al., 2015).

Calcium-mediated signaling has been elucidated in plant defense responses against chilling, heat shock and salinity stresses (Reddy and Reddy, 2004). Ca^{2+} mediated stress signaling in plants under salt stress has been described in Figure 2.3. Stress-induced expressions of

Ca^{2+} sensors by multiple genes have been reported in soybeans (DeFalco et al., 2010) and *A. thaliana* (Reddy and Reddy, 2004). Recent studies have suggested that calcium-binding TFs have a vital position in stress signaling (Reddy et al., 2011). Such DNA-binding TFs maintain the homeostasis of ROS and regulate other intracellular signaling networks (Nookaraju et al., 2012; Zeng et al., 2015). Ca^{2+} mediated signaling is highly robust and evolved due to its ability to process multiple stimuli at the same time, and shares tightly regulated crosstalk with other signaling networks due to its architectural structures (Dodd et al., 2010). Plants regulate their Ca^{2+} signaling to manipulate the biochemical and molecular processes that influence their physiological, developmental and stress-related responses (Nookaraju et al., 2012). However, it has not yet been clarified how Ca^{2+} signaling brings specificity to the response and how it identifies its downstream target proteins (Zeng et al., 2015). The need of the hour is to enhance our knowledge regarding Ca^{2+} mediated signaling and understand how it helps cope with environmental stresses so that stress-tolerant crop can be developed.

When plants are exposed to stress, a transient fluctuation in calcium levels affects the signaling network. Such fluctuations create unique stress-associated calcium signatures that are deciphered by signal transduction pathways. For the reestablishment of normal Ca^{2+} concentration, there are several cytosolic Ca^{2+} buffering mechanisms, including Ca^{2+}/ATPase pumps and Ca^{2+}/
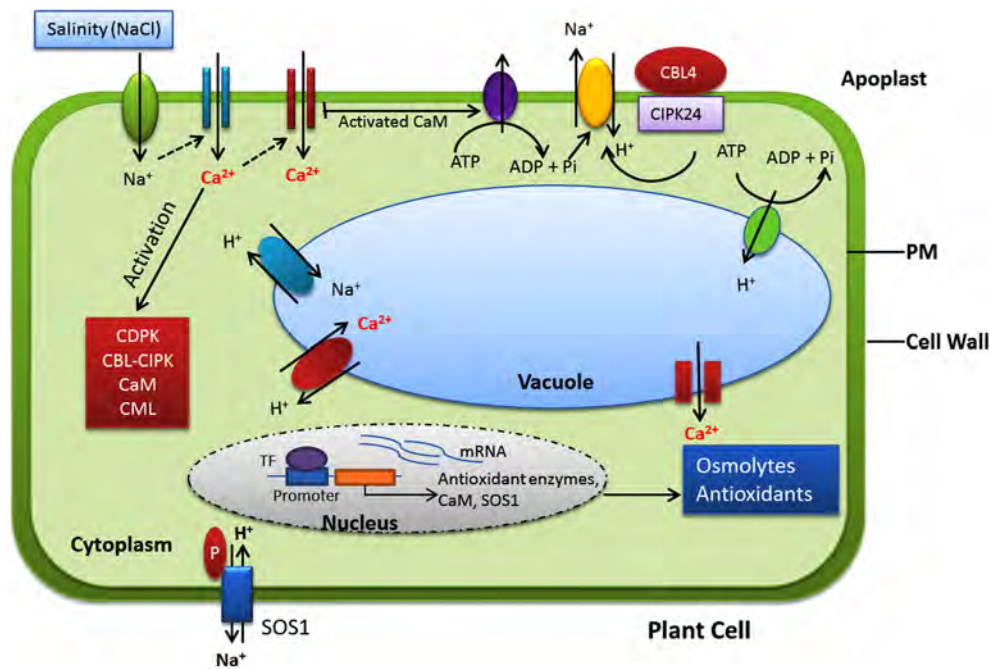
FIGURE 2.3 Ca^{2+} mediated signaling in plants under salt stress. Plant perceives salt stress by increased level of Na^+ and causes Ca^{2+} accumulation which cause hydroxyl radical formation and activation of CBL and CDPKs which leads to Na+efflux. Where, PM=Plasma membrane; DACC=Depolarization activated cation channel; HACCs=Hyperpolarization activated cation channel; cGMP=Cyclic guanosine monophosphate; cAMP=Cyclic adenosine monophosphate; InsP3R=inositol 1,4,5-trisphosphate receptor-like channel; cADPR=cyclic ADP-ribose-activator ryanodine receptor-like channel; CDPKs=Ca2+dependent protein kinases; CaM=Calmodulin; CIPKs=CBL-interacting protein kinases; and CBL=Calcineurin B-like proteins (Kurusu et al., 2015; Wilkins et al., 2016).

H^+ antiporter, which terminate Ca^{2+} mediated signaling (Bose et al., 2011). Several phytochemicals help plants restore their health, either by normalizing Ca^{2+} concentration, after the stress, in a feedback mechanism, or by elevating Ca^{2+} concentration to create a prompt response against stress. Take the example of polyamines (PA) and H_2O_2, which are the representative of phytoprotectants. PA, synergistically, affects Ca^{2+} efflux under stress conditions, whereas H_2O_2 activates various Ca^{2+} channels that affect cytosolic ionic homeostatic (Demidchik et al., 2002; Pei et al., 2000). Moreover, there is a crosstalk between PA and ROS, which results in the oxidation of PA into H_2O_2 and OH^-, which, ultimately, causes Ca^{2+} influx across the plasma membrane (Moschou et al., 2008).

