

Parvaiz Ahmad
Mohd Rafiq Wani *Editors*

Physiological Mechanisms and Adaptation Strategies in Plants Under Changing Environment

Volume 2

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Preface

Environmental stresses such as salinity, drought, flooding, extreme temperatures, nutrient deficiency, or toxicity in addition to deteriorating soil conditions pose major intimidation to agriculture and food security worldwide. The productivity loss is elicited by a series of morphological, physiological, biochemical, and molecular stress-induced changes. Such an adverse situation is in contrast with the mounting global food demand and becomes even more testing in developing countries where they cause severe food insecurity and ruthless poverty for large populations predominantly in rural areas. Global population is escalating at a distressing rate and is anticipated to reach beyond nine billion by the end of 2050. While plant productivity is being seriously constrained by a range of abiotic stresses, feeding the world population under such horrid environment is a major disquiet for all nations. Water stress, on one hand, affects in excess of 70 million hectares of rice-growing land globally, whereas salt and nutrient stresses render more than one hundred million hectares of agricultural land uncultivable, thereby resulting in low outputs, poor human nutrition, and abridged educational and employment avenues. Knowledge and technology in biological science is expanding leaps and bounds, thus it becomes imperative to keep ourselves updated with the advances in plant abiotic stresses to meet the current scientific challenges, particularly the growing food demand for world population. In this scenario, it is urged that such strategies should be adopted which may be used to get maximum crop stand and economic returns from stressful environments. By employing contemporary tools and techniques, strenuous attempts are being made worldwide to understand how plants respond to these stresses. In this context, the book “*Physiological Mechanisms and Adaptation Strategies in Plants under Changing Environment*” Volume 2 will prove an indispensable source for scientists, students, and others seeking advancements in this area of research.

The present volume comprises of 13 chapters and each chapter has different research scope from the other. Chapter 1 throws light on biochemical and molecular approaches for drought tolerance in plants. Here, the authors scrupulously review the effects of drought stress on biochemical parameters especially proline metabolism in plants besides recounting the mechanism of drought resistance on physiological, molecular, and enzymatic basis. Chapter 2 addresses the heavy-metal

attack on freshwater side: physiological defense strategies of macrophytes and ecotoxicological ops, wherein the authors have comprehensively put in their efforts in elaborating the role of Cd and Cu pollution for inducing heavy-metal stress at all organization levels. The authors reveal that physiological responses remain very sensitive to the xenobiotic levels and constitute the first step towards the development of histological protection against the free radicals. Chapter 3 is about the secondary metabolites and environmental stress in plants: biosynthesis, regulation, and function. In this chapter, recent developments on structural and regulatory genes involved in the biosynthesis of secondary metabolites are explicitly discussed.

Chapter 4 is about the major phytohormones under abiotic stress, where the authors uncover the pivotal role of phytohormones in plants for adapting to changing environments by mediating growth, development, nutrient allocation, and source/sink transitions. Furthermore, the chapter summarizes the recent progress concerning the essential role of phytohormones in plant responses to abiotic stress, which has brought change in transcriptomics, metabolomics, and proteomics. Chapter 5 is regarding the nitric oxide and its role in plants under abiotic stress. In this chapter, the author presents the comprehensive synthesis of nitric oxide and its role in many physiological and developmental processes in addition to signaling molecule interactions with plant hormones and defense gene regulations under environmental stresses. Chapter 6 describes brassinosteroids: improving crop productivity and abiotic stress tolerance. The chapter focuses on the exogenous application of effective doses of brassinosteroids (BRs) in stress-affected plants, which play crucial roles in wide spectrum of biochemical, physiological, growth and developmental processes, besides defending them from adversaries of environmental stresses.

Chapter 7 deals with ethylene and its role in plants under environmental stress. In this chapter, it is highlighted that ethylene acts via complex signaling pathway leading to the activation of *Ethylene Response Factor (ETR)* genes which represent one of the largest transcription factor families in the plant kingdom. Chapter 8 describes the scenario of climate changes in the context of agriculture. Here, the authors painstakingly discuss the contributing factors to global warming in addition to global distribution of synthetic organic compounds, alteration in biochemistry of elemental cycle, and impact of climatic changes on the productivity of plants. Chapter 9 is concerned with the role of protective compounds in stress tolerance. This chapter highlights how protective compounds alleviate the effects of environmental stresses, especially drought and salt and function as metabolic signals for broader influence on physiological responses and metabolic adjustments vis-à-vis stressful conditions.

Chapter 10 deals with the growth patterns of tomato plants subjected to two non-conventional abiotic stresses: UV-C irradiations and electric fields. This chapter covers the effects of the exposition of tomato to UV-C radiation and DC-electric field in bringing the significant alterations in plant growth. The protection of tomato plants against UV-C, combined with growth-promoting effects of electro-culture, could allow farmers to grow better crops in less time and at lower cost. Chapter 11 is about rhizobacteria and the restoration of heavy-metal contaminated soils. In this chapter, the authors enumerate the panoply of mechanisms used by microorganisms to cope

up with metal stress and mobilize their plant growth promotion traits in association with their host plants with special emphasis to actinobacteria in metal contaminated lands. Chapter 12 deals with potassium and sodium transport channels under NaCl stress, where the authors have discussed in detail the pathways for Na⁺ and K⁺ transport across the plasma membrane, tissue distribution of these ions, and their intracellular compartmentalization. Chapter 13 is about *Jatropha curcas*: an overview. The chapter encompasses different aspects of *Jatropha* plantation and its uses including in soil conservation under stressful conditions. In addition, the chapter also includes the information about phytochemical constituents of *Jatropha* and its possible allelopathic effects.

