

PREFACE

Environmental stresses, such as heavy metals, drought, radiation, salts, pesticides, temperature, etc. are major factors collectively called abiotic stresses, which limit agricultural productivity. Abiotic stress factors negatively influence the survival, biomass production, and yield of staple food crops of up to 70%. In recent years, much attention has been given for developing strategies to alleviate the adverse effects of abiotic stresses on crops in order to fulfill the food demand of increasing population. Chemical application and agronomical crop management practices have been used to alleviate abiotic stresses with some success. During the last decade, extensive work has been carried out to understand plant hormone-mediated enhancement in abiotic stress tolerance using physiological, biochemical, genetic, molecular, and genomic approaches for crop breeding and management. This book has compiled recent research on plant hormone mediated regulation of abiotic stress tolerance in plants with special emphasis on crops.

This book consists of fourteen chapters dealing with recent research made in the direction of plant hormone and abiotic stress tolerance in crop plants. Chapter One deals with abiotic stress and crop productivity. Chapters Two and Three deal with the role of polyamines, ROS, and melatonin in the regulation of abiotic stresses. Chapter Four extensively elaborates the significance of the multigene family in the improvement of crops under stress conditions. Chapters Five and Six deal with the interaction of plant hormones and their subsequent impact on plant abiotic stress tolerance. Chapter Seven, Eight and Nine comprehensively deal with the role of abscisic acid and gibberellic acid signaling in the regulation of abiotic stress tolerance in crops. Chapters Ten through Thirteen describe the role of brassinosteroids cross talk, interaction and signaling in the regulation of abiotic stress tolerance in crops. Chapter Fourteen deals with the emerging role of oxylipins in the regulation of abiotic stress in crops. Chapter Fifteen deals with the role of jasmonic acid and salicylic acid signaling in the regulation of abiotic stress tolerance. This book has gathered recent information of plant hormone research and abiotic stress tolerance in crops. The authors hope that this book will be very useful for graduate and post graduate students and researchers.

Chapter 1 - Major abiotic stresses viz. drought, cold, salinity and heat are known to reduce the yield of food crops worldwide. To improve abiotic stress tolerance of crops through traditional plant breeding approaches had limited success due to multigenic nature of stress tolerance. In the recent past years, molecular techniques have been used to understand the mechanisms by which plants perceive environmental signals and further their transmission to cellular machinery to activate adaptive responses. Studies on physiological and molecular

mechanisms of abiotic stress tolerance have led to characterization of a number of genes associated with stress adaptation. Microarrays techniques have proven to be invaluable in generating a list of stress related genes. Some of these genes are specific for a particular stress while others are shared between various stresses. Interestingly, a number of genes are shared in abiotic and biotic stress responses. This highlights the complexity of stress response and adaptation in plants. There is a whole cascade of genes involved in abiotic stress tolerance; starting from stress perception to transcriptional activation of downstream genes leading to stress adaptation and tolerance. A number of these genes have been discovered but the authors still do not have the complete list with all interactions. There is also significant number of genes with unknown functions found to be regulated by abiotic stresses. Understanding the function of these genes and their interaction with other known genes to effect stress adaptation is required. The recent discovery that microRNAs regulate gene expression adds another layer of complexity to the authors' understanding of abiotic stress tolerance. Significant amount of work will be needed to identify microRNAs associated with abiotic stress response, and understand their interaction with each other and their mechanism of regulating abiotic stress response. The promising side is the development of next-generation sequencing techniques that has allowed deep sequencing of mRNAs and microRNAs associated with abiotic stress response. A complete understanding on physiological and molecular mechanisms especially signaling cascades in response to abiotic stresses in tolerant plants will help to manipulate susceptible crop plants and increase agricultural productivity in the near future.