2.4 EFFECT OF PHYTOPROTECTANTS ON TRANSCRIPTIONAL NETWORKING

Plants tolerate abiotic stresses through one of the principal stress controllers known as transcription factors (TFs). TFs are DNA-binding regulatory proteins mainly encoded by early stress-responsive genes, and comprise approximately 7% of the coding genome of plants (Udvardi et al., 2007). TFs regulate the transcription of other proteins by either blocking or recruiting RNA polymerase to DNA in a sequence-specific manner (Riechmann and Ratcliffe, 2000). They take part in almost all physiological, developmental and defense mechanism of plants, thus playing vital roles in plant survival and adaptation (Lindemose et al., 2013). Due to extensive diversity, TFs have been classified into gene families: myelocytomatosis oncogene (MYC)/myeloblastosis oncogene regulon (MYB), APETALA 2/ethylene responsive element binding factor (AP2/ERF), basic leucine zipper (bZIP), heat shock factor (HSF), NAC,WRKY, Cys2Hizinc fingers (C2H2 ZF), MADS-box, nuclear factor Y (NFY) and ten others (Hirayama and Shinozaki, 2010; Reguera et al., 2012; Yamaguchi-Shinozaki and Shinozaki, 2006). A noteworthy fraction of TFs, including bZIP, C2H2 ZF, AP2/ERF, MYB, WRKY, NAC and bHLH, has been characterized as coordinator of abiotic stress signaling, which confers tolerance to plants in order to promote growth and development, as depicted in Figure 2.4 (Lindemose et al., 2013).

bZIP TFs are a member of the vast family of dimerizing TFs that is present in all the eukaryotes and plays
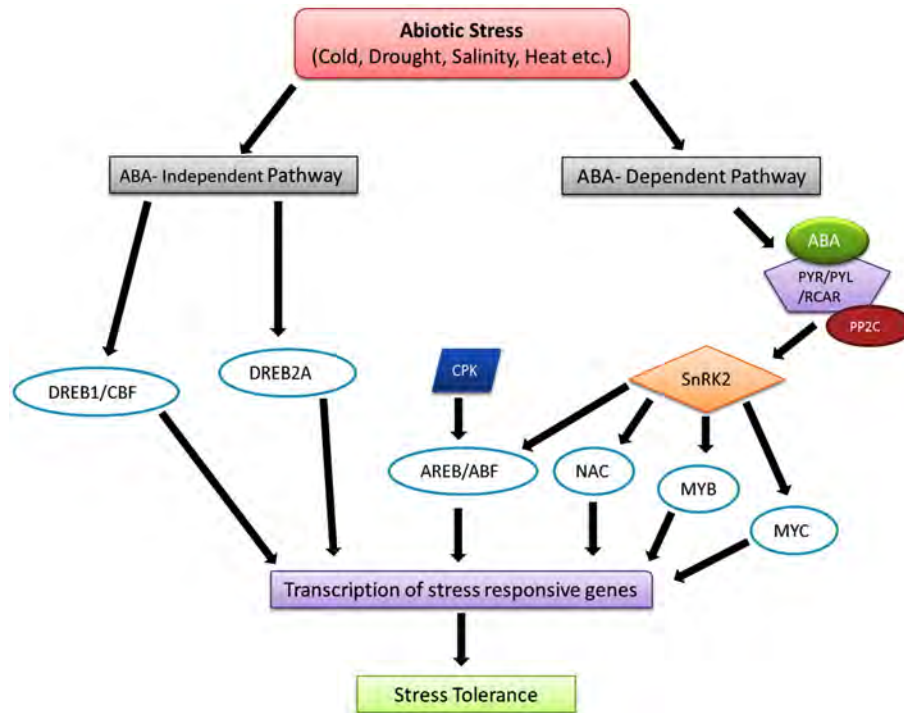
FIGURE 2.4 Transcriptional networking under abiotic stress (Joshi et al., 2016; Kumar, 2014).

an essential role in ABA signaling. ABA-mediated phosphorylation leads to activation of bZIP that control the ABA-responsive genes expression by interacting with their promoter region, which contains ABA-responsive elements (ABREs) (Soma et al., 2017). Elevated bZIP expression in response to ABA, salinity, low temperature and drought has been observed in *Glycine max, A. thaliana*, wheat and rice (Gao et al., 2011; Lindemose et al., 2013).

C2H2 ZF proteins are transcriptional repressors, having an ERF-associated amphiphilic repression (EAR) domain which regulates stress responses (Ciftci-Yilmaz et al., 2007). Improved tolerance against salinity, osmotic pressure and heat stress has been observed in plants with an enhanced level of C2H2 ZF proteins (Mittler et al., 2006). These proteins transcriptionally repress plant growth under stress condition by inhibiting auxin-responsive growth-related genes (Kodaira et al., 2011). While under an unstressed condition, they downregulate ABA-responsive genes (Jiang et al., 2008). It has been observed that C2H2 ZF overexpression can induce tolerance in plants against drought and salt stress by manipulating H_2O_2 homeostasis (Huang et al., 2009).

Dehydration-responsive element binding-protein (DREB), AP2, ERF and ABI3/VP1 (RAV) are the four main subfamilies of plant AP2/ERF TFs. Among these TFs, DREBs are well characterized transcriptional regulators of ABA-dependent abiotic stress responses (Mizoi

et al., 2012). DREBs consist of six members that interact with dehydration-responsive element/C-repeat element (DRE/CRT) to induce defense responses against cold, heat, salinity and drought (Haake et al., 2002; Liu et al., 1998). DREB TFs have the capability to enhance drought tolerance in plants, but several reports have observed deformation in the growth of plants due to overexpression of these TFs (Yang et al., 2010).