Chapters contributed in this book have been published keeping intact author's justifications; however, suitable editorial changes were made, wherever considered necessary. In spite of our best efforts, there is a chance of some errors still creeping in the book, for which we seek reader's feedback. We wish to express our appreciation to the well-versed contributors, who readily accepted our invitation to write the chapters. Moreover, we would like to thank Springer Science+Business Media, LLC, New York, particularly Eric Stannard (Editor Botany), Flora Kim (Developmental Editor), Andy Kwan (Assistant Editor), and all the other staff members of Springer, who were directly or indirectly associated with us in the current project for their constant support and efforts in bringing out the timely publication of this volume.

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About the Editors



Dr. Parvaiz Ahmad (Editor) Dr. Parvaiz Ahmad is Assistant Professor in Botany at S. P. College, Srinagar, Jammu and Kashmir, India. He has completed his post-graduation in Botany in 2000 from Jamia Hamdard, New Delhi, India. After receiving Doctorate degree from Indian Institute of Technology (IIT) Delhi, India, he joined International Centre for Genetic Engineering and Biotechnology, New Delhi in 2007. His main research area is Stress Physiology and Molecular Biology. He has published more than 30 research papers in peer-reviewed journals and 19 book chapters. He is also an editor of 6 volumes (5 with Springer NY USA and 1 with Studium Press Pvt. India Ltd., New Delhi, India). He is the recipient of Junior Research Fellowship and Senior Research Fellowship by CSIR, New Delhi, India. Dr. Parvaiz has been awarded Young Scientist Award under Fast Track scheme in 2007 by Department of Science and Technology (DST), Govt. of India. Dr. Parvaiz is actively engaged in studying the molecular and physio-biochemical responses of different agricultural and horticultural plants under environmental stress.



Dr. Mohd Rafiq Wani (Co-editor) Dr. Mohd Rafiq Wani is currently Assistant Professor in Botany at Government Degree College (Boys), Anantnag, University of Kashmir, India. Dr. Wani did his Masters in Botany in 2003 with specialization in “Genetics and Plant Breeding” from Aligarh Muslim University (AMU), Aligarh, UP, India. After obtaining the Degree of Doctorate in 2008 for his research work on “Chemical Mutagenesis in Mungbean” from the same University, he joined Department of Higher Education, Government of Jammu and Kashmir in 2009. He teaches a

range of bioscience-related subjects at undergraduate/post-graduate levels. At present, his research interests are mainly focused on the improvement of pulses through induced mutations and exploring the physiological and biochemical responses of crop plants to a range of biotic and abiotic stresses. As a part of his research endeavour, Dr. Wani has extensively researched and written on the issues of induced chemo-mutagenesis among the food crops, with special reference to pulses. He has around twenty eight (28) research publications to his credit, published in various international and national journals of repute. Moreover, he has also submitted several book chapters to various research-oriented volumes. Dr. Wani, while constantly working for his academic and research interests, is currently in the process of editing many volumes of books on the subjects of plant stress physiology and induced plant mutagenesis with reputed international publishers. In addition, he is an editorial member and reviewer of few online journals pertaining to plant sciences, besides being the life member of various scientific societies like Indian Society of Pulses Research and Development (ISPRD) and Indian Society of Genetics and Plant Breeding (ISGPB).

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Chapter 1

Biochemical and Molecular Approaches for Drought Tolerance in Plants

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Subzar Ahmad Sheikh, Mohd Rafiq Wani, Saiema Rasool,
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1 Introduction

Plants are subjected to variety of abiotic stresses such as drought, temperature, salinity, air pollution, heavy metals, UV radiations, etc. (Ahmad et al. 2008a; Ahmad and Prasad 2012a, b). Abiotic stress adversely affects crop production worldwide, decreasing average yields for most of the crops to 50 % (Bray et al. 2000). Abiotic stress hampers all the metabolic processes and affect the normal functioning of plant (Ashraf et al. 2006, 2009; Jaleel et al. 2007a, b, c, 2008a, b, c; Azooz et al. 2009; Koyro et al. 2012; Katare et al. 2012; Ahmad and Prasad 2012a, b). Drought is one of the major abiotic stresses occurring in many parts of the world and is the main limiting factor in crop production (Ashraf et al. 2006, 2009; Jaleel et al. 2007a, b, c). Due to an increasing world population, drought stress will lead to a serious food shortage by 2050 as the population is expected to reach ten billion. Water stress may result either from an insufficient water availability because of

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drought or from an excessive presence of water activity in the plant's environment (Jaleel et al. 2007a, b). Water deficit means the absence of sufficient moisture content necessary for normal plant growth and its life cycle (Zhu 2002; Sankar et al. 2008). Plant experiences drought stress either when the roots face water deficit or because of the enhanced transpiration rate and both these conditions often coincide under arid and semiarid climates (Sankar et al. 2007a; Sakcali et al. 2008).

Drought accelerates the effect of other stresses to which plants are subjected to and several different abiotic stresses (like salt and cold stress) result in water stress (Ahmad and Prasad 2012a, b). The general effects of drought on plant growth are well known, but the effects of water deficit at biochemical and molecular levels are not well understood (Shao et al. 2008a). Plant species possess distinctive indicators of stress tolerance at whole plant, tissue, or cellular level (Munns 2002). Sufficient evidences favour the view that adaptive osmotic adjustment is mediated by proline and glycine betaine (GB), that also helps in protecting the subcellular structures in stressed plants. Proline accumulation has been advocated as a selection criterion for stress tolerance (Azooz et al. 2004; Jaleel et al. 2007d; Ahmad et al. 2008b). Proline accumulation has been reported in many plants on exposure to the stresses like temperature, drought, salt, heavy metal, etc. (Sairam et al. 2002; Ahmad et al. 2006, 2011a, 2012a, b; John et al. 2009; Katare et al. 2012). Enhanced proline level enables the plant to maintain low water potentials (Jaleel et al. 2007e, 2008d, e). As the water potential decreases, the compatible osmolytes involved in osmoregulation accumulate, resulting in additional water absorption thus overcoming the immediate effect of water shortages (Azooz 2004; Ahmad and Sharma 2008; Jaleel et al. 2009). The main role of these osmolytes is probably to insulate plant cells against the destructive effects of stress by preserving the osmotic balance by stabilizing the structure of key proteins such as Rubisco, by protecting the macromolecular structure and function and helps to adapt stress injury (Bohnert and Jensen 1996).

