Chapter 2
Drought Tolerance: Role of Organic Osmolytes, Growth Regulators, and Mineral Nutrients

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Contents

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1 Introduction

World population is increasing at an alarming rate and is expected to reach 8.3 billion by 2030 (FAO 2010). In many densely populated developing countries of the world, expansion of arable land has become more difficult as a result of rapid urbanization, industrialization, and water scarcity (Rengasamy 2010). In future, food grain production has to be increased by 57 % so as to ensure sufficient food for the growing population (Wild 2003). In past few years, no doubt, an increase in productivity of certain major crops has been reported but repeating the same success in future for increased food production seems to be difficult.

Among various abiotic stresses, drought is one of the major environmental constraints limiting crop productivity worldwide (Masoumi et al. 2010; Khamssi et al. 2011; Batlang et al. 2013). About 25 % of the world's agricultural land is affected by drought stress (Jajarmi 2009). Changes in global climate have made this situation even more serious (Anand et al. 2003). Water shortage and soil water losses due to changes in environment and excessive land use are challenges to crop production (Xia et al. 2005). Maintaining higher plant productivity under environmental stresses is the main challenge which modern agriculture is facing (Gill and Tuteja 2010). Drought stress affects both source and sink, thereby causing reduction in yield in a time-dependent manner with respect to the severity of stress and plant developmental stage (Blum 1996). Drought stress imposes osmotic stress leading to loss of turgor and oxidative stress through production of reactive oxygen species (ROS) that results in loss of membrane integrity, protein denaturation, and oxidative damage to other biomolecules. As a consequence of such changes, inhibition of photosynthesis, metabolic dysfunction, and damage to cellular structures occurs causing growth perturbances, reducing fertility, and premature senescence (Munns and Tester 2008). Plants respond differently to water deficiency in different periods of their growth. The generative phase and the beginning of flowering are most frequently the period of the greatest sensitivity to water deficit.

2 Adaptations to Drought Stress

Distribution of plant species depend upon the prevailing environmental conditions. Tolerant plants can survive the extreme harsh environmental conditions at which the growth of sensitive ones is negatively influenced (Munns and Tester 2008). Higher tolerance to adverse environmental conditions is because of different stress response mechanisms. Plants adopt different strategies to cope with drought stress. The strategies adopted include escape, avoidance, and tolerance strategy (Levitt 1980; Chaves et al. 2002; Blum 2005; Ahmad and Sharma 2008; Rasool et al. 2013). Ephemeral plants have rapid phenological development, completing their life cycle during a period of adequate moisture and forming dormant seeds before the onset of dry seasons. Ephemerals never really experience the drought stress. In avoidance strategy, plants somehow reduce the impact of stress factor, even though the stress is present in the environment. Avoidance strategy, generally results in maintaining the favorable internal water content either by conserving water which is brought about by closing the stomata, leaf rolling, and heavy pubescence or by increasing the water uptake through development of deep root system and water spenders (Ruiz-Sanchez et al. 2007). On the other hand, in tolerance strategy, plant endures drought without undergoing injury, retaining the capacity of normal growth and development when rehydrated. In tolerance, plants mitigate the stress by maintaining high water potential through accumulation of compatible osmotic solutes. The accumulation of compatible solutes is well regarded as a basic strategy for the protection and survival of plants under abiotic stress conditions (Chen et al. 2007).

Responses of plant species to drought stress depend on several factors including duration and severity of the drought period as well as its inherent tolerance mechanisms. Severe and prolonged periods of drought stress result in oxidative damage due to the overproduction of ROS (Smirnoff 1993). Among various physiological and developmental mechanisms that a plant species adopts to tolerate periods of water deficit, accumulation of osmotically active solutes is the most commonly reported mechanism. By the accumulation of solutes, turgor and turgor-dependent processes are maintained, thereby allowing cell enlargement and plant growth during water stress and stomata to remain partially open and CO_2 assimilation to continue at low water potentials that are otherwise inhibitory (Pugnaire et al. 1994).

Drought is a multidimensional stress, affecting plants at various levels of their organization (Yordanov et al. 2000). Stress-imposed effects are often manifested at phenological, morpho-physiological, biochemical, and molecular levels (Bahrani et al. 2010). Accumulation of compatible organic solutes (Da Costa and Huang 2009), changes in endogenous levels of certain phytohormones (Seki et al. 2007; Dobra et al. 2010), and overexpression of stress-responsive genes (Xiong and Yang 2003; Jaleel et al. 2006) do occur in response to stress. Most of these responses are directly triggered by the changes in water status of the cell (Chaves et al. 2003). In connection to this, plant hormones such as abscisic acid (ABA), jasmonic acid (JA), and salicylic acid (SA) are involved in a complex signal transduction network, thereby coordinating growth and development with plant responses to the changing environment (Jiang and Zhang 2002; Fujita et al. 2006; Szalai et al. 2010). In order to improve plant tolerance to stress, understanding of complete physio-biochemical responses of plant is pivotal (Jaleel et al. 2006; Ahmad and Sharma 2008; Ahmad et al. 2008a, b, 2010a).

3 Osmoregulation and Osmolytes

Osmoregulation/osmotic adjustment is the general response of plants to water stress so that solute content of the cell is increased. In order to maintain turgor and water uptake for normal growth, plants under stress need to maintain internal water potential well below that of soil which is usually acquired by increasing concentration of cell osmotica, either through uptake of solutes from soil solution or by increased synthesis of compatible solutes (Tester and Davenport 2003; Ahmad and Sharma 2008). Cytoplasm accumulates low molecular mass compounds in order to accommodate the ionic balance in the vacuoles (Zhifang and Loescher 2003). These compatible osmotic solutes do not interfere with normal metabolic reactions but rather, they replace water in these reactions (Ahmad and Sharma 2008; Koyro et al. 2012). Accumulation of these osmolytes is proportional to change in external osmolarity (within species-specific limits), thereby protecting cellular structures and maintaining osmotic balance to support continued water influx (Hasegawa et al. 2000). Majority of these compatible osmolytes are organic solutes, while some are essential ions such as K^+ (Yokoi et al. 2002; Ahmad and Sharma 2008). However, the accumulation varies within the genus as well as plant species. Majority of the organic solutes accumulated are sugars (fructose, glucose, trehalose, and raffinose), sugar alcohols (glycerol and methylated inositols) (Bohnert and Jensen 1996), quaternary amino compounds (proline, glycine betaine, proline betaine, tertiary amines), and sulfonium compounds (choline *O*-sulfate, dimethyl sulfonium propironate) (Yokoi et al. 2002). Osmolyte accumulation is mandatory in plants for osmotic adjustment under water limiting conditions, but osmolyte accumulation mainly depends upon water status, crop growth stage, and cultivar (Shao et al. 2006). Due to accumulation of osmolytes, water status of cell and subcellular structures is maintained and membranes as well as proteins are protected from denaturing effects of osmotic stress (Ashraf and Foolad 2007).