MYBs are characterized by the presence of R1, R2 and R3 sequence repeats of the MYB domain (Dubos et al., 2010). Out of them, the R2R3 subfamily has occupied a vital position in ABA-dependent abiotic stress response. MYBs have an antagonistic role between ABA and Jasmonic acid (JA)-mediated signaling (Jung et al., 2010). Induced MYB expression in plants has been observed in response to ABA, osmotic stress, cold stress and drought stress by joining auxin and ABA signals (Seo et al., 2009).

WRKY TFs have been divided into three groups based on the number of interacting domains and their association with a zinc finger-like motif (Li et al., 2011). Earlier, these were only associated with biotic stress, but now evidence is available for their role in the abiotic stress response. For instance, ABA sensitivity, heat stress tolerance, drought tolerance and salt sensitivity have been observed in plants with overexpression of WRKY (Jiang and Deyholos, 2009). WRKY68 involves ABRE bZIP, a factor that plays a central role in ABA-dependent plant

responses. Transcriptional regulation by WRKYs is complex because of their antagonistic and agonistic roles in various situations. For example, WRKY40 enhances ABA sensitivity while WRKY60 reduces ABA sensitivity (Liu et al., 2012).

NAC is a widely spread plant TF family which reprograms the transcription of plant stress-responsive genes. The word NAC has been derived from three genes with a conserved domain: no apical meristem (NAM), ATAF, and cup-shaped cotyledon (CUC2) (Aida et al., 1997; Souer et al., 1996). NAC TFs have an N-terminus conserved domain consisting of approximately 150–160 amino acids whose functions are linked with DNA binding, homo/hetro-dimerization and nuclear localization (Olsen et al., 2005; Ooka et al., 2003). During stress conditions, NAC genes contribute to the formation of a complex signaling network that makes them potential nominees for conferring stress tolerance (Nuruzzaman et al., 2013).

bHLH proteins are positive regulators of ABA-dependent or independent stress-responsive genes (Bailey et al., 2003). Among bHLH TFs, MYC2 has a principal role in the crosstalk among various cellular signaling pathways, including salicylic acid (SA), JA, ABA, auxin and Gibberellin signaling pathways (Kazan and Manners, 2013). Drought, salinity, mannitol and cold tolerance have been reported in bHLH92 overexpressing plants (Jiang et al., 2009).

Molecular studies have revealed that plants regulates their physiological, developmental and defense response through fine-tuning transcriptional networking. Phytoprotectants directly or indirectly involve various TFs that regulate the expression of stress-responsive genes. For example, both glutathione (GSH) and nitric oxide (NO) are effective entrants of phytoprotectants that work through various TFs under stress. GSH offsets stress-induced oxidation by changing gene expression directly or with the help of transcription factors. It has an important role in signal transduction and ROS signaling at multiple levels. It also acts as redox sensor and helps plants tolerate oxidative stress (Srivalli and Khanna-Chopra, 2008). Thus, GSH is one of the powerful phytoprotectants that can confer tolerance to plants against abiotic stresses. NO is a gaseous biologically active molecule that emerged as a significant antioxidant and signaling molecule. NO triggers many kinds of redox-associated gene expressions to establish tolerance against plant stress (Sung and Hong, 2010). Furthermore, plant hormones as phytoprotectants mediate plant adaptive responses to biotic or abiotic stresses. Hormones recognize stress signals that stimulate transcriptional network to produce plant adaptive responses under stress (Pandey et al., 2017). In a nutshell, phytoprotectants greatly affect the transcriptional networking that helps plants overcome abiotic stress.

2.5 PHYTOPROTECTANTS AFFECTING OXIDATIVE STRESS MECHANISM (ROS PRODUCTION)

Due to abundant molecular oxygen in plants environment, all plant cells confront conditions such as environmental stresses or UV radiations when some toxic chemical entities called reactive oxygen species accumulate in them. ROS include hydroxyl radical (HO•), superoxide anion ($O_2^{•-}$) and hydrogen peroxide (H_2O_2) which, if uncontrollably produced, can lead to far-reaching damage to the cell by degrading proteins, inactivating enzymes or altering gene actions (Choudhury et al., 2013; Mittler et al., 2004).

However, with time, plants have evolved mechanisms to use ROS as chemical signals to mitigate the effects of abiotic stress by regulating ROS network genes, which are comprised of almost 152 genes. Such ROS-regulatory networks involve redox-sensitive transcription factors (TFs), receptor proteins and inhibition of phosphatases by ROS. Thus at any given time, an active balance between ROS-producing and ROS-scavenging pathways promotes cellular well-being (Choudhury et al., 2013).

Upon exposure to numerous abiotic stresses, plants display unique expression patterns of ROS-scavenging and producing enzymes. These changes have been observed in many forms, such as: altered levels of byproducts of lipid peroxidation, increase in enzymes such as peroxidases, glutathione-S-transferase, and CAT, and accumulation of phytoprotectants which act as antioxidants, such as ascorbate, phenolic compounds, carotenoids, alkaloids, sucrose and trehalose (Choudhury et al., 2017).