Water stress tolerance is a natural phenomenon in all plant species, but it varies from species to species. Improving the efficiency of water use in agriculture is associated with increasing the fraction of the available water resources that is transpired, because of the unavoidable association between yield and water use (Lawlor 2002). During last few decades, lots of physiological works have been conducted under drought stress in crop plants (Shao et al. 2008a, b; Zhao et al. 2008). Although the drought tolerance mechanism is still unclear, but it can be to some extent explained on the basis of ion homeostasis mediated by stress adaptation effectors, toxic radical scavenging, osmolyte biosynthesis, water transport, and long distance response coordination (Reddy et al. 2005). Due to the complexity of the interactions between stress factor and various molecular, biochemical, and physiological phenomena affecting plant growth and development, the abiotic stress tolerance is complex phenomenon (Ashraf and Harris 2004; Ahmad and Sharma 2008; Ahmad et al. 2010a; Hakeem et al. 2012). Some small and electrically neutral molecules act as osmoprotectants and stabilize proteins and membranes against the denaturizing effect of some abiotic stresses and are nontoxic at molar concentrations (Munns 2002).

Natural osmoprotectant concentrations in cytoplasmic compartments are osmotically significant and have pivotal roles in maintaining cell turgidity and the driving

force for water uptake under stress (Rontein et al. 2002). One of the four most common responses against stress in plants is overproduction of different types of compatible solutes. Accumulation of osmotically active biomolecules plays an imperative role to develop the stress tolerance. These are low molecular weight organic metabolites called compatible solutes which do not inhibit other cellular functions. It is an adaptive mechanism that enables protection of cell turgor and restoration of water status of cells without disturbing the normal cellular function. The compatible solutes include proline, sucrose, polyols, trehalose, and quaternary ammonium compounds (QACs) such as glycine betaine (GB), alanine betaine, proline betaine, choline-*O*-sulphate, hydroxyproline betaine, etc. (Azooz et al. 2004; Ashraf and Foolad 2007; Ahmad and Sharma 2008; Koyro et al. 2012; Rasool et al. 2013). Compatible solutes protect plants from stress through different means including contribution to cellular osmotic adjustment, detoxification of reactive oxygen species (ROS), protection of membrane integrity, and stabilization of enzymes/proteins (Ahmad and Sharma 2008; Koyro et al. 2012; Grant 2012; Sofo et al. 2012; Rasool et al. 2013). Proline and glycine betaine accumulation help to adapt the stress injury as they provide an environment attuned with macromolecular structure and function (Sankar et al. 2007b). Foliar application of various organic solutes enhances tolerance to abiotic stress and this approach significantly contributes in increasing the crop production under stressed environment.

2 Effects of Drought on Biochemical Parameters

2.1 Soluble Proteins

Changes in protein expression, accumulation, and synthesis have been observed in plants on exposure to drought stress (Cheng et al. 1993). Drought stress brings quantitative as well as qualitative changes in proteins (Riccardi et al. 1998). Stress-induced protein accumulation may provide a storage form of nitrogen and is used by the plant later and have been proved to play a role in osmotic adjustment. Nayer and Reza (2008) demonstrated that drought stress induced expression of 50 proteins in two varieties of maize. Riccardi et al. (1998) has reported a significant quantitative variation in 78 out of 413 leaf proteins, with 38 exhibiting differential expression in two genotypes of maize during water deficit. A relationship has been reported to exist between the accumulation of drought-induced proteins and physiological adaptations during water stress (Bray 1993). Dehydrins, the proteins synthesized in response to drought stress, belong to group II late embryogenesis-abundant proteins (Close 1996). These group II proteins defend protein structure and act as molecular chaperones during stress. Four names have been designated for this protein family—RAB, LEA D-11, LEA (II), and DHNs (dehydrins) (Dure et al. 1989).

Dehydrin (dehydration-induced) genes expresses in the embryos during the late stages of embryogenesis. These are also induced in vegetative tissues during normal

growth conditions and in response to stresses like drought, low temperature, and salinity leading to cellular dehydration. They are distributed in a wide range of organisms including algae, yeast, cyanobacteria, and higher plants. Dehydrins are mainly found in cytosol, nucleus mitochondria, vacuole, and the vicinity of plasma membrane (Rorat 2006). Dehydrin gene expression has been observed to be drought-regulated in both drought-tolerant and drought-susceptible cultivars (Wood and Goldsbrough 1997). Dehydrins have been most extensively studied in relation to drought stress. They are believed to play an important role in the stability of membrane proteins and in osmotic adjustment (Dure et al. 1989) like that of compatible solutes. The dehydrins may also be playing the role by binding with ions accumulated (ion sequestering) under drought stress and in controlling the solute concentration in the cytoplasm. Dehydrins may also have a cryo-protective role in macromolecular stabilization by binding water molecules to their hydrophilic surfaces, which reverses or prevents cellular protein denaturation (Jiang and Huang 2002).