3.1 Proline

Proline is an amino acid that plays multifunctional role in stress defense. It is actively involved in osmoregulation, scavenging of free radicals, and as a molecular chaperone for stabilizing protein structure, thus protects plant cells from damaging effects of various environmental stresses (Verbruggen and Hermans 2008; Ahmad and Sharma 2008; Szabados and Savoure 2010; Koyro et al. 2012; de Carvalho et al. 2013). Accumulation of proline in response to various environmental stresses is well documented (Ahmad 2010; Ahmad et al. 2010b, 2011, 2013; Azooz et al. 2011; Katare et al. 2012; Kim and Nam 2013). Water stress-induced increase in proline has been reported in rice (Pandey and Agarwal 1998), *Medicago sativa* (Slama et al. 2011), wheat (Jatav et al. 2012), and *Arabidopsis* (Ju et al. 2013). Besides its role in stress tolerance, accumulation of proline is possibly a useful drought injury sensor in plants (Zlatev and Stotanov 2005). Tolerant plant genotypes show large accumulation of proline which is often correlated with increased stress tolerance (Katare et al. 2012; Ahmad et al. 2012a, b). As a consequence of drought stress, the concentration of proline in plant leaves increases tenfold in leaves of *Lotus japonicus* (Signorelli et al. 2013).

Biosynthetic and catabolic pathways of proline determine its level (Szabados and Savoure 2010). Proline is biosynthesized from glutamate by sequential action of γ-glutamyl kinase (γ-GK), pyrroline-5-carboxylate synthetase (P5CS), pyrroline-5-carboxylate (P5C), and P5C reductase (P5CR) (Hong et al. 2000; Yamada et al. 2005). In most plant species, P5CS is encoded by two genes and P5CR is encoded by one (Armengaud 2004). Proline can also be synthesized by alternative pathway from ornithine, employing ornithine-delta-aminotransferase (d-OAT)

(Miller et al. 2009). Proline synthesized in cytoplasm or chloroplasts is transported to mitochondria where it is catabolized to P5C through the sequential action of proline dehydrogenase (PDH) or proline oxidase (PROX) and P5C is then converted to glutamate by enzyme P5C dehydrogenase (P5CDH).

Proline level in plants is controlled by two important enzymes, PROX and γ-GK (Girija et al. 2002; Ahmad and Sharma 2008; Koyro et al. 2012). Increased proline accumulation during stress may be due to the activation of proline synthesis through glutamate pathway involving γ-GK, glutamyl phosphate reductases, and P5CR enzymes. During stress, increase in activity of γ-GK and decrease in activity of PROX has been reported by Jaleel et al. (2007) in *Catharanthus roseus* and Ahmad et al. (2010b) in *Morus alba*, thereby helping plants to maintain sufficient levels of proline to combat/ameliorate detrimental effects of stress.

Under stress conditions, proline synthesis is enhanced in plants and on recovery from stress, its catabolism is enhanced. It has been reported that overexpression of P5CS in *Nicotiana* and *Petunia* resulted in increased proline accumulation and enhanced salt and drought tolerance (Hong et al. 2000; Yamada et al. 2005). Rice and tobacco plants overexpressing *Arabidopsis* d-OAT has increased proline levels and greater tolerance to stress (Roosens et al. 2002; Qu et al. 2005).

Proline accumulation is a highly regulated process involving a set of protein kinases that is ubiquitous for stress tolerance including drought. These proteins include SNF-related protein kinases 2 (SnRK2s, i.e., SnRK 2.2, SnRK 2.3, and SnRK 2.6) which are activated on exposure to stress (Boudsocq et al. 2004). It has been reported in *Arabidopsis* mutants that ABA-responsive SNF-related protein kinases 2 (SnRK2)-induced ABA-dependent proline accumulation, therefore imparts more tolerance to osmotic stress (Fujii et al. 2011). Another family of SNF-related protein kinases, that enhance proline levels, is SnRK3s. These are calcineurin B-like (CBL) calcium binding proteins also known as CBL-interacting kinases (CIPKs) and overexpression of OsCIPK03 and OsCIPK12 has been reported to increase tolerance of rice to cold and drought by causing significant increase in proline (Xiang et al. 2007). In addition to the abovementioned protein kinases, *Arabidopsis* calcium-dependent protein kinase 6 (CDPK6) (Xu et al. 2010) and soybean calmodulin GmCAM4 (Yoo et al. 2005) have been reported to contribute positively so as to enhance proline content and stress tolerance in *Arabidopsis*, thereby indicating a key role for intracellular calcium signals in proline metabolism. Variety of abiotic stress responses in plants are regulated through MAPK (mitogen-activated protein kinase) cascades and it has been reported that several MAPKs are activated on exposure to various environmental stresses resulting in increased proline accumulation and tolerance as well (Kong et al. 2011; Zhang et al. 2011). Moreover, genetic manipulation of MAPK signaling pathway results in altered plant stress tolerance (Xiong and Yang 2003; Shou et al. 2004a, b). Proline accumulation can be induced by ABA as well as by other stress-related protein kinases. In addition to the abovementioned positive regulation of proline accumulation by several protein kinases, it shall be pointed out that it may also be regulated negatively, e.g., maize protein phosphatases type 2C (PP2C) regulate various processes of development and responses to environmental stress but have been reported to regulate proline accumulation negatively (Liu et al. 2009; Umezawa et al. 2010).

3.2 Glycine Betaine

Glycine betaine (GB) plays an important role in plant tolerance to stress, enzyme activity, membrane integrity, ROS detoxification, and osmotic adjustment. Glycine betaine (*N*,*N*,*N*-trimethylglycine), one among the quaternary ammonium compounds (glycinebetaine,β-alaninebetaine,choline-*O*-sulfate,and3-dimethylsulfoniopropionate and proline betaine), is dipolar and exists as neutral molecule at physiological pH (Le Rudulier et al. 1984) which is known to play protective role in plants under stress (Yang et al. 2003) and its accumulation has positive associations with stress tolerance (Ashraf and Foolad 2007; Kathuria et al. 2009). GB is mainly found in chloroplasts and plays a pivotal role in protection of thylakoid membranes and other key components of photosynthetic machinery such as ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and oxygen evolving complex from stress-induced inactivation and dissociation, thereby maintaining the photosynthetic efficiency (Yokoi et al. 2002). Moreover, it stabilizes the association of the extrinsic PS II complex proteins and maintains the highly ordered state of membranes at nonphysiological temperatures and salt concentrations (Papageorgiou and Murata 1995).