Among the various chemicals which act as phytoprotectants in abiotic stress conditions, soluble sugars which, by definition, are mono and di saccharides, display dual roles, acting both as mediators of ROS production like in mitochondrial respiration and as antioxidants in oxidative pentose phosphate pathways (PPP). The current topic comprehends how ROS production is mediated by phytoprotectants such as soluble sugars and affects oxidative mechanisms that cause damage to plants (Couée et al., 2006). In plants, ROS are accumulated in several different cellular sources, such as NADPH oxidase located in cell membrane, electron transport chain in chloroplast and mitochondria, β-oxidation of fatty acids and the glycolate oxidase stage of photorespiration in peroxisomes and respiration in mitochondria, respectively (Doudican et al., 2005; Møller, 2001).

Soluble sugars have the effect of increasing ROS production in plants during an increase in photosynthetic activity. In contrast, a decrease in soluble sugars negatively regulates the expression of photosynthetic genes even in normal daylight conditions, especially the genes involved in the expression of the Calvin cycle. Such type of regulation of gene expression by soluble sugar and light simultaneously is better understood thanks to the elucidation of the relationship between light and sugar accumulation. This situation is compounded in abiotic stress conditions such as chilling stress, where sugar accumulation is considered to act as cold protectant (Ciereszko et al., 2001; Havaux and Kloppstech, 2001).

Similarly, a condition of fluctuation in carbohydrate levels or carbohydrate starvation at specific developmental stages may also increase ROS production. This is due to the fact that ADP regeneration is significantly decreased and the electron transport flow, through cytochrome c oxidase, results in increased ROS in mitochondria (Dutilleul et al., 2003). Sugar starvation is also thought to activate lipid mobilization and β-oxidation in peroxisomes. This involves the stimulation of acyl co-A oxidase, the protein, and mRNA activity levels, as illustrated in Figure 2.3. Such ROS activation facts are also confirmed by transcriptomic analysis where sugar stress activates oxidative enzymes such as catalases (Contento et al., 2004).

Besides, soluble sugars and the interactive roles of some phytohormones (auxin, brassinosteroid and ABA) have also been observed for ROS production. Auxins can induce the production of ROS and regulate ROS homeostasis, suggesting a relationship between auxin signaling and oxidative stress. For example, auxins activate a Rho-GTPase (RAC/ROP) that interacts with NADPH oxidases, resulting in apoplastic ROS production (Duan et al., 2010). On the contrary, ROS activate a MAPK signaling cascade which inhibits auxin-dependent signaling and triggers oxidative signaling cascades (Kovtun et al., 2000). Auxin-induced changes in cellular redox status, brought about by auxin-induced ROS production, regulate the plant cell cycle (Vivancos et al., 2011). Although plant cells are equipped with numerous other protectants which help in scavenging the ROS produced and mitigate the consequences of abiotic stresses, the part played by such protectants as dual-role entities is also helpful in understanding valuable ROS-production-mediated effects imparted to plant cells during normal activities. An overview of this mechanism is depicted in Figure 2.5.
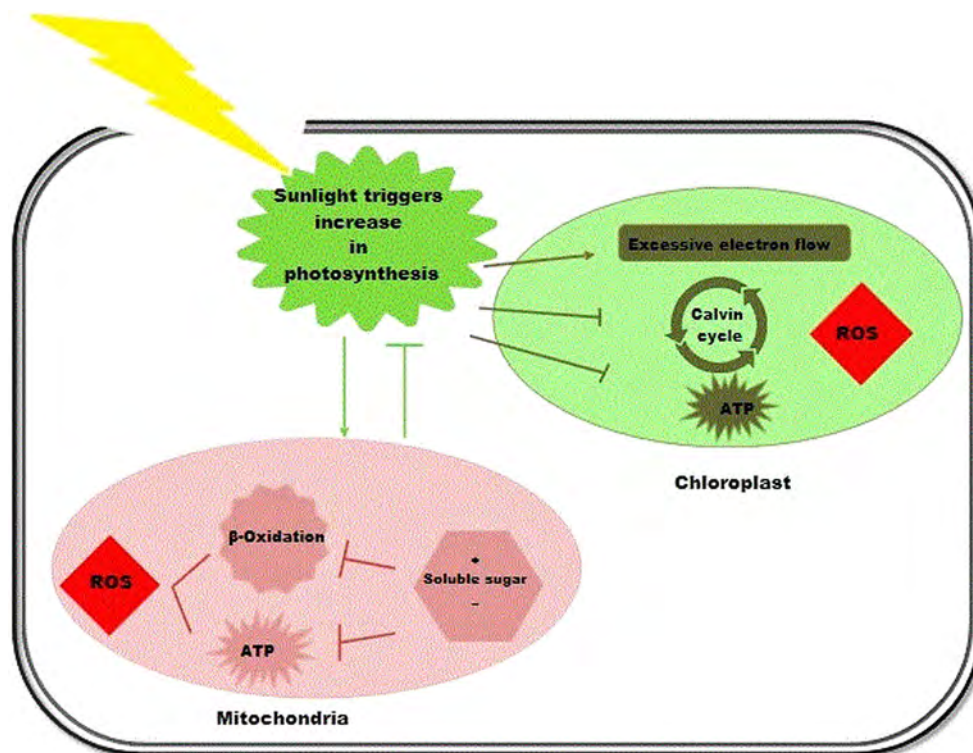

FIGURE 2.5 High photosynthetic activities stimulate accumulation of soluble sugars which in turn downregulate the expression of photosynthetic genes and increase electron flow leading to ROS generation.