In many plants, like some maize cultivars, sorghum, wheat, and cocksfoot, the drought-induced expressions of dehydrin genes have been identified (Nayer and Reza 2008; Shao et al. 2009). Dehydrin-like proteins can be detected in the roots and leaves of drought-stressed plants and probably protect them from further dehydration damage (Tuğçe and Yasemin 2005). Drought either induces earlier expression of dehydrin-like proteins by accelerating the development, or changes the water potential which results in the expression of dehydrin-like proteins (Nayer and Reza 2008). de Rodríguez et al. (2002) observed in sunflower that leaf soluble proteins decreased during water stress. A contrasting result was observed by Ashraf and Mehmood (1990), who reported association between degree of drought resistance and protein contents. According to Irigoyen et al. (1992) and Tahkokorpi et al. (2007) under water stress, the nature of plant species and the type of tissue modulate the concentration of soluble proteins. Under stress, the reduction in protein content may be due to an increase in proline content (Chen et al. 1999). The decreased protein content may be due to the hydrolysis of protein or the inhibition of protein synthesis by oxidative stress leading to the accumulation of proline (Feng et al. 2003). Protein metabolism of the plants has been associated with the adaptation to environmental changes.

2.2 Free Amino Acids

Amino acids (protein, non-protein, and amides) have been reported to accumulate in plants subjected to stress (Mansour 2000). The accumulation of free amino acids accounts for most of the osmotic potential changes in sorghum (Yadav et al. 2005). Accumulation of free amino acids in higher contents has been reported under stress conditions in soybean (Fututoku and Yamada 1981), wheat (Munns and Weir 1981; Hamada 2000), durum wheat (Morgan et al. 1986), olive (Anjuthakur et al. 1998), coconut (Kasturi and Rajagopal 2000), groundnut (Asha and Rao 2002), *Vicia faba* (Ismail and Azooz 2002), *Oryza sativa* (Hsu and Kao 2003) and bell pepper

(Nath et al. 2005). Amino acid accumulation plays a crucial role in drought tolerance through osmotic adjustment in different plants such as *Catharanthus roseus* (Jaleel et al. 2007a) and *Abelmoschus esculentus* (Sankar et al. 2007b).

Chartzoulakis et al. (2002) has observed contrasting results by indicating that no significant increase occurs in total free amino acid content under water stress. According to Greenway and Munns (1980), accumulation of amino acids helps plants to overcome water deficit conditions through osmotic adjustment. Amino acids and other soluble nitrogenous compounds play an essential role in plant metabolism by being the primary product of inorganic nitrogen assimilation and precursors of protein and nucleic acids. Because of the importance of soluble nitrogenous compounds, there has been much interest in the influence of environmental stress on their metabolism. One of the main responses of plants to environmental stress is amino acid accumulation (Aspinall and Paleg 1981). The total soluble sugar and free amino acid content increases under stress at all the growth stages which indicate their possible involvement in osmotic adjustment (Yadav et al. 2005). Osmotic adjustment is one of main mechanisms that alleviates some of the detrimental effects of water stress (Morgan 1984) and has been identified as a chief criterion of yield stability and drought tolerance in several crops including sorghum (Chimenti et al. 2002).

2.3 Proline

Proline is an important osmolyte which plays a pivotal role in membrane stabilization and protein structure besides regulate the accumulation of usable nitrogen. Proline is induced in response to various environmental stresses (Ahmad and Jhon 2005; Ahmad et al. 2006, 2007, 2010b, 2011a, 2012a, b) and occurs in cytosol where it helps in osmotic adjustment. Proline production, during salt or water stresses, probably plays a role in tolerance to these stresses in wheat (Azooz 2002), rice (Hsu and Kao 2003), soybean (Porcel et al. 2004), pea (Ahmad and Jhon 2005; Ahmad et al. 2008b), *Vicia faba* (Ismail and Azooz 2002), mulberry (Ahmad et al. 2006) and mustard (Ahmad 2010). Singh et al. (1972) were probably the first who tried to establish a correlation between proline accumulation and drought resistance in barley cultivars. They showed that drought-resistant cultivars of barley accumulated higher quantities of free proline than the susceptible ones. Depending on the species and the extent of stress, the proline accumulation under abiotic stresses accounts for concentrations of few millimolars (Delauney and Verma 1993; Bohnert and Jensen 1996). Two enzymes pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductases (P5CR) play an important part in proline biosynthetic pathway (Delauney and Verma 1993; Koyro et al. 2012).

According to Nanjo (1999), in higher plants, the osmotic stress stimulated free proline accumulation and is regulated by a rate-limiting enzyme P5CS. Further, the antisense transgenics in *Arabidopsis* with P5CS cDNA show morphological alterations in leaves that were hypersensitive to osmotic stress. In *Arabidopsis*, the proline

deficiency has been found to affect specifically the structural proteins of cell walls, suggesting that proline is an osmoregulator in osmotolerance and morphogenesis in plant (Reddy et al. 2004). Many workers have reported that water deficit induced proline accumulation at vegetative stages in sorghum (Yadav et al. 2005), bell pepper (Nath et al. 2005), *Gossypium hirsutum* (Ronde et al. 1999), wheat (Demir 2000; Hamada 2000) and *Cyamopsis tetragonoloba* (Shubhra and Ooswami 2003). In salt-tolerant alfalfa, proline concentration in the root rapidly doubles, while in the salt-sensitive plants, the response is slow (Petruša and Winicov 1997). Ahmad et al. (1981) reported that salt-tolerant ecotypes of *Agrostis stolonifera* accumulated more proline in response to salinity than salt-sensitive ecotypes. Some other stresses have also been found to be inducing proline accumulation, e.g. chilling in cucumber plant (Feng et al. 2003), chilling and drought in soybean (Heerden and Krüger 2002).