Chapter 2 - Drought, a meteorological condition resulting from extensive period of deficient precipitation, is a severe limiting factor that impacts plant productivity and sustainable agriculture, thus also the affected country's economy. Scarcity of water affects the normal growth of plants, suppresses photosynthesis enhancing photorespiration, reduces leaf size, stem extension, root proliferation and restricts the expression of full genetic potential of the plants leading to serious loss in agricultural productivity. An increased rate of photorespiration during drought produces excess amount of reactive oxygen species (ROS) that damage cellular membranes, macromolecules and can lead to denaturation of functional and structural proteins. To survive in such adverse condition, plants undergo several adaptations. They generate antioxidants (ROS scavengers) that include enzymes such as catalase, superoxide dismutase (SOD), ascorbate peroxide (APX) and glutathione reductase. Along with these, some non-enzyme molecules such as ascorbate, glutathione, carotenoids and anthocyanin are also produced. Another group of macromolecules, known as polyamines, are produced and accumulated by plants and have been implicated in drought stress adaptation. Polyamines have a double-edged role as a potential ROS scavenger as well as a source of ROS. Thus, these groups of aliphatic polycations seem to play a crucial part in maintaining cellular ROS homeostasis during drought stress. An increased level of polyamines in plant can be effective against all types of stress. On the contrary, excess polyamines can also act as a deterrent. Hence, the main objective of this review is to explore ROS as a major cause of oxidative stress and to discuss the polyamine's action of scavenging ROS together with maintaining stable homeostasis of ROS in plant body during drought stress.

Chapter 3 - Abiotic stresses encompass multiple environmental conditions like salinity, drought, extreme temperature, radiation stresses and heavy metal toxicity. Such harsh conditions are challenging for plants to complete their life cycle, causing detrimental effects

on crop productivity. To address food security issues, the recent focus on melatonin as an antioxidant agent and positive regulator of abiotic stress tolerance seems relevant. Plants exposed to stress conditions have elevated endogenous melatonin levels. Furthermore, transgenic lines overexpressing melatonin biosynthetic genes or those treated exogenously with melatonin are found to exhibit improved growth and developmental patterns under several abiotic stress conditions. The present chapter highlights a comprehensive discussion on the recent advances in the field of melatonin research with context to mitigation of multiple abiotic stresses in plants at the physiological, biochemical and molecular levels.

Chapter 4 - With augmentation in the genetic knowledge, the use of gene-function analysis and development of gene transformation methods for crop improvement has taken place in current times. Such development of genetically improved crops requires improved molecular technologies and controlled manipulation of multiple genes. Application of genetic engineering for development of improved crop plants is one of the best methods to deal with crop improvement issues. The genetically engineered plants are insect, pest and virus resistant, also tolerant to water deficit condition and have an increased nutritional value. Genetic manipulations of the crop plants are the key concern of geneticist by synthesis of novel organic compounds and pharmaceutically vital proteins. Genetic engineering has seen a gradual modification from a single gene transformation to multigene transformation (MGT). A large number of agronomic traits in plants are generally controlled by multiple genes. Now a days, multigene transformation or multigene engineering is accepted as a novel approach to develop plants with desired phenotype. This book chapter discusses metabolic pathways of multigene engineering, various multigene engineering approaches including nuclear, chloroplast and mitochondrial multigene engineering. It also emphasizes on the application of multigene engineering and forecast of future role of multigene approach in crop improvement.

Chapter 5 - Various anthropogenic activities decrease the fertility of agricultural lands that ultimately reduce the plant growth and yield. Attempts are being made on developing novel strategies to enhance crop productivity and stress tolerance responses, by recognizing various stress markers and genes to counteract stress signals and maintain growth and yield under harsh conditions. Phytohormones are synthesized in very small amounts and work as chemical messengers to communicate cellular activities in higher plants. They play key roles and coordinate various signal transduction pathways during abiotic stress response. They regulate external and internal stimuli. Interaction of plant hormones with each other play significant role in boosting defense response under abiotic stress by modulating gene expression. Mechanisms regulating synthesis, mode of action and signaling of hormones for the production of genetically modified crop plants with increased tolerance against stress signals are being identified.

Chapter 6 - Stress has been defined as an altered physiological condition caused by factors that tend to disrupt the equilibrium. External stress can be of biotic or abiotic origin. The major abiotic stresses viz., drought, high salinity, cold, and heat negatively affect the agriculture worldwide. Dehydration stress is induced by drought, salinity and temperature severity. The drought or salt stress triggers many common reactions in plants. Both stresses cause cellular dehydration, leading to osmotic stress. Plants induce various morphological, biochemical and physiological changes in order to acclimatize and endure drought and salt stress. Phytohormones play vital roles in tolerance of plants against both stresses. Plants respond to external stimuli like drought and salt stress by initiating signaling pathways which

trigger the expression of appropriate responses. These signaling pathways comprise a network of protein-protein reactions and signaling molecules.