Plants synthesize GB in chloroplast from either glycine or choline via two distinct pathways: (1) dehydrogenation of choline or (2) N-methylation of glycine and enzymes involved in choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH) (Nye et al. 1997). Increase in glycine betaine content under stress conditions has been reported in many plants but the increase may be more pronounced in leaves than in roots, e.g., *Haloxylon recurvum* (Wang and Nil 2000). In most of the crop plants, concentration of naturally accumulated GB may not be sufficient enough to mitigate the deleterious effects of various environmental stresses (Subbarao et al. 2001). Accumulation of GB in response to stress has been reported in many crops, e.g., bean (Gadallah 1999), peanut (Girija et al. 2002), sorghum (Yang et al. 2003), and mustard (Ahmad 2010). But the concentrations accumulated vary with plant species, for example, sorghum accumulates manifold more GB than maize (Murata et al. 1992). Stress-tolerant species accumulate GB in high concentrations than sensitive ones (Agastian et al. 2000). Plants that accumulate low concentration of GB, exogenous application can be a useful tool to reduce the adverse effects of environmental stresses (Makela et al. 1998; Yang and Lu 2005). It has been reported that exogenous application of glycine betaine increased tolerance of tomato (Makela et al. 1998) and rice plants to salt stress (Lutts 2000). In maize, exogenous supply of glycine betaine caused considerable increase in yield, RWC, proline, and antioxidant enzyme activity but reduced lipid peroxidation under normal as well as drought conditions (Lv et al. 2007; Anjum et al. 2012). In addition, water-limited conditions increased the yield and yield components have been reported in several other crops such as rice (Rahman et al. 2002), sunflower (Iqbal et al. 2005), maize (Ali and Ashraf 2011), bean (Abou El-Yazied 2011), and *Triticum aestivum* (Aldesuquy et al. 2012).

However, many important crop plants like maize, potato, tomato, and eggplant lack the capability to synthesize GB in adequate amounts (Zwart et al. 2003). In such cases, both the exogenous application of GB and the introduction, via transgenes, of the GB biosynthetic pathway have become imperative to increase their tolerance to different abiotic stresses. This increased tolerance to abiotic stresses will be useful for understanding the mechanisms through which GB protects plants against abiotic stresses. So far, genetically modified plants containing transgenes for production of GB have faced the limitation of being unable to produce sufficient amounts of glycine betaine required to mitigate the stress, but applying glycine betaine exogenously to plants under stress conditions has gained more attention (Ashraf and Foolad 2007). Introduction and overexpression of choline oxidase (Cod A) gene from *Arthrobacter globiformis* and BADH genes from Spinach/*Atriplex* have been widely used for GB production in transgenic plants. Introduction of Cod A gene in *Arabidopsis thaliana* (Hayashi et al. 1997), *Oryza sativa* (Alia and Murata 1998), and *Lycopersicum esculentum* (Kathuria et al. 2009) and BADH gene in *Triticum aestivum* (Wang et al. 2010) have been reported to increase the tolerance to drought, salinity, and cold stresses by increasing the membrane integrity, enzyme activity, photosynthesis regulating ROS detoxification and also yield.

3.3 Polyamines

Polyamines are group of naturally occurring nitrogenous compounds with aliphatic structure that are implicated in several processes such as growth, development as well as responses to various environmental stresses (Ahmad et al. 2012c). Moreover, polyamines due to their hydrophilic properties are involved in the maintenance of pH and in scavenging of active oxygen compounds, therefore are considered as mediators in protective reactions against different stresses (Kovacs et al. 2010). Polyamines protect membrane from disintegration and alleviate oxidative stress (Groppa and Benavides 2008; Alcazar et al. 2011; Hussain et al. 2011; Ahmad et al. 2012c). Putrescine (PUT), spermidine (SPD), and spermine (SPM) are commonly occurring polyamines in higher plants and may exist free or covalently bound to small molecules such as phenolic compounds as well as to macromolecules such as nucleic acids and proteins in soluble-conjugated or insoluble bound forms (Kusano et al. 2007; Duan et al. 2008). In addition to these, uncommon polyamines like homospermidine, cadaverine, and canavalmine have also been reported in several biological systems including plants. At the physiological pH, polyamines usually exist as cations. This polycationic nature of polyamines is one of their important properties affecting their biological activities (Valero et al. 2002). Polyamine levels vary depending on plant species and the stress duration (Liu et al. 2008). It has been suggested that stress-tolerant plants have increased polyamine levels as compared to sensitive ones and polyamines with higher number of amino groups (SPM and SPD) are more effective in scavenging of ROS than the ones with less number of amino groups (PUT) (Kubis 2008).

Polyamines serve as messengers of stress signals (Liu et al. 2007). As a result of acid neutralizing and antioxidant capability, polyamines show antisenescence, anti-stress effects, and membrane and cell wall stabilizing abilities (Zhao and Yang 2008). Role of polyamines in modulating the defensive responses of plants to various environmental stresses is well documented (Alcazar et al. 2011).

Exogenous application of polyamines has been suggested as an effective approach for enhancing stress tolerance of crops and crop productivity as well. Exogenous application of PUT have been successfully utilized in enhancing plant tolerance to high temperature (Murkowski 2001), cold (Nayyar and Chander 2004), osmotic stress (Liu et al. 2004), salinity (Verma and Mishra 2005), drought (Zeid and Shedeed 2006), heavy metals (Wang et al. 2007), water logging (Arbona et al. 2008), and flooding (Yiu et al. 2009). Furthermore, it has been reported that genetic transformation of plants with genes that code for the enzymes involved in polyamine biosynthesis resulted in increased stress tolerance in various plant species (Liu et al. 2007). Transgenic plants overexpressing these genes show increased tolerance to multiple environmental stresses including salinity, drought, and low and high temperatures. This tolerance to multiple abiotic stresses is of practical importance as plants are often encountered by several concurrent forms of environmental stresses during their life cycle (Wi et al. 2006; Prabhavathi and Rajam 2007; Wen et al. 2008).