Significant variations in proline content among ten wheat genotypes, under water deficit stress, were reported by Hong-Bo et al. (2006). Sawhney and Singh (2002) reported accumulation of proline under chemical applied desiccation stress in wheat. According to Reddy et al. (2005), proline is known to be involved in reducing photo damage in the thylakoid membranes by scavenging and/or reducing the production of O_2^- . Also, it can be inferred that proline acts as a free radical scavenger and may be more effective in overcoming stress than acting as simple osmolyte (Reddy et al. 2004) as reported in *Catharanthus roseus* (Jaleel et al. 2007a). Proline accumulation in plants is caused not only by the activation of proline biosynthesis, but also by the inactivation of proline degradation, thereby resulting in a decrease in the level of accumulated proline in dehydrated plants like groundnut (Girija et al. 2002). According to Morot-Guadry et al. (2001), reduced leaf water potentials results in manifold increase in proline concentrations and at this stage photosynthesis is known to be quite reduced. Gupta et al. (2000) reported increased proline accumulation, when water stress was followed by simultaneous increase in leaf water potential in chickpea. In water-stressed plants, proline accumulation is maximum at flowering stage and minimum at vegetative stage, with a rapid accumulation in the stem (including sheaths) and roots as compared to the leaves, with the roots being net proline importers (Singh et al. 1973). Overexpression of P5CS in transgenic tobacco plants showed elevated levels of proline and tolerance to salt and drought stress (Kavikishore et al. 1995). Proline accumulation could be used as selection criterion for stress-resistant genotypes. Such studies open a new avenue of research for metabolic engineering in several agriculturally important crop plants for drought resistance (Kavikishore et al. 1995).

2.4 Glycine Betaine

Glycine betaine (GB) is one of the most abundant QACs produced in higher plants like onion (Mansour 1998), rice (Mohanty et al. 2002), sorghum (Yang et al. 2003), mustard (Ahmad 2010) and mulberry (Ahmad et al. 2010b) under stressful environmental conditions. Overexpression of betaine aldehyde dehydrogenase (BADH)

induced by stress, leads to GB synthesis, e.g. in barley (Nakamura et al. 2001) and sunflower (Manivannan et al. 2007). According to Rhodes and Hanson (1993), in higher plants, GB is synthesized in chloroplast from serine via ethanolamine, choline, and betaine aldehyde. Choline monoxygenase (CMO) converts choline to betaine aldehyde, which is then converted to GB by BADH. This pathway has been identified in all GB-accumulating plant species (Weretilnyk et al. 1989; Luo et al. 2012). During dehydration stress, GB localized in chloroplasts showed increase in concentration and plays an important role in chloroplast adjustment and protection of thylakoid membranes which leads to maintenance of photosynthetic efficiency and membrane integrity (Yokoi et al. 2002). Different plants experience GB accumulation in response to different stresses, e.g. sugar beet, spinach, barley, wheat, sorghum, and maize (Hunag et al. 2000; Yang et al. 2003; Zhang et al. 2012). Exogenous application of GB to naturally low-accumulating or non-accumulating plants, may help to ameliorate the adverse effects of environmental stresses (Yang and Lu 2005; Reddy et al. 2013).

Exogenous application of GB ameliorates the adverse effects and improved the growth of temperature-stressed plants, e.g. *Lycopersicon esculentum* (Makela et al. 1998a, b; Park et al. 2006), salt-stressed *Oryza sativa* (Lutts 2000), *Lolium perenne* (Hu et al. 2012) and drought-stressed *Lycopersicon esculentum* (Rezaei et al. 2012), *Carica papaya* (Mahouachi et al. 2012). Foliar application of GB improved the growth and yield of water-stressed plants viz. *Nicotiana tobaccum* (Agboma et al. 1997b), *Gossypium hirsutum* (Gorham et al. 2000), *Glycine max* (Agboma et al. 1997c), *Zea mays* (Agboma et al. 1997a) and *Triticum aestivum* (Aldesuquy et al. 2012). According to Storey and Wyn-Jones (1975), the accumulation of glycine betaine might be serving as an extracellular osmoticum and could be closely correlated with the elevation of osmotic pressure as in *Spartina x townsendii*. According to Kavikishore et al. (1995), glycine betaine can maintain the osmoticum of plant, provided its basal metabolism sustains a high rate of GB synthesis to facilitate osmotic adjustment for water stress tolerance. Under stress, glycine betaine protects membranes, metabolic enzymes, and also stabilizes PSII protein pigment complexes (Papageorgiou and Morata 1995). Yang et al. (2003), while working on sorghum revealed that the level of glycine betaine biosynthesis is dependent on the nature and severity of environmental stresses. However, there are few reports which demonstrated that certain plants do not show such positive correlation with exogenous application of GB (Meek et al. 2003).

3 Proline Metabolizing Enzymes

Several workers have discussed proline metabolism from time to time (Ahmad et al. 2010b, 2012a, b). A number of plants respond to osmotic stress by accumulating high concentration of proline mainly because of stimulated proline biosynthesis (Rudulier et al. 1984). In plants like soybean and moth bean, proline biosynthetic pathway has been well characterized (Delauney and Verma 1993; Hu et al. 1992).

Two proline biosynthetic pathways are present in plants: the glutamate pathway and ornithine pathway; the former appears to play a predominant role under osmotic stress (Rhodes 1987; Ahmad and Sharma 2008; Koyro et al. 2012). In glutamate pathway, enzyme complex pyrroline-5-carboxylate synthetase (P5CS) converts glutamic acid into γ -semialdehyde (GSA). The glutamic acid γ -semialdehyde is converted into pyrroline-5 carboxylic acid (P5C) by non-enzymatic cyclization. The enzyme γ -1-pyrroline-5-carboxylate reductase (P5CR) converts P5C into proline (Treichel 1986; Fujita et al. 2003). The P5C synthetase probably regulates proline synthesis (Bogges et al. 1976). The enzymes γ -glutamyl kinase and γ -glutamyl phosphate reductase form an enzyme complex called P5C synthetase as the resulting product. Glutamic GSA is non-enzymatically converted to γ -1-pyrroline-5-carboxylate (P5C). The conversion of ornithine to proline in plants with P2C or P5C as intermediate has been debated by many workers for long (Adams and Frank 1980; Stewart 1981).