2.6 PHYTOPROTECTANTS AS ROS SCAVENGERS

With the span of evolution, as discussed above, green plants have learned to mitigate the effects of ROS through different phytoprotectants that can be non-enzymatic, like carotenoids, ascorbate (AsA), tocopherol and glutathione, or enzymatic, like catalase (CAT), superoxide dismutase (SOD) and glutathione-S-transferase. They act as redox buffers and influence the expression of the genes involved in abiotic stresses (Foyer and Noctor, 2005). Here, we will elaborate on the roles of such protectants in mitigating oxidative stress through ROS scavenging and helping plants cope with abiotic stresses.

Ascorbic acid (AsA) is a powerful antioxidant which is present in all plant tissues, particularly in actively photosynthesizing tissues such as meristems. It works as a reductant for numerous free radicals such as $O_2^{\bullet}$, $HO^{\bullet}$ and H_2O_2. This forms the basis of its action as an antioxidant. Plants contain sufficient amounts of AsA. It not only scavenges ROS but also maintains other antioxidant components such as α-tocopherols through the AsA-GSH cycle (Smirnoff, 2000). AsA metabolism and recycling involve enzymes such as mono-dehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR) (Meena et al., 2017), which are increased during certain abiotic stresses such as high temperature and confer tolerance to plants against stress. The AsA recycling system ensures the maintenance of sufficient amounts of AsA, which confer heat stress tolerance to plants. Experiments carried out on *Arabidopsis* under high-temperature stress support the fact that overexpression of DHAR in cellular compartments substantially increases AsA levels 2–4.25 times, which lowers membrane damage and improves chlorophyll content as compared to normal plants (Wang et al., 2010).

Another important protectant is glutathione (GSH), which occurs abundantly in almost all subcellular compartments such as mitochondria, endoplasmic reticulum and cytosol, whereby it manifests substantial ROS-scavenging capacity. It can act as ROS scavenger either directly by reacting with free radicals such as $HO^{\bullet}$ and $O_2^{\bullet}$, or else by indirectly maintaining the levels of other antioxidants such as tocopherol and zeaxanthin in a reduced state. Additionally, it is a substrate for some other enzymatic antioxidants such as glutathione-S-transferases (GST) and glutathione peroxidase (GPX) (Hasanuzzaman et al., 2013). The mechanism of action of GSH is such that the onset of abiotic stress stimulates its accumulation. Increased GSH concentrations counterbalance the stress-initiated oxidation of GSH and cause changes in gene expression directly or through interaction with regulatory proteins and/or transcription factors. This increase is equally important in signal transduction and defense against ROS and works through a multilevel control mechanism, which includes the coordinated activation of genes encoding GSH biosynthetic enzymes and GR (Srivalli and Khanna-Chopra, 2008). Thus, GSH acts as a redox sensor of environmental cues, and the increase in GSH helps plants tolerate oxidative stress.

As amphiphilic antioxidants and protectants, Tocopherols contribute to ROS scavenging in photosynthetic membranes. They limit the extent of lipid peroxidation by reducing free radicals such as lipid peroxyl ($LOO^{\bullet}$) to their respective hydroperoxides (Maeda et al., 2005). They are also part of numerous ROS-controlled signaling networks, phytohormones and some other antioxidants and therefore are appropriate candidates for influencing abiotic stress signaling. Studies indicate that α tocopherols are not important for plant survival under optimal conditions, but an adequate amount of redox-state tocopherol in chloroplasts helps in imparting tolerance to plants against abiotic stresses. Exogenous application of α-tocopherol on *H. annuus* seeds grown under salt stress markedly enhanced activities of antioxidative enzymes and mineral nutrient content, and minimized salt-induced leaf senescence (Hasanuzzaman et al., 2013).

Taken together, all cellular compartments are equipped with antioxidants to scavenge ROS immediately at the site of production by local antioxidants. However, if the stress is severe or the antioxidant capacity is not sufficient to cope with it, then free radicals (H_2O_2) can leak into the cytosol and move to other cellular compartments. Cells are also equipped with mechanisms which allow them to combat the production of excessive H_2O_2 by transporting it in vacuoles for detoxification. Vacuoles are rich in protectants such as flavonoids and ascorbate, which scavenge them there and help plants stabilize themselves on the onset of abiotic stresses (Gechev et al., 2006).

2.7 PHYSIOLOGICAL AND MOLECULAR ADAPTATIONS IN RESPONSE TO PHYTOPROTECTANTS

The utmost requirement of every plant on the inception of an environmental stress is to allocate its energy in such a way that it adapts itself better to the environment while maintaining its growth and productivity. These functions demand a change in physiology within plants, such as the activation of many metabolic reactions, ion

homeostasis and plant hormonal signaling leading to the expression of stress-responsive genes (Ahmad and Wani, 2013). Phytoprotectants act as chemical barriers to resist environmental constraints and help plants remain physiologically stable. However, depending on the severity of the stress encountered, the physiological adaptation may not be robust enough to resist the stress and the plant may suffer. We will explore different types of physiological and molecular adaptation which occur in plants due to phytoprotectants and improve the effects of a protectant in producing stress-tolerant crops.

Abiotic stresses such as drought, cold and salinity induce several alterations in plants physiology, in the form of low water and nutrient availability, accumulation of toxic concentrations of salts, lower seed germination rate, early senescence and, in severe cases, plant mortality (Ahmad and Wani, 2013). Several potential low-molecular-weight organic compounds, including compatible solutes produced in plants under osmotic stress, have a potential role in the adaptation of plant physiology with respect to external conditions.