Plants deficient in arginine decarboxylase (ADC) and spermidine synthase (SPDS) are unable to synthesize sufficient PUT and SPM, respectively, therefore are sensitive to stress (Yamaguchi et al. 2007; Cuevas et al. 2008), whereas overexpression of ADC leads to greater synthesis of PUT and enhanced tolerance to drought (Alcazar et al. 2010; Alet et al. 2011). Tobacco plants overexpressing ornithine decarboxylase (ODC) showed increased tolerance to salt stress (Kumriaa and Rajam 2002). Moreover, it has been reported that *Arabidopsis* plants overexpressing SPDS showed greater tolerance to drought, salinity, and cold stress (Kasukabe et al. 2004). Scaramagli et al. (2000) reported that increase in insoluble-conjugated PUT levels was closely associated with polyethylene glycol-induced stress acclimation in potato. Liu et al. (2004) reported an increase in the polyamine levels in leaves of drought-tolerant wheat seedlings under osmotic stress, indicating the role of polyamines in facilitating osmotic stress tolerance of wheat seedlings.

4 Growth Regulators

4.1 Abscisic Acid

Growth hormones help plants to adapt to changing environments by mediating growth, development, nutrient allocation, and source/sink transitions (Peleg and Blumwald 2011). ABA, a 15-carbon sesquiterpenoid compound resembling terminal portion of some carotenoid molecules, is synthesized in chloroplast and other plastids by mevalonic acid pathway from 40-carbon precursor, zeaxanthin. Zeaxanthin epoxidase (ZEP), 9-cis-epoxycarotenoid deoxygenase (NCED), alcohol dehydrogenase (ABA2), and abscisic aldehyde oxidase (AAO3) are the main enzymes mediating its biosynthesis.

ABA is involved in many cellular processes like germination, gravitropism, and guard cell-mediated stomatal opening (Levitt 1980). ABA plays an important role in the adaptation of plants to environmental stress. Regulation of water balance and osmotic stress tolerance is a well-established function of ABA (Takahashi et al. 2000; Zhu 2002). Under stress conditions, in addition to its well-established role in closing of stomata, ABA increases the ion influx across root cell membrane and also mediates the greater synthesis and accumulation of active osmotic solutes (e.g., proline, trehalose), thereby helping in bringing osmotic adjustment (Nayyar et al. 2005). ABA accumulates under drought stress and degrades gradually upon removal of stress. Since ABA mediates so many stress responses, starting from the perception of stress signal upto changes in gene expression, which ultimately leads to increased ABA in plants (Zhang et al. 2006). Pospisilova et al. (2005) reported that ABA pretreatment further increased the endogenous ABA level in maize seedling. Presoaking seeds with ABA was reported to significantly enhance the activities of antioxidant enzymes in maize seedlings subjected to water stress (Jiang and Zhang 2002). Similarly, Boominathan et al. (2004) found that relative water content of ABA-treated plants was higher under drought stress. Moreover, exogenous application of ABA under water stress increased the grain weight in susceptible wheat cultivars (Nayyar and Walia 2004).

The role of ABA in plants exposed to drought stress has been well studied. ABA has a potential role in regulating the plant water status and growth. Increased expression of genes encoding enzymes and proteins involved in enhancing drought tolerance has also been attributed to increased ABA (Luan 2002; Zhu 2002). During stress, ABA produced in root is transported to shoot for regulating stomatal movements and leaf growth (Zhang et al. 1987; Zhang and Davies 1990a, b). The pH and ionic conditions in the xylem play an important role in this transport (Wilkinson et al. 1998; Bacon et al. 1998; Hartung et al. 2002). Source of ABA appearing in the xylem during drought has been debated. Some are of the opinion that it comes only from the root (Zhang et al. 1987), while some have reported that ABA comes from both root and leaves. Root-sourced ABA is usually involved in the initial sensing of drought to regulate the stomatal conductance so that the excess water loss may be reduced, but under severe and prolonged stress, leaf water deficit becomes unavoidable and older leaves may wilt because of weak hydraulic link or less control over stomatal conductance, increasing ABA concentration in the xylem (Zhang and Davies 1989a, b). Concentration of ABA in xylem has direct influence on leaf conductance and it has been reported that leaf conductance also responds to the flux of ABA into leaves per unit time, indicating its role in regulation of stomatal movements and due to stress-induced changes in transpiration rate, this role may be marginalized (Jarvis and Davies 1997). However, there are certain reports indicating that stomata responds to xylem ABA concentration rather than its flux, e.g., when leaf conductance has decreased considerably as a result of water stress (Jackson et al. 1995). By following the amount of ABA entering the leaves during the process of ABA-induced stomatal closure, it has been reported that changes in leaf conductance are due to xylem ABA and the rapid metabolism of this xylem-derived ABA in the leaves is very essential in order to prevent its accumulation and stomatal movements to be sensitively regulated (Jia and Zhang 1999).

ABA is important for growth and development of plants under water stress (Zhang and Davies 1990b). But increment in the concentration of xylem ABA, beyond certain limits, can restrict shoot growth (Gowing et al. 1990). However, it should be noted that shoot and root respond differently to ABA levels. Sharp et al. (2000) and Spollen et al. (2000) have reported that better growth of roots under water stress is attributed to higher amounts of ABA accumulated in the roots. Maintenance of better root growth under water deficit has positive association with drought tolerance. ABA has dual role in regulating physiology of plant, i.e., inhibitory as well as stimulatory (Finkelstein et al. 2002). Under stress conditions, when it is accumulated beyond certain limits to help plant survival, it may inhibit processes such as stomatal opening and plant size expansion for quite large time, but under normal conditions, when accumulated concentration is normal, it promotes vegetative growth (Sharp et al. 2000; Spollen et al. 2000) and post-germination development (Cheng et al. 2002). He and Cramer (1996) have reported that accumulation of ABA in lower concentrations increased salt tolerance of *Brassica napus*. Excess accumulation of ABA as a result of salinity has often been reported to induce inhibition of leaf expansion in different species (He and Cramer 1996; Montero et al. 1998).