3.1 γ -Glutamyl Kinase

The γ -glutamyl kinase is an important enzyme regulating proline synthesis. The induction of proline accumulation may be due to a stimulated proline synthesis through glutamate pathway involving activity of many enzymes like γ -glutamyl kinase, glutamyl phosphate reductase, and Δ -pyrroline-5-carboxylate reductase (Girija et al. 2002). The enzyme γ -glutamyl kinase belongs to an amino acid kinase family and its predicted three-dimensional model has been constructed on the basis of crystal structures of three related kinases (Fujita et al. 2003). In the glutamate pathway, enzyme γ -glutamyl phosphate reductase converts glutamate to GSA. This product spontaneously cyclizes to (P5C) γ -1-pyrroline-5-carboxylate which is then reduced by NADPH to proline by the enzyme γ -1-pyrroline-5-carboxylate reductase (Fujita et al. 2003). Muthukumarasamy et al. (2000) reported higher γ -glutamyl kinase activity in NaCl-stressed radish. Variation in γ -glutamyl kinase activities has been reported in tomato in different regions (Fujita et al. 2003) and mulberry (Ahmad et al. 2012b).

3.2 Proline Oxidase

Under water stress, a drastic reduction in proline oxidation was observed by Flowers and Hanson (1969) in beans, by Sells and Koeppel (1981) in *Zea mays* and by Ahmad et al. (2010b) in *Morus alba*. Proline is converted to glutamate by proline oxidase. Thus proline oxidase also influences the free proline level. In plant proline biosynthesis, enzyme γ -1-pyrroline-5-carboxylate synthetase is the rate-limiting enzyme and is subjected to feedback inhibition by proline. Under stress conditions, the feedback regulation of P5CS is lost in plants (Hong et al. 2000).

4 Polyamines in Response to Drought Stress

Environmental stress factors like salinity, temperature, drought affects the growth and development of plants globally. Abiotic stress causes an accumulation of excess concentrations of active oxygen species (AOS) resulting in oxidative damage at cellular level. AOS being highly toxic, damages many biomolecules such as DNA, RNA, lipids, and protein (Smirnov 1993; Pourtaghi et al. 2011; Masoumi et al. 2011; Ahmad et al. 2010a, 2011b; Ahmad and Umar 2011). Osmotic imbalance and membrane stability damage are the most frequent symptoms during dehydration stress. Drought is one of the important stresses responsible for crop loss worldwide. Water scarcity threatens the agricultural systems and limits the crop production. To enhance the high tolerance of crops for better productivity, polyamines (putrescine, spermidine, and spermine) play a key role to overcome this problem as these are known to accumulate to a higher concentration under unfavourable conditions (Ahmad et al. 2012c). Polyamines have protective role as scavengers of AOS, consequently, results in an improved adaptation ability and growth of plants under drought stress (Türkan and Demiral 2009). Polyamines are low molecular weight natural compounds present in all living cells that are nontoxic at higher concentration, protecting them from dehydration injury, thereby acts as osmoprotectants and compatible solutes (Reddy et al. 2004; Shao et al. 2005; Ahmad et al. 2012c; Todorova et al. 2013; Lutts et al. 2013).

Putrescine, spermidine, and spermine are polyamines that occur in free form as cations but are often conjugated to micromolecules and also to various macromolecules. Polyamines are implicated in a variety of fundamental and developmental processes of plants, including transcription, RNA modification, protein synthesis, and modulation of enzyme activities (Tonon et al. 2004). It has been observed that spermine, spermidine contents in shoots of *Phaseolus vulgaris* have been found to increase substantially under drought stress alone or in combination with pretreatment of H₂O₂ (Abass and Mohamed 2011). Loka et al. (2013) also reported that spermidine, putrescine, and total polyamines increased significantly in cotton flower and its sun tending leaf under water deficit stress. However, it has been observed that exogenous spermidine and spermine stimulated the growth and reduced the membrane damage in jack pine seedlings (Rajasekaran and Blake 1999). Hence, spermidine may serve as signalling regulator in stress signalling pathway, thus developing stress tolerance mechanism in plants. Furthermore, polyamines have been shown to prevent senescence due to their acid-neutralizing and antioxidant properties and also for their membrane and cell wall stabilizing abilities (Zhao and Yang 2008). Besides, it also plays an important role in regulating the plants defense response to drought stress (Yamaguchi et al. 2007).

The mechanism of drought resistance, through which roots are most likely associated, is drought avoidance. Genotypes comprising deep, coarse roots with capability of branching and penetration, higher root to shoot ratio, elasticity in leaf rolling, early stomatal closure, and high cuticular resistance are reported as main constituents of drought avoidance (Samson et al. 2002; Wang and Yamauchi 2006).

To meet the growing water shortage, it becomes necessary to accomplish drought resistance in plants and needs a deeper understanding of drought resistance mechanisms (Serraj et al. 2011). Significant knowledge in the physiology of drought response can also contribute to plant breeding efforts towards drought resistance cultivars (Serraj et al. 2009). Root traits are known to be critical for increasing yield under soil-related stresses (Serraj et al. 2004; Lynch 2007). Polyamines have been reported in different plant cultivars in response to drought stress (Galston et al. 1997; Bouchereau et al. 1999; Guerrier et al. 2000). Their accumulation in plants causes the removal of ROS resulting in better survival in subsequent stresses, maintaining turgor (Islam et al. 2003) and photosynthetic activity (Galston et al. 1997). It has been well documented that genetic transformation with several polyamine biosynthetic genes (ADC, ODC, SAMDC, SPDC) have been shown to improve significantly the environmental stress tolerances in different plant species (Liu et al. 2007).