Osmolytes are important phytoprotectants comprising amines (polyamines), amino acids (Pro), sugars (sucrose trehalose), and sugar alcohols (sorbitol, mannitol), which have a role in maintaining cell turgor, lessening ionic toxicity and protecting cell structures. Enhanced levels of sugar in drought- and salt-tolerant rice varieties suggest that these protective compounds can contribute to stress tolerance in rice (Ahmad and Wani, 2013).

Reports suggest that, alternative protective functions of osmolytes have a role in adapting plant physiology to environmental conditions. Rice plants grown under salt stress accumulate soluble nitrogenous compounds such as polyamines (PA), betaines, imides and amino acids along with certain proteins. Salt stress has been shown to increase the content of a polyamine called putrescene (put), which is involved in developing tolerance to salt (Do et al., 2014). Exogenously applied PA has also shown an ability to overcome the damaging effects of salinity in several other plant species (Mansour, 2000). The physiological role of PA-induced adaptation in salt stress has been extensively studied. Due to their polycationic nature, PA can directly interact with the surface of membranes or indirectly affect some membrane-binding enzymes maintaining their structure. They also act as ROS scavengers and ammonia detoxifiers, but due to their low number, their contribution is less felt in osmotic adjustments as compared to other osmoprotectants (Mansour, 2000) (Kushad and Dumbroff, 1991).

A common alleviator of many stresses is the amino acid proline (pro), which is elevated during abiotic stress conditions such as salinity, drought, intense radiation and oxidative stress. Due to its antioxidative potential, it maintains redox balance, stabilizes enzymes and protects cellular structures (Ahmad and Wani, 2013). Studies on transgenic *Arabidopsis* with 90% lower contents of proline than the wild type ascertained that they produce significantly more ROS and lipid-peroxidation products (Székely et al., 2008). Proline is also considered as an osmotic adjustment agent under abiotic stresses and functions by lowering cellular osmotic potential, permitting the reabsorption of water to take place. Proline also has a role in stabilizing membrane structures and protecting cell membrane against salt-induced injuries. On a molecular level, this membrane stabilization involves a decreased accumulation of Na^+ and Cl^- in shoots and thus enhances growth in response to proline treatment on salt-affected plants (Mansour, 2000)

Plants accumulate non-reducing sugars such as trehalose in high concentrations under distinct abiotic stresses such as cold, salinity and drought. Stress moderately increases its levels, which helps stabilizing proteins and membranes (Ahmad and Wani, 2013). Trehalose is also a precursor of glucose and is catabolized by trehalose to give glucose (Brodmann et al., 2002; Goddijn et al., 1997). Trehalose treatments cause an increase in the transcription of antioxidant enzyme genes such as superoxide dismutase, ascorbate peroxidase, and catalase in salt-stressed rice plants. Trehalose-treated plants recover immediately compared to non-treated plants (Nounjan et al., 2012).

2.8 PHYTOPROTECTANTS AFFECTING STRESS SIGNALING IN DIFFERENT CROPS

Abiotic stresses are considered as one of the utmost constraints to crop production across the globe. It has been estimated that more than 50% of yield reduction is the direct result of abiotic stresses. This is becoming a threatening scenario for food security all over the world (Rodríguez et al., 2005). Numerous signaling compounds such as phytohormones, Nitric oxide (NO), sugars and Hydrogen Peroxide display expedient effects in crop plants to combat stresses. In this section, we will describe a few such signaling protectants, which are induced upon stress perception and regulate the expression of genes through signal transduction pathways which enable plants to better adapt to environmental conditions.

Nitric oxide (NO) is a significant signaling molecule and antioxidant which is induced under several environmental conditions and helps plants acclimatize to environmental adversities. NO has been reported to play a significant role in alleviating adverse effects in

wheat seedlings. The exogenous application of NO continuously improved the antioxidant system of plants by increasing the level of antioxidants and antioxidative enzymes such as AsA, GSH, APX, GST and MDHAR, which further leads to the generation of a cascade of events that cause physiological adaptations in the plant in numerous forms, such as reduced lipid peroxidation and H_2O_2 content (Nahar et al., 2015). In grapevines, NO accumulation was observed under drought stress, which suggested its potential signaling role in drought. This role was also strengthened when similar results were obtained in other crops, such as maize seedlings grown under stress. In this case, an exogenous treatment of NO scavenger (cPTIO) increased NO scavenging, and an application of NO-donor (SNP) reduced NO scavenging, which strengthens the role of NO as a cellular messenger to mediate adaptive responses in plants against drought stress (Hao et al., 2008).

It was generally thought that hydrogen peroxide (H_2O_2) is a byproduct of aerobic metabolism and a harmful free radical entity. But recent studies suggested its role as redox-signaling molecule and mediator of plant adaptive responses under stress. An exogenous treatment of plants with H_2O_2 imparted tolerance to salinity stress by enhancing the activities of antioxidants and minimizing membrane lipid peroxidation in roots and leaves of maize as an acclimation process (de Azevedo Neto et al., 2005).

Furthermore, accumulation of H_2O_2 at low levels can induce tolerance to high-temperature stress in a few plants. Rice seedling, when pre-treated with a low amount of H_2O_2 (less than 10 mM), were found to have greater quanta yield from photosystem II and thus a better survival rate of green tissues as compared to untreated seedlings. Additionally, this enhanced the activities of antioxidative enzymes and the expression of stress-related genes such as those encoding small heat-shock protein 2, Δ-pyrroline-5-carboxylate synthase and sucrose-phosphate synthase, which have vital signaling roles in enhancing tolerance to high-temperature stress in rice seedlings (Uchida et al., 2002). The role of phytoprotectants in developing tolerance in green plants is unquestionable but a robust response to stress imparts multiple signaling cascades.