ABA has an important role in signaling plant responses to drought and salt stresses, thereby triggering the expression of drought-responsive genes. As revealed from sequencing studies, among the various stress-responsive genes that are regulated by ABA, only few have been identified for having any probable physiological functions. In ABA-dependent pathway, synthesis of new proteins may or may not be required (Bray 2002). In such pathways, when the synthesis of new proteins is not required, the presence of ABA-responsive element (ABRE) at the promoter domain of ABA-responsive gene is ubiquitous which upon binding to transcription factor (TF) leads to ABA-induced gene expression, e.g., in *Arabidopsis*, ABA-induced expression of dehydration-responsive gene (rd29B) has two ABREs essential and two transcription factors (bZIP) (Uno et al. 2000). However, when synthesis of proteins is required for the ABA-dependent gene expression, de novo synthesis of new proteins is the prerequisite. These genes do not have any ABREs (Leung and Giraudat 1998; Bray 2002). Expression of some genes may be dependent as well as independent of ABA (Shinozaki and Yamaguchi-Shinozaki 1997), e.g., gene rd29A, which is important for water stress, has two types of regulatory *cis*-elements at its promoter, one ABA-dependent and the other is ABA-independent (Ingram and Bartels 1996; Leung and Giraudat 1998).

Under osmotic stress conditions, transcription levels of ABA biosynthetic genes are upregulated. Increased expression of the ZEP gene, under drought stress, has been reported in roots of *Nicotiana plumbaginifolia* (Audran et al. 2001) and leaves of *Arabidopsis* (Xiong et al. 2002). Moreover, stress-induced overexpression of NCED gene is well documented (Thompson et al. 2000; Tan et al. 2003). Under water stress conditions, accumulation of ABA is accompanied by transient increase in NCED transcript and proteins (Qin and Zeevaart 1999). Overexpression of AtNCED3 is highly induced by dehydration, although other NCED genes also contribute positively but their role is minor (Tan et al. 2003). In addition, transgenic

Arabidopsis plants overexpressing NCED show greater ABA levels and increased desiccation tolerance. Similar results have been reported in transgenic tomato and *Nicotiana plumbaginifolia* (Thompson et al. 2000). Exogenous application of ABA has been reported to induce the expression of NCED gene in ABA-deficient mutants (Xiong et al. 2002).

4.2 Salicylic Acid

Salicylic acid (SA) is an endogenous growth regulator of phenolic nature, actively involved in plant growth, development, and several other physiological processes including germination, fruit ripening, flowering, photosynthesis, stomatal conductance, ion uptake and transport (Shakirova 2007), biogenesis of chloroplast, interaction with other organisms, and protection of plants against multiple environmental stresses such as ozone and ultraviolet radiation (Sharma et al. 1996), salinity (Borsani et al. 2001), freezing (Janda et al. 1999), herbicides (Ananieva et al. 2004), heavy metals (Ahmad et al. 2011), osmotic stress (Shi and Zhu 2008), and drought (Sadeghipour and Aghaei 2012). Salicylic acid (SA) acts as a signal involved in the expression of specific responses in plants to biotic and abiotic stresses.

SA induces systemic acquired resistance (SAR) in plants to different pathogens (Metraux 2001). SA has been reported to induce accumulation of lectins in wheat (Shakirova and Bezrukova 1997), synthesis of heat shock proteins, and activation of protein kinase in tobacco exposed to osmotic stress (Burkhanova et al. 1999; Mikolajczyk et al. 2000), suggesting the role of SA in anti-stress mechanisms. Salicylic acid (SA) has long been considered as signal molecule and is known to reduce the oxidative damage caused by salinity stress (Azooz et al. 2011; Sajid and Aftab 2012) and this ability of SA to produce a protective effect in plants under different abiotic stresses has increased the interest of researchers.

Exogenously applied salicylic acid in plants has been reported to enhance the efficiency of several developmental, physiological, and biochemical processes. It has been reported that exogenous application of SA enhances transpiration rate (Rai et al. 1986), seed germination and yield (Raskin 1992), membrane permeability (Barkosky and Einhellig 1993), growth, and photosynthesis (El-Tayeb 2005). Moreover, exogenously applied SA is involved in the defense against pathogen attack and more recently its role has been widely investigated in both biotic and abiotic stresses (Shi et al. 2006). The role of SA in inducing stress tolerance in plants is well documented, e.g., it enhances the resistance of plants against drought and salt stress (Tari et al. 2002) besides metal stress (Ahmad et al. 2011). SA has been found to induce heat stress tolerance in mustard (Dat et al. 1998), chilling tolerance in maize (Janda et al. 1999), drought tolerance in wheat (Singh and Usha 2003), heavy metal stress tolerance in barley (Metwally et al. 2003), and salinity tolerance in barley (El-Tayeb 2005). Singh and Usha (2003) have reported that under drought, application of salicylic acid to wheat increased the moisture content, total chlorophyll content, nitrate reductase activity, carboxylase activity of Rubisco, superoxide dismutase activity, and dry matter accumulation. Moreover, exogenous application of salicylic acid has been reported to maintain the stability of membranes, enhance photosynthetic rate and K^+/Na^+ ratio (Kaydan et al. 2007), and increases proline content and activities of antioxidant enzymes, thereby mitigating the deleterious effects of stress (Shakirova et al. 2003). Agarwal et al. (2005) have reported that under water stress conditions, application of SA to wheat enhanced the chlorophyll and relative water content while caused considerable reduction in hydrogen peroxide and lipid peroxidation.

There are certain reports indicating that exogenous application of SA does not help in mitigation of drought-induced negative effects (Waseem et al. 2006). Nevertheless, it should be noted that before applying SA, one should have a thorough knowledge about the effective means and methods of application so as to increase the efficiency of exogenously applied SA which is believed to depend on several factors including the species, developmental stage, the manner of application, and the concentration of SA as well (Borsani et al. 2001; Horvath et al. 2007; Joseph et al. 2010). Few other methods which have been reported to protect different plant species against abiotic and biotic stresses include presoaking of the seeds, addition of SA to the hydroponic solutions, tissue culture media and spraying with SA solution (Horvath et al. 2007; Sakhanokho and Kelley 2009). In recent years, tissue culture technique has been extensively utilized for screening and developing stress-tolerant plants. Under in vitro conditions, impact of varying SA concentrations on growth and induction of salt tolerance in *Hibiscus* plants have also been reported (Sakhanokho and Kelley 2009). Moreover, salicylic acid has an affinity to bind with the enzymes like catalase, ascorbate peroxidase, and carbonic anhydrase that are involved in metabolism of free radicals and redox homeostasis (Slaymaker et al. 2002). Any kind of imbalance in this homeostasis triggers the induction of defense responses in plants (Torres et al. 2002; Durrant and Dong 2004). Application of salicylic acid has been reported to increase the activities of the antioxidant enzymes in wheat (Agarwal et al. 2005), *Brassica juncea* (Yusuf et al. 2008), and broad bean (Azooz et al. 2011). Under water stress, salicylic acid-induced activity of antioxidant enzymes has also been reported in *Ctenanthe setosa* (Kadioglu et al. 2010). Moreover, exogenously applied salicylic acid to wheat (Shakirova et al. 2003) and *Brassica juncea* (Yusuf et al. 2008) under salinity and water stress, respectively, alleviated the synthesis and accumulation of proline—a good indication of increased stress tolerance.