Transgenic plants overexpressing ADC, SPD have been reported to endure multiple stresses including drought. Transgenic approaches demonstrate that polyamines play essential roles in stress tolerance and open up the possibility to design new strategies to increase the plant survival in adverse environments. Variation in polyamine contents has been examined significantly in plants exposed to single as well as combined stresses (Capell et al. 2004; Kasukabe et al. 2004; Liu et al. 2007). As compared with stress-intolerant plants, Kasukabe et al. (2004) revealed that stress-tolerant plants showed twofold enhancement in polyamine biosynthesis. Polyamines linked to phospholipids function as membrane surface stabilizers (Wang et al. 2006), protect against stress via stabilizing protein structure to prevent proteins from degradation by conjugating to proteins (Waie and Rajam 2003; Verma and Mishra 2005). Water deficit inhibited the seed germination and seedling growth and indicating that the root zone extensively affects the growth and development, thereby leading to poor productivity or death of the plant (Grzesiak et al. 1996; Dhanda et al. 2004). Similar reports have been found in *Vicia faba* by El-Tayeb (2006). Okçu et al. (2005) investigated the reduction of shoot growth of pea as compared to root growth under water stress. Photosynthesis under drought stress has been observed to inhibit by causing changes in chlorophyll contents, damage photosynthetic apparatus, decreases the activities of Calvin cycle enzymes and ultimately the crop yield (Monakhova and Chernyadev 2002).

In recent years, several reports established that thylakoid-bound polyamines help in the regulation of structure and function of the photosynthetic apparatus (Imai et al. 2004). Zlatev and Yordanov (2004) have observed a considerable inhibition of photosynthesis owing to stomatal closure under drought stress. To deal with this stress, plants instigate reprogramming of transcriptional, post-transcriptional, and metabolite processes that restrict water loss. Application of exogenous polyamines has been reported to improve drought tolerance against the perturbation of biochemical processes (Yang et al. 2007; Alcázar et al. 2010), but mechanisms of their action in modulating physiological phenomena especially in photosynthesis are not fully understood (Bae et al. 2008). Both photosynthetic rate and water-use efficiency in leaves of rice subjected to dehydration stress for 7 days were extensively enhanced by spraying plants with 10 μ M Put, Spd, and Spm solutions, among which

Spm was found to be the most effective (Farooq et al. 2009). Moreover, use of 0.1 mM exogenous Spd has been found to increase the yield of tomato seedling by preventing stomatal closure and stimulating CO₂ uptake during the later period under drought stress (Zhang et al. 2010).

Absorption of polyamines by the seedlings seems to be effective in improving root and shoot growth thereby, balancing the cellular membrane and showed vigorous growth. Therefore, they have been implicated in a wide array of biological processes, growth, development, and abiotic stress responses including drought (Galston et al. 1997; Liu et al. 2007; Do et al. 2013) in plants. Liu et al. (2007) also ascertained that stress-tolerant plants increase their endogenous polyamine levels to a finer extent than sensitive ones. The polyamine overproducing transgenics have greater stress tolerance (Galston et al. 1997) and uses of exogenous polyamines confer protection from many abiotic stresses (Nayyar and Chander 2004). By means of genetic manipulation, modifications in PA biosynthesis resulted in enhanced abiotic stress tolerance. Kasukabe et al. (2004) reported that the transgenic *Arabidopsis*, overexpressed SPDS of *Cucurbita ficifolia* under 35S promoter, showed enhanced drought tolerance.

Capell et al. (2004) found that transgenic rice expressing ADC of *Datura* (stress tolerant) accumulated a much higher level of polyamines than its wild type, hence achieving higher water stress tolerance. Use of biosynthetic inhibitors like DFMA, DFMO, and CHA affects the growth of several crop species by increasing the stress injury and reducing the water content of roots. Liu et al. (2004), Amooaghaie and Moghym (2011) and Amooaghaie (2011) found that the addition of exogenous PAs to water-stressed soybean seedlings retarded growth reduction and inhibited the loss of membrane stabilization. These results clearly indicate that polyamines are involved in stress-adaptive responses and, thereby act as tolerance enhancers in various crops. Under drought stress, osmotic stress induced a greater increase in putriscine and spermidine contents in tolerant species of *Lycopersicon pennellii* than the sensitive *Lycopersicon esculentum* (Santa-Cruz et al. 1997). Likewise, tolerant sugarcane varieties due to greater activity of arginine decarboxylase and ornithine decarboxylase induced a greater increase of putriscine synthesis (Zhang et al. 1996). Further evidence is supported by the fact that the adaptive role of polyamines was higher in terrestrial reeds than in swamp reed ecotypes (Wang et al. 1995).

The transformation of tobacco with S-adenosylmethionine decarboxylase led to increased polyamine biosynthesis and improved drought tolerance (Waie and Rajam 2003). Due to increase of spermine content and the level of other polyamines, yield of soybean plant has been found to grow tremendously; suggesting polyamines an efficient protection against drought-induced stress (Simon-Sarkadi et al. 2006). Putriscine content from transformed soybean also brought an enhancement in poplar (Guerrier et al. 2000) and rape plant (Aziz and Larher 1995). As a result, exogenous polyamines in transgenic plants, during stress periods, might contribute to their greater ability to alleviate stress damage. Spermine content known to prevent senescence has been well studied in different plants (Kaur-Sawhney and Galston 1991; Tiburcio et al. 1994). This induces increase in protein, RNA, and DNA synthesis, reduces RNAase activity and chlorophyll loss (Kaur-Sawhney and Galston 1979) and inhibits specific protease activity of senescing oat leaves (Kaur-Sawhney et al. 1982).