Chapter 7 - Some plant responses to stress are mediated by phytohormone abscisic acid (ABA). ABA regulates molecular, physiological, growth etc. processes in response to abiotic stress. ABA-mediated stress response comprised of stress perception, signaling, gene transcription and response. The plasma membrane receptors such as SOS1, HKs and RLKs can sense the stress stimuli and then induce the ABA-signaling pathway. ABA as a second messenger regulates the ABA signaling complex/ABA signalosome comprised of RCAR/PYR/PYLs, PP2Cs, and SnRK2s elements. Subsequently, activation of phosphorylation cascade induces transcription factors such as DREB, AREB/ABFs, bZIP, MYC/MYB. The transcription factors binding to cis-elements in the upstream regions of promoter of genes control the expression of abiotic stress-responsive genes. The cis-acting elements of DRE/CRT, ABRE and MYCRS/MYBRS are common in the promoter region of numerous ABA-responsive genes. The binding of transcription factors to cis-elements of gene induce stress-tolerance genes (e.g., LEA, HSPs, COR, TFs, ERA1, P5CS, PP2C, RD29, etc.) and ABA biosynthesis genes (e.g., NCDE, ABA3/LOS5, MCSU, etc.). The expression of ABA-responsive genes leads to ABA biosynthesis and increasing stress tolerance through stomatal closure, osmolyte accumulation, ion homeostasis, growth regulation and etc. In conclusion, ABA through activation a complex network of actions increases plant tolerance under unfavorable condition of salt, drought, cold and osmotic stresses.

Chapter 8 - Plant growth, development, survival and adaptability under various environmental conditions greatly depend upon the plant growth hormones. Changes in their content will alter many signal transduction pathways and enable plants to coordinate among its various growth and developmental processes to survive adverse conditions. Gibberellins (GAs) are such plant hormones whose role and signal transduction pathways in abiotic stress condition are evident and increasingly being researched nowadays. GA signalling in positive or negative growth regulation varies with respect to the particular abiotic stress plant is subjected to. In shallow long submergence and shading stress, increased GA levels help plant to grow more and escape the stress condition, while in short deep submergence and salt, cold and osmotic type of stresses plant restricts its growth by reducing GA content and contribute to fight against stress condition. GA signalling mechanism involved in various developmental and abiotic stress condition is mediated through an important GA signalling molecule called DELLA protein. DELLA protein regulates a complex network of genes and transcription factors. It also interacts with components of other hormone signalling pathways thereby integrating multiple signalling pathways in response to various developmental and abiotic stress conditions. The GA signalling pathway comprises active GAs biosynthesis, their perception, signal transduction and inactivation, each of which is subject to regulation by different abiotic stress signals. This chapter reviews the past and present knowledge on how stress modulates GA signalling and imparts stress tolerance.

Chapter 9 - Plants adapt to drought and salinity integrating developmental and growth responses environmentally activated. Phytohormones tightly control the adaptive processes and coordinate the cellular responses to drought and salinity. Recent studies have uncovered novel roles of gibberellins (GAs) and abscisic acid (ABA) demonstrating that both phytohormones are involved in the whole plant responses to affront the stressful environmental signaling for growth and development. In this chapter, the authors emphasized the role and the crosstalk of GAs and ABA mediating plant responses under drought and

salinity. The function of DELLA proteins as central regulators in the GA and ABA crosstalk is also emphasized.

Chapter 10 - Plants are continuously under the influence of various environmental stresses that includes biotic and abiotic stresses. Abiotic stresses are prevalent in present day's plants because of several anthropogenic factors like pollution and global warming as well as greenhouse gases. Brassinosteroids (BRs) are the potential growth hormones that mitigate the negative impact of stresses in plants. BRs are plant poly hydroxyl steroids, recognized as a new kind of phytohormones that play an essential role in plant development. It occurs in plants at low concentrations and has been detected in all plant organs (pollen, anthers, seeds, leaves, stems, roots, flowers, and grains) and also in the insect and crown galls. BRs show structural similarity with animal and insect steroid hormones. Over the few past years, studies at molecular, genetic and proteomic level have established the complete BRs signaling pathway and exposed the important regulatory mechanisms in plants. However, to focus some important and recent studies in this chapter, the authors have discussed the currently available data on BR signaling pathway and the latest findings on their regulatory mechanisms in plants under abiotic stresses.