4.3 Ethylene

In addition to its usual role in plants, ethylene is also involved in defense against a wide variety of environmental stresses (Bleecker and Kende 2000). Increased ethylene biosynthesis is triggered in plants under various environmental stresses including water stress, thereby suggesting its pivotal role in plant acclimation to stress (Gomez-Cadena et al. 1996). The effects of ethylene, whether transitory or long term, vary considerably among species (Hall and Smith 1995). Although examples of abscission of leaves in response to water deficit stress are compelling, exogenous application of ethylene or the ethylene precursor (1-aminocyclopropane-1-carboxylate) enhances leaf abscission, whereas inhibitors of ethylene synthesis (e.g., aminoethoxyvinylglycine and Ag^+) reduce leaf senescence (Taiz and Zeiger 1998). Ethylene is believed to be involved in stomatal closure but seems rather contradictory. In *Arabidopsis*, ethylene has been reported to inhibit ABA-induced stomatal closure (Tanaka et al. 2005) because H_2O_2-induced stomatal closure results in loss of function in *Arabidopsis* mutants, therefore suggesting an important role of ethylene in guard cell ROS signaling and stomatal closure (Desikan et al. 2005).

Ethylene is biosynthesized from methionine. Two main enzymes involved in the biosynthesis of ethylene are 1-aminocyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase (ACO) that catalyze the conversion of *S*-adenosyl-L-METHIONINE to ACC and the oxidative cleavage of ACC to ethylene, respectively (Zarembinski and Theologis 1994). Normally the activity of ACC synthase (ACS) is very low in tissues that produce less amounts of ethylene, but upon stimulation, its activity is induced rapidly so the reaction catalyzed by this enzyme is considered as rate limiting and regulatory step in induction of ethylene biosynthesis (Kende 1993). Moreover, the activity of this enzyme is also regulated by phosphorylation and dephosphorylation of proteins at the posttranslational level, thereby altering its turnover rate (Chae et al. 2003). In addition to this, induction of genes coding ACS and ACO under changing environmental conditions or endogenous cues, also enhance the ethylene biosynthesis in plants (Wang et al. 2002).

Under stress, plants produce ethylene in greater concentrations and the stress signal perceived triggers cellular responses further downstream. Protein kinases involved in regulation of ethylene synthesis under stress conditions covert these signals into cellular responses, thereby acting as important mediators of signal transduction cascade in cells (Chang and Karin 2001). Studies carried on transgenic tobacco using protein kinase and phosphatase inhibitors reveal that overexpression of NtMEK2 DD causes activation of SIPK, a tobacco MAPK, thereby resulting in increased ethylene production which coincides with the increase in ACS activity, followed by the activation of a subgroup of ACS and ACO genes, suggesting the role of MAPK in activation of ACS and posttranscriptional regulation (Kim et al. 2003).

Stress signaling cascade largely depends on transcription factors and their expression levels have direct bearing with plant adaptation to adverse environment (Schenk et al. 2000). Among several transcription factors that have been identified, ethylene response factors (ERFs) are known to be important (Zhang et al. 2009). ERFs are implicated in biotic and abiotic stress-induced transcription (Riechmann and Meyerowitz 1998; Hu et al. 2008) but among the various ERF genes, only a few are known to mediate responses to abiotic stress (El-Sharkawy et al. 2009). ERFs are DNA binding proteins that are specific to plants (Hao et al. 1998). It has been reported that ERF family genes are implicated in several stress responses like high salinity (Dubouzet et al. 2003), freezing (Yang et al. 2005), and drought (Yamaguchi-Shinozaki and Shinozaki 2006). Overexpression of the tobacco transcription factor NtERF1 leads to increased salt tolerance (Huang et al. 2004). *Arabidopsis thaliana* overexpressing *Helianthus annus* transcription factor Hahb-4 exhibits a characteristic phenotype essential for tolerance to water stress. Moreover this transcription factor is involved in ethylene-mediated signaling pathways and its expression is regulated by water availability (Manavella et al. 2006).

Particular type of ethylene-responsive transcription factor induces/enhances tolerance to stress in particular plant species. For example, expression of tomato ERF5 has been reported to impart regulation of stress responses in *Arabidopsis thaliana* at transcriptional level (Chuang et al. 2010). In transgenic tomato plants, overexpression of SlERF5 resulted in high tolerance to drought and salt stress which was accompanied by increased relative water content (Pan et al. 2012). Zhang et al. (2010) showed that transgenic rice overexpressing JERF3 exhibited better drought and osmotic stress tolerance which is reflected in increase in the contents of soluble sugars and proline. In addition, overexpression of JERF3 led to the upregulated expression of two OsP5CS genes in response to drought stress and also activated the expression of stress-responsive genes, including WCOR413, OsEnol, and OsSPDS2 under normal conditions.

5 Mineral Nutrients

5.1 Calcium

Calcium is one of the macronutrients required for normal growth and development of plants. It is implicated in regulating a number of fundamental cellular processes involving cytoplasmic streaming, thigmotropism, gravitropism, cell division, cell elongation, cell differentiation, cell polarity, photomorphogenesis, plant defense, and stress responses. As a divalent cation (Ca^{2+}), it acts as an intracellular messenger in the cytosol (Marschner 1995; Nobuhiro and Mittler 2006), has structural role in the cell wall and cell membranes and as a counter cation for anions in the vacuoles (White and Broadley 2003). Calcium provides strong structural rigidity to cells by forming cross-links within the pectin polysaccharides (Easterwood 2002). In plants, Ca^{2+} is usually stored as calcium oxalate crystals in plastids. Better plant growth, the structural integrity of stems, and the quality of fruit produced are strongly coupled to Ca^{2+} availability. Calcium is also known to act as an activator of many enzymes like ATPase, phospholipases, amylase, and succinate dehydrogenase. Studies carried on *Phaseolus vulgaris* L. suggested that Ca^{2+} is associated with stomatal closure, decrease of hydraulic conductivity, sap flow, leaf dry weight, leaf K^+ and Mg^{2+} concentrations, and inhibition of CO_2 assimilation (Cabot et al. 2009).