2.9 ROLE OF PHYTOPROTECTANTS IN CROSSTALK MECHANISMS

Plants induce the production of unique metabolites comprising numerous signaling molecules when subjected to stresses. Stress perception by specific plant receptors initiate stress responses by triggering particular

signal transduction pathways that ensure the survival and well-being of the stressed plant. Oxidative burst, ROS, ion efflux and influx, especially that of Ca^{2+} through Ca^{2+} signaling, acidification or alkalinization of cytoplasm, nitric oxide, abscisic acid signaling, jasmonates signaling, lipid signaling and cyclic nucleotides including cyclic guanosine monophosphate (cGMP) and cyclic adenosine monophosphate (cAMP), are among the signaling components that directly or indirectly participate in plant abiotic stress responses. Integration of different signaling pathways by transcription factors or other signaling components gives rise to the essential crosstalk of signaling pathways that is crucial for plant welfare under stress conditions (Zhao et al., 2005).

Crosstalk of signaling pathways helps plants regulate the expression of arrays of genes in a spatiotemporal manner to create a wide range of defense responses against abiotic stresses. Crosstalk of signaling pathways can occur either at transcription, translation, RNA splicing/editing or post-translational modification level. Transcription factors (TFs) are converging points for almost all the signaling pathways and they can be synthesized or activated either directly through stress signals/signal transduction pathways or indirectly by the feedback mechanism regulated by other TFs (Liu et al., 1999). Association of various signaling pathways through TFs has been observed under the influence of drought, cold, wounding, salinity, pathogens and hormonal treatment (Denekamp and Smeekens, 2003; Eulgem et al., 2000; Liu et al., 1998).

ROS production is central to oxidative stress that changes redox status within a cell. ROS regulate the wide range of genes involved in defense and antioxidant responses (Kandlbinder et al., 2004). Application of phytoprotectants mainly affects ROS signaling by interfering in the antioxidant system, thus accelerating ROS scavenging by enhancing ascorbate peroxidase and catalase activities. They manipulate lipid signaling by upregulating lipid peroxidation under osmotic stress (Cruz et al., 2013). Furthermore, they change membrane permeability by improvising potential gradient of ions across cellular membranes in stress conditions. Moreover, they crosstalk with nitrogen metabolic pathways, photosynthetic pathways and hormonal pathways to bring coordination in plant growth and development under stress (Zhang et al., 2013). Several phytoprotectants have been reported in the following examples that mediate crosstalk with nitric oxide (NO) signaling, lipid signaling, hormonal signaling and Ca2+ signaling through ROS signaling.

Nitric oxide (NO) is one of the potential phytoprotectants that crosstalk with ROS signaling. NO can work

either agonistically or antagonistically with ROS in plant defensive response (Neill et al., 2002). NO signaling also causes the accumulation of cGMP and cAMP though the help of Ca2+ signaling, thus creating specific defense responses in stressed plants (Lamotte et al., 2004).

Salicylic acid (SA) is a phytohormone that affects plant growth and development. It has a major part in biotic stresses but its role in abiotic stresses has been discovered recently. SA has also been included in the list of phytoprotectants because of its anti-stress program. It causes the accumulation of IAA and ABA but does not influence cytokinin levels (Sakhabutdinova et al., 2003). SA has been reported to induce crosstalk of signaling pathways, which takes place at the level of NO and ROS production under salt stress. It has also been suggested as a functional link to control various stressors (Gémes et al., 2011).

Tocopherols are amphiphilic antioxidants having four isomers that lessen the ROS level in photosynthetic membranes and limit lipid peroxidation (Garg and Manchanda, 2009). Furthermore, they take part in an intricate signaling network regulated by antioxidants, phytohormones and ROS (Munne-Bosch, 2005). Polyamines, on the other hand, are low-molecular amines that regulate a wide range of plant adaptive immune responses. They show high biological activities as they are involved in plant growth and development, membrane stabilization, gene expression and adaptation to abiotic stresses. Polyamines also have a role in signaling molecules as they are an essential signal for crosstalk between hormonal signaling and ABA signaling, and induce NO in plants (Alcázar et al., 2010; Tun et al., 2006). Thus, tocopherols and polyamines are the kind of molecules that can serve as candidates to influence plant cellular signaling. The interaction of different transcription factors under abiotic stress has been shown in Figure 2.6 for further understanding.