Chapter 11 - Apart from their primary role in growth and developmental processes, plant hormones have been identified to play a vital role in abiotic stress control. The adaptation of plants to several environmental stresses has been reported to be regulated by fluctuations in phytohormones which are stress responsive. Recent studies on phytohormones have strongly indicated the importance of their crosstalk leading to regulation and tolerance of abiotic stresses. Numerous studies on brassinosteroids have also suggested their regulatory roles in controlling the functions of other hormones. It has also garnered importance as a stress alleviator which is reported to curb environmental stresses like exposure to heavy metals, pesticides, chemical fertilizers, temperature extremes and water stress. The studies pertaining to the interplay of brassinosteroids with other plant hormones under stress have provided an insight into the functioning and probable modulation of gene expression that alters the signaling mechanisms. The present chapter reviews the studies indicating the crosstalk of brassinosteroids with other hormones.

Chapter 12 - Brassinosteroids (BRs) are a class of steroid plant hormones that participate in the regulation of numerous developmental processes, including root and shoot growth, vascular differentiation, fertility and seed germination, and tolerance to biotic and abiotic stresses. The utilization of BRs in protecting plants from adverse environmental stress has positive prospects because these compounds are non-toxic, non-genotoxic, biosafe and eco-friendly. In this way, they could have diverse applications in agri- and horticulture. However, the hormonal control of plant development and stress adaptation relies on a complex network of synergistic and antagonistic interactions between various hormones.

The authors focus on how the crosstalk between brassinosteroids and other hormones, such as auxin, abscisic acid, gibberellins, ethylene, cytokinins, jasmonate and salicylic acid, influences the adaptation of plants to various abiotic stress.

Chapter 13 - Brassinosteroids (BRs) are steroidal plant-hormones that control several physiological functions in plants including cell elongation, seed germination, cell division, senescence, vascular-differentiation, reproduction, root development and also respond to various biotic and abiotic stresses. Drought, flood, excessive heat, chilling, salinity, inappropriate light, presence of heavy metals and other pollutants are some common abiotic stresses to which plants are exposed. These stresses have harmful effects on the growth and

development of plants. A multifarious interaction of signaling tumblers are necessary for the insight of extracellular stimulus and consequent commencement of proper responses to the stress at the molecular level. A receptor kinase-mediated pathway has been involved in the BR signal transduction. In present chapter the authors provide a synopsis of the brassinosteroids signaling during different abiotic stresses. Also the BR perception, its receptors, transcription factors and mechanisms of termination of BR signals have been discussed in detail.

Chapter 14 - Oxylipins are lipophilic signalling molecules, derived from oxygenation of polyunsaturated fatty acids by enzymatic (e.g., Jasmonic acid, divinyl ethers) or non-enzymatic pathways (e.g., phytoprostanes) leading to the synthesis of various products such as jasmonates, aldehydes, ketones, oxyacids, alcohols and hydrocarbon gases. Enzymes such as allene oxide synthase (AOS), hydroperoxide lyase (HPL), divinyl synthase (DES), peroxygenase (POX), reductase, etc. catalyse the biosynthetic pathway of oxylipins. Under abiotic stress, high content of ROS formation and activation of biosynthesis of oxylipins have been reported. In this chapter, the authors have focused on the various biosynthetic pathways, signalling and role of oxylipins in plant development and defense mechanism under various abiotic stresses.

Chapter 15 - Jasmonic acid (JA) is biosynthesized from linolenic acid by the octadecanoid pathway and is considered a plant hormone. There are many derivative compounds and metabolites collectively called jasmonates, which have different physiological actions. The major function of JA and its various metabolites is to regulate plant responses to abiotic and biotic stresses as well as plant growth and development. Plant growth and development processes include growth inhibition, senescence, tendril coiling, flower development and leaf abscission. JA is also responsible for tuber formation. It has an important role in response to wounding of plants and systemic acquired resistance. Salicylic acid (SA) is a phenolic compound with a broad distribution in plants. It has been found that SA plays an important role in the regulation of physiological and biochemical process of plants growth and development such as ripening, flowering in thermogenic plants, seed germination, ion uptake and transport. SA also is an important signaling molecule involved in local and systemic responses to pathogen attacks. Besides it has been found that SA plays a role during the plant response to abiotic stresses such as drought, chilling, heavy metal toxicity, heat, and osmotic stress. In particular, the exogenous application of SA is effective in providing resistance to the plants against different abiotic stress factors. Furthermore, SA may function in crosstalk with other phytohormones, reactive oxygen species (ROS) and glutathion (GSH) in events involved in the transcription of sets of defense genes.