In the absence of a stimulus, the plant cells maintain low cytosolic Ca^{2+} concentration (100 nM), but in response to an external stimuli including light, touch, wind, hormones, and biotic and abiotic stresses, the cytosolic concentration of calcium is rapidly elevated via an increased Ca^{2+} influx due to the release of Ca^{2+} by Ca^{2+} channels from endoplasmic reticulum, plasma membrane, and other cell organelles and then quickly returns to the normal level by Ca^{2+} efflux through Ca^{2+}/H^+ antiporter and Ca^{2+} pumps (Bush 1995). One of the most common signaling pathways causing increase in concentration of calcium in cytosol in response to external stimulus is the phospholipase C enzyme-mediated pathway. Enzyme phospholipase C is activated after the signal perception by cell surface receptors including G protein-coupled receptors and receptor tyrosine kinases. Activated phospholipase C hydrolyzes the membrane phospholipid PIP2 to form 1,4,5-trisphosphate (IP3) and diacylglycerol (DAG) that act as secondary messengers. DAG is also involved in the activation of protein kinase C enzyme, while IP3 after diffusing into the endoplasmic reticulum binds to receptor (IP3 receptor), a Ca^{2+} channel, thus releasing Ca^{2+} from the endoplasmic reticulum. This stimulus-specific increase in cytoplasmic calcium is called as calcium signature (Evans et al. 2001). Current evidences indicate that apart from IP3, cyclic ADP ribose (cADPR) also influences the activity of Ca^{2+} channels and plays an important role in elevating calcium levels in cytosol. The transduction of Ca^{2+} signals into various biochemical and morphological responses is a very complex and specific phenomena that is controlled by several factors. Specific signal induces a specific Ca^{2+} signature in different cell types (Kiegle et al. 2000). Furthermore, in plant cells, Ca^{2+} acts as a secondary messenger, thereby coupling a range of extracellular stimuli with intracellular responses (Sarwat et al. 2013). The specificity of eliciting appropriate physiological response is due to the temporal and spatial changes of Ca^{2+} and the extent of its amplitude as well (McAnish and Hetherington 1998; Allen et al. 1999), while the nature and intensity of stimulus is specified by amplitude and duration of Ca^{2+} transients. Ca^{2+} binding proteins (sensors) help in decoding and transducing the calcium signatures by activating specific targets and pathways (Shao et al. 2008b; Ahmad et al. 2012d).

Increase in the concentration of cytosolic calcium leads to the activation of various Ca^{2+} sensor proteins that convert these signals into a wide variety of biochemical changes. Different Ca^{2+} sensors that exist in higher plants include calmodulin (CaM), calcium-dependent protein kinases (CDPK), and CBL protein which play a crucial role in abiotic stress signaling in plants (Das and Pandey 2010; Ahmad et al. 2012d). Binding of Ca^{2+} to the sensor molecule induces conformational change in the sensor molecule and exposes the hydrophobic pockets, thereby facilitating interactions of the sensor protein with a variety of target proteins. These kinases are reported to play an important role in inhibition of autophosphorylation and enhancing substrate phosphorylation (Patil et al. 1995). Calcium and Ca^{2+} sensor calmodulin (CaM) regulate the expression of structural and regulatory genes by acting on transcription factors (TFs), thereby modulating their activity or Ca^{2+}-loaded CaM may directly bind to promoter sequences to regulate gene expression, thus, indicating the role of CaM as a transcription factor. Ca^{2+}/CaM complex may bind directly with transcription factors so as to regulate their DNA binding affinities or indirectly by associating with complex transcriptional machinery that consists of Ca^{2+}/CaM complex, transcription factor binding protein (TFBP), and transcription factors. TFBP serves as a bridge between Ca^{2+}/CaM and TFs, while Ca^{2+}/CaM complex regulates gene expression by modulating the phosphorylation status of TFs through the activity of CaM binding protein kinase and protein phosphatase (Kim et al. 2009). Moreover, plant species overexpressing these protein kinases are more tolerant to drought, salinity, and cold stresses. In transgenic rice, overexpression of OsCDPK7 enhanced the induction of stress-responsive genes, resulting in increased tolerance to stress (Saijo et al. 2000). In *Arabidopsis*, it has been reported that under drought and salt stress conditions, expression of AtCPK10 and AtCPK11 is induced indicating their possible role in osmotic stress signaling (Urao et al. 1994). *Arabidopsis* plants overexpressing the CBL5 protein showed enhanced tolerance to high salt or drought stress (Cheong et al. 2010).

Ca^{2+} supplementation under drought stress have been reported to enhance water conservation and improve the hydrophobicity of cellular membranes while lowering its permeability through its interaction with the phosphates and proteins in cellular membranes, thus strengthening their stability (Shao et al. 2008a). Ca^{2+} protects membranes from hydration, improves the cohesion of cell walls, maintains protoplasm viscosity, and enhances cellular dehydration resistance. Thus, Ca^{2+} can stabilize plant cells and enhance drought tolerance through its direct effects on structural basis of the plant (Shao et al. 2008b; Ma et al. 2009). Schaberg et al. (2011) reported that addition of calcium increased the concentrations of amino acids, alanine and γ-aminobutyric acid (GABA) and the polyamines, putrescine (PUT) and spermidine (SPD) as well as chlorophyll content in red spruce (*Picea rubens*) under low temperature stress. Abdel-Basset (1998) reported that under drought stress, calcium supplementation caused significant increase in fresh weight, dry weight, chlorophyll, and relative water content, while reduced the membrane leakage in *Vicia faba*.

5.2 Potassium

Potassium (K) is an important macronutrient required for growth and development of plants both under normal and stress conditions (Agarwal et al. 2009). Potassium is actively involved in many basic biochemical and physiological functions such as osmoregulation, enzyme activation, and stomatal movements reducing excess uptake of ions such as Na and Fe in saline soils (Epstein and Bloom 2005; Amtmann et al. 2008; Ahmad et al. 2012c; Wang et al. 2013). Potassium is implicated in transport of inorganic anions and metabolites. Moreover, it maintains the transmembrane voltage gradients for cytoplasmic pH homeostasis (White and Karley 2010).