During water stress, the activation of ethylene hormone causes membrane leakage, eventually leads to senescence in plants (Hipkins and Hillman 1985). Ethylene evolution increases the rate of degradation of chlorophyll in *Cucumis sativus* cotyledons (Abeles and Dunn 1989). Here, polyamines impede senescence by inhibiting ethylene production (Apelbaum et al. 1985) or by stabilizing cell membrane against enzymatic degradation and solute leakage (Kaur-Sawhney et al. 1978). To determine the specificity of ROS-driven transcript expression, Gadjev et al. (2006) showed how the accumulation ROS in a variety of subcellular compartments altered gene expression. Their experiments included transgenic plants with certain disorder of ions and enhanced activities of antioxidant enzymes (catalase, cytosolic ascorbate peroxidase, or copper/zinc superoxide dismutase) by exogenous application of oxidative stress-causing agents (methyl viologen, *Alternaria alternata* toxin, 3-aminotriazol, and ozone) to plants. The disruptions in antioxidant enzymes included experiments in which the enzyme activity was reduced or completely abolished. This analysis showed that a majority of the transcripts responding to the stress were altered only in one experiment, i.e. by one species of ROS. The authors considered these transcripts to be “hallmarks for a specific oxidative stress characterized by the chemical identity of the produced ROS and/or the subcellular site of its production” (Gadjev et al. 2006). A bulk of genes that had a change in expression level responded only in one experiment, highlighting that the type of ROS and/or the subcellular location of its generation determines the gene response. The genes that had the largest change in expression were three ethylene-responsive element-binding proteins, supporting a connection between ethylene and singlet oxygen as was previously observed by Danon et al. (2005), who observed that by blocking ethylene production, the cell death that normally occurs in flu mutants upon moving from dark to light was partially blocked. These genome-wide expression inventories have shed light on early response and downstream transcripts, especially altered in their expression, by a particular type of ROS and hinted at transcripts or pathways that serve as integrative points of ROS-mediated plant responses. The identification of ROS sensors and signalling components which are responsible for this remarkable selectivity and specificity of ROS signalling within the cell remains a major challenge.

5 Genetic Engineering and Drought Stress

Tolerance to drought stress is controlled by many genes to improve the yield of crops. In this regard, scientists are under a challenge to develop the drought-tolerant plants that mitigate the water limitation and thereby, accelerate the production to meet the global needs (Ozturk et al. 2002; Yang et al. 2004; Montalvo-Hernández et al. 2008; Macková et al. 2013). During scarcity of water, changes in gene expression patterns have been observed from early response gene (signal transduction, transcription and translation factors) to late response genes, i.e. water transport, osmotic balance, oxidative stress, and damage repair (Ahmad and Prasad 2012a, b;

Yu et al. 2013). Bray (2002) observed an adaptive response in plants as a consequence of such changes. Gene knowledge initially obtained from *Arabidopsis* have been transformed to important food plants to certain extent and have shown to develop stress tolerance against drought condition (Zhang et al. 2004; Rai et al. 2013; Yu et al. 2013; Li et al. 2013). Such transgenics, with several stress inducible genes, resulted in their increased tolerance to drought and other abiotic stresses (Umezawa et al. 2006a; Kumar et al. 2013). Seki et al. (2003) observed the expression pattern of about 1,300 genes in *Arabidopsis* also demonstrated that many stress inducible genes like osmoprotectant, chaperons, and detoxification enzymes directly protect against environmental stress. The ability of responsive genes to survive under these stress conditions has become exceptionally important (Chinnusamy et al. 2007; Shinozaki and Yamaguchi-Shinozaki 2007).

Various metabolites viz., polyamines, carbohydrates, proline, glycine betaine, and trehalose have been shown to be associated with drought resistance and utilizes the related genes to transfer them to sensitive plants that have been evolved through different biochemical pathways (Ahmad et al. 2013). The gene TPS1 encoding trehalose-6-phosphate, crucial for the biosynthesis of trehalose was engineered into tobacco (Romero et al. 1997). It was shown that transgenic plants exhibited drought tolerance by determining the water loss from detached leaves. Simultaneously, transgenic potato plants encoding gene TPS1 also showed higher drought resistance (Yeo et al. 2000). These studies have been correlated with the accumulation of polyols in many plants and animals (Bohnert and Jensen 1996). Polyols act as osmolytes as well as scavengers against water deficit (Bohnert et al. 1995). An enzyme pyrroline-5-carboxylate synthetase for proline synthesis encodes gene P5CS. Overexpression of this gene in transgenic tobacco plants resulted in accumulation of proline, conferring drought resistance and showing better growth over control plants (Kavikishore et al. 1995). This overproduction of proline showed enhancement in root biomass and flower development under dehydration stress (Kavikishore et al. 1995). Same gene has been found to be incorporated into rice, petunia as well as in soybean by Su and Wu (2004), Yamada et al. (2005), de Ronde et al. (2004) respectively. Similarly, the bacterial gene SacB in *Bacillus subtilis*, encoding for levan-sucrase, was used for transformation of *Nicotiana* plants, the resultant transgenics produced, showed accumulation of bacterial fructans and hence better performance under PEG-mediated drought stress over control (Pilon-Smits et al. 1995). Both the genes betA encoding for choline dehydrogenase and betB encoding for betaine dehydrogenase are involved in the biosynthesis of glycine betaine. Holmstrom et al. (1994) showed that transformation of betB gene to tobacco plant caused the accumulation of glycine betaine conferring drought resistance. This build-up of glycine betaine in transgenic plant provides an adaptive response to water stress and can be attributed to protein stabilization, scavenging oxygen radicals as well as regulation of osmotic effects.

Bacterial mannitol phosphate dehydrogenase engineered (mE1D) gene in tobacco plants showed increased biomass due to the accumulation of mannitol in the cytoplasm (Tarczynski et al. 1992, 1993). Similar gene in the egg plant was observed to endure drought stress (Prabhavathi and Rajam 2007). In polyamine