2.10 PHYTOPROTECTANTS AND SIGNALING PATHWAY ENGINEERING

Humans have struggled for food security since the beginning of their existence. Climate change and population growth has led to resource depletion, ultimately threatening food security worldwide. But due to advancements in genetic engineering in the current era, it has become possible to overcome these threats (Koning, 2017). Continued efforts are being made to develop new biotechnology approaches for improving crop varieties in an efficient and effective manner. The production of *Bacillus thuringiensis* (*Bt*) bacterial proteins in plants is a landmark in genetically engineered crops (Haq et al.,
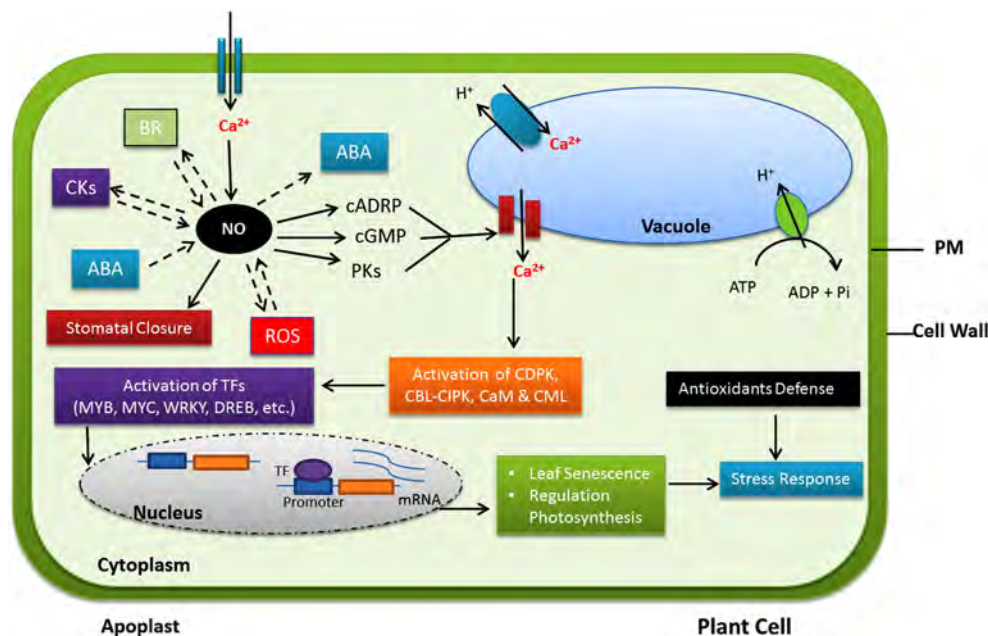
FIGURE 2.6 Phytoprotectants including nitric oxide and polyamine interact with abiotic stress signaling to generate stress responses in stressed plants. CKs cause the production of NO which induces ABA signaling, thus controlling the physiochemical reaction in a stressed plant. Furthermore, application of PAs and BR with NO promotes plant defense response against abiotic stresses. Where, NO=Nitric oxide; PAs=Polyamines; ABA=abscisic acid; ROS=Reactive Oxygen Species; CDPKs=Ca2+ dependent protein kinases; CBL=Calcineurin B-like proteins. BR=Brassinosteroid; and CKs=Cytokinins CaM=Calmodulin; and CIPKs=CBL-interacting protein kinases (Asgher et al., 2017; Besson-Bard et al., 2008).

2004). Many studies have been conducted on various phytoprotectants regarding their application in plants, their role in the stress signaling network and metabolic response. A genetic transformation approach has been exploited to support plant phytoprotection under stress conditions and improved performance of crops has been observed under suboptimal conditions. Activation or inhibition of the biosynthetic and catabolic pathways can lead to an accumulation of these protectants.

Glycine betaine (Du et al.), an amine, protects plants by activating the ROS detoxification system. In genetically modified tomatoes, a 10–30% increase in production is evidence that GB is a potential candidate to protect plants against drought and cold (Park et al., 2007). Transgenic maize tolerant to drought and cold has confirmed the suitability of GB as a target for genetic engineering (He et al., 2013). γ-aminobutyric acid (GABA), an amino acid, has been associated with carbon-nitrogen pool and ROS scavenging (Liu et al., 2011). Trehalose is a non-reducing sugar playing a significant role in stress responses. Genetic analysis has demonstrated that GABA is a potent candidate for the role of phytoprotectant for biosynthetic pathway engineering to produce transgenic plants against salt and drought stress (Nounjan et al., 2012; Renault et al., 2010).

Polyols and simple sugar have also been targeted for genetic engineering because of their role as osmoprotectants. Polyols act as a molecular chaperone. and thus play a supportive role in ROS scavenging. Accumulation of straight chain polyols such as mannitol increases the tolerance of plants such as *A. thaliana*, poplar, wheat and tobacco to salinity and drought stresses (Ahmad and Wani, 2013), while a higher expression of sorbitol has been reported as being toxic due to inference in carbon metabolism (Llanes et al., 2013). Thus, mannitol biosynthetic pathway genes are a strong candidate for pathway engineering. With every passing day, research is being conducted to exploit biotechnology approaches to create plant crops with stress tolerance traits. But still, a better understanding is needed to fill the gaps in pathway engineering.

2.11 CONCLUSION AND FUTURE PROSPECTIVE

Global climate deterioration and various abiotic stresses such as heat, drought and cold adversely affect plant growth and development. Plants exert different immune responses by coordinating their physiological and molecular responses, which are important defense strategies. However, adjustment to environmental conditions involves different signaling cascades simultaneously, which makes this adaptation process more complex. A rapidly changing environment demands novel approaches to overcome threats to plant development. Using phytoprotectants as immuno-boosters under stress conditions is an interesting approach as it enhances photosynthetic rate, yield and antioxidative capacity.

Phytoprotectants such as proline and sugar can function as signaling molecules and have an obvious influence on various physiological and metabolic processes. There exists high integration between these protectants and the transcriptional activation of stress-responsive genes, ROS scavenging and calcium-mediated protective responses against environmental stresses. Extensive research has been conducted in order to understand plant abiotic stress signaling pathways mediated by phytoprotectants through the aid of powerful molecular tools including transcriptome and proteome analyses. To acquire more insights into the underlying molecular mechanism(s), a genetic transformation approach can be used to enhance the endogenous production of protectants, which will result in better performing crops under suboptimal conditions. Furthermore, novel pathways can be established in plants by introducing genes from other species. More sophisticated and high throughput techniques can be employed in genetic engineering to improve the networks of stress signaling mediated by phytoprotectants in plants, thus helping them combat abiotic stresses in a better way.

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