Potassium deficiency causes considerable reduction in leaf area, photosynthesis, and nitrogen metabolism, which ultimately result in reduced plant growth (Ebelhar and Varsa 2000). As a result of reduction in production of photoassimilates due to potassium deficiency, the sink tissues also get restricted supply of photoassimilates. Due to this reduction in partitioning of photoassimilates, the quantity as well as quality of the yield gets affected (Pettigrew and Meredith 1997; Meille and Pellerin 2004). The very first response of plants to potassium deficiency is the reduction in growth rate, and later beginning of chlorosis and necrosis in older leaves (Mengel and Kirkby 2001). Potassium deficiency induces disturbances in turgor, stomatal opening, water relations, and photosynthesis (Marschner 1995; Mengel and Kirkby 2001). Stomatal regulation largely depends upon the distribution of potassium in epidermal cells, guard cells, and leaf apoplast (Shabala et al. 2002). Supplying sufficient potassium levels has been reported to help plants to maintain higher leaf water potential, turgor potential, relative water content, and lower osmotic potential in several crop plants like wheat (Sen Gupta et al. 1989), maize (Premachandra et al. 1991), and *Vigna radiata* (Nandwal et al. 1998) grown under water stress.

Plants suffering from environmental stresses like drought have a larger internal requirement for K and deficiency of potassium results in overproduction of ROS (Cakmak 2005). Potassium has been reported to reduce the detrimental effects of ROS by enhancing photosynthetic electron transport while inhibiting the activity of membrane bound NAD(P)H oxidases.

Potassium promotes root growth under water stress conditions (Sangakkara et al. 1996) because potassium and magnesium enhances transport of sucrose to developing root for their normal growth and development. Moreover, it also enhances the ion uptake, as potassium itself is one among the main constituents of the phloem sap, thus maintaining the osmotica and, thereby mitigating the adverse effects of moisture stress in plants by increasing the translocation and maintaining the water balance within the plants (Jeschke et al. 1997; Walker et al. 1998). In addition to this, activity of several enzymes which are involved in drought resistance is enhanced by the supplementation of appropriate potassium and its adequate concentration in cytoplasm as well (Kant and Kafkafi 2002). Plants with appropriate K levels have enhanced membrane fluidity because potassium maintains the higher ratio of unsaturated to saturated fatty acids in membranes (Wilkinson et al. 2001). Moreover, potassium supplementation has been reported to increase the synthesis of many organic solutes like proline, free sugars, and free amino acids, under normal and water stress conditions, which contribute to osmotic adjustment. Under normal and water stress conditions, potassium-induced increase in proline has been reported in rice (Pandey et al. 2004) and wheat (Jatav et al. 2012). Potassium-induced increase in free sugars under water stress has been reported in rice by Pandey et al. (2004). In sorghum, potassium has been reported to overcome the ill effects of water stress and maintains the higher tissue water content (Umar et al. 1993). Plants accumulate osmolytes under stress conditions, thereby reducing osmotic potential and maintaining RWC (Gupta et al. 2000). Drought-induced proline accumulation and hydrolysis of macromolecules into simpler mono, disaccharides, and amino acids may lead to accumulation of osmotica.

Evidences are emerging from the molecular studies that potassium might be involved in regulating the plant stress responses (Ashley et al. 2006; Wang and Wu 2010). Low potassium status triggers several signaling cascades such as up regulation of K transporters, synthesis of ROS, and phytohormones including jasmonic acid (JA) and ethylene. In addition to up regulation of transport proteins, potassium deficiency also triggers several other responses in roots. All these strategies enable plant species to adapt with the changing environmental conditions. It has been reported that increase in ROS and phytohormone levels is accompanied by transient increase in transcripts coding potassium transporters and channels, suggesting possible regulatory role of potassium in plant stress responses (Cheong et al. 2007; Jung et al. 2009). Cheong et al. (2007) suggested that in K-deficient plants and drought-induced ABA may trigger Ca flow which acts as secondary messenger and initiates the uptake of K by roots and the regulation of stomatal guard cells. Ca signaling, which regulates leaf transpiration and root K uptake, involves membrane localized Ca sensor-interacting proteins. Jung et al. (2009) reported the increased ethylene and ROS production in K-deficient plants. This phytohormone signal is important for changes in root morphology and plant tolerance to low K supply.

6 Conclusion and Future Perspectives

Abiotic stresses cause considerable reduction in yield especially in arid and semi-arid regions of the globe. Around 40–45 % of the agricultural land affected by drought stress and global climate change has made the problem even graver by causing reduction in arable land. Drought stress causes alterations in normal plant metabolism. Exposure to environmental stresses triggers the generation of ROS in different cellular organelles, especially chloroplasts and mitochondria. ROS cause disturbances in normal functioning of the cell by affecting several cellular macromolecules including DNA, lipids, proteins, carbohydrates, and their overproduction which ultimately can lead to cell death. In order to mitigate the stress, plants have evolved many adaptive mechanisms. Greater synthesis of various organic osmolytes such as proline, glycine betaine, free sugars, and polyols is considered as good indication of greater tolerance to stress. To ameliorate the damaging effects of ROS, plants are well equipped with enzymatic as well as nonenzymatic antioxidants. Positive effects of organic osmoprotectants and antioxidative defense system in combating stress-induced damage are well established. Osmolytes are known to play a role in osmotic adjustment, thereby maintaining the internal water content of cell, besides protecting subcellular structures. Moreover, synthesis of certain growth regulators is upregulated in plants under stress. Growth regulators act as signal molecules and play pivotal role in sensing and combating with the incoming stress. Proper mineral nutrition can enhance the performance of plants, both under normal and stressed conditions by preventing the oxidation of polyunsaturated fatty acids (PUFA), thereby preventing membrane leakage and excessive formation of free radicals.

The biggest challenge to plant scientists is to develop stress-tolerant plant varieties. In order to enhance the stress tolerance, researchers have to look for defined sets of markers. In connection to this, genetic manipulations in important crops are gaining pace, but it should be kept in mind that the genes incorporated should not only enhance the tolerance at certain plant growth stages but at the whole plant level as well. Genomics, proteomics, and ionomics have been contributory towards the understanding of various plant responses to abiotic stresses. These techniques will help to identify unknown links, cross talk across different stress signaling pathways that could be exploited to enhance the plant tolerance to particular abiotic stress. Keeping global climate change in mind, model plants should be developed for increasing the understanding of tolerance mechanisms and interactions with increasing concentration of CO_2 so as to assess them as suitable future crop plants. At the same time, lack of thorough understanding of drought tolerance mechanisms at genetic and physiological levels and their contributions towards the stress tolerance have been a major limitation to develop drought-tolerant plants.

Our present knowledge about causes and consequences of water stress has still many dark areas and we should enhance our efforts towards these issues. Plant biotechnologists have so far been successful to some extent in developing stress-tolerant varieties but there is much more which still remains to be done.

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