Chapter 9
Importance of Protective Compounds in Stress Tolerance

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1 Introduction

Environmental conditions determine plant growth and development. Optimal growth of plants is adversely affected by abiotic stresses such as drought and salt stress (Kintisch 2009). Soil salinity and drought stress result in crop loss affecting about 40 % of the arable lands across the globe (Wang et al. 2003). During last decade, increase in environmental stresses and global warming result in the necessity of developing new crop cultivars that are stress tolerant. Developing tolerant lines for salt and drought stress was more important and convenient owing to their already elaborated tolerance mechanisms reported in various plants (Gregory et al. 2005). Physiological responses to drought, cold, and salt stress are similar resulting in impaired plant growth, altered photosynthetic activity via reduction in the dark reaction of photosynthesis, accumulation of reactive oxygen species (ROS), alterations in ion transport and compartmentalization, faults in the osmotic responses of the cell (Schulze et al. 2002) and changes in metabolite profiles (Shulaev et al. 2008). Low-molecular-weight organic compounds are considered to have protective functions and are accumulated as a consequence of osmotic stress without any metabolic alterations (Bartels and Sunkar 2005). Compatible solutes include organic compounds that serve as tools for osmotic adjustment and protect membranes and proteins from denaturation which reduce impacts of drought stress on plants. They also alleviate ion toxicity resulting from salt stress and maintain ion imbalance. This chapter will focus on importance of osmoprotective compounds for the acclimation to extreme environmental conditions and their role in impeding deleterious effects of environmental stresses.

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2 Osmolytes

Osmolytes are considered as compatible solutes which contribute to cell turgor, protect cellular structures, and alleviate ion toxicity. These solutes mediate osmotic adjustment under drought stress by stabilizing internal potential and maintain osmotic balance (Parida and Das 2005). These protective compounds comprise mainly of amino acids (Pro), quaternary amino acid compounds (alanine betaine, glycine betaine, and proline betaine), amines (polyamines), sugars (glucose, fructose, sucrose, trehalose, raffinose, and fructans), sugar alcohols (mannitol, glycerol, and sorbitol), and sulfonium compounds (choline-*O*-sulfate, dimethylsulfoniopropionate) (Parida and Das 2005; Shulaev et al. 2008; Ahmad and Sharma 2008; Koyro et al. 2012; Dedemo et al. 2013). However, there are contradictory reports suggesting that osmolytes may have alternative protective functions. However, lower concentrations of organic osmolytes in several halophytes indicate that these compounds might not be important for osmotic adjustment (Gagneul et al. 2007). This statement is supported by transgenic tobacco which produces proline at high rates but does not make any osmotic adjustment compared to control tobacco plants, under salt and drought stress (Kishor et al. 1995). In addition, osmoprotectants may also serve in stabilization of redox balance, maintenance of proper protein folding and signaling (Rosgen 2007).

High salinity or dehydration can alter structure of proteins and modify the proteins followed by their denaturation and finally accelerated degradation. However, osmolytes can protect proteins from aggregation or degradation by preserving their native conformations, folding of proteins, and improve their thermodynamic stability so that they can function under stress conditions (Bolen and Baskakov 2001; Street et al. 2006). In addition, osmoprotective compounds have roles in the adaptation process to extreme environmental conditions (Rontein et al. 2002). For instance, high levels of sugars or polyols, quaternary amino acid compounds such as GB, alanine betaine, and proline are produced by halophyte species (Arbona et al. 2010; Lugan et al. 2010). Salt tolerance of halophytic *Limonium* species are related to accumulation of high level of quaternary ammonium compounds such as choline-O-sulfate, GB, and alanine betaine (Hanson et al. 1991). Composition and concentration of these solutes in plants can vary considerably, depending on species and type of the environmental stress (Yancey 2005; Sanchez et al. 2008; Dedemo et al. 2013). For instance, GB is dominant in *Plumbaginaceae* species adapted to dry environments, alanine betaine is apparently more typical in species growing on saline soils, and proline betaine has been detected in plants adapted to arid environments (Hanson et al. 1994; Majumder et al. 2010).

Osmoprotectants are significant for salt and drought stress tolerance in cereals (Garcia et al. 1997; Reguera et al. 2012). High levels of proline and sugar in drought and salt tolerant rice varieties suggest that these protective compounds can contribute to stress tolerance of rice (Roychoudhury et al. 2008). Similarly, glucose, fructose, sucrose, fructan, proline and quaternary ammonium compounds are accumulated in wheat under drought conditions (Bowne et al. 2012; Maevskaya and Nikolaeva 2013).

It has been shown that the accumulation is well correlated with drought tolerance of wheat (Kerepesi et al. 1998; Bajji et al. 2001). Increase in both proline and GB levels of sorghum have been recorded upon water deficit and high salt concentration (Wood et al. 1996; Chen and Murata 2011). However, an accumulation of proline in tolerant sorghum does not contribute to its drought tolerance (Premachandra et al. 1995). Like other extremophile plants, halophytic wild rice *Porteresia coarctata* Roxb. is known to synthesize and accumulate myo-inositol and pinitol for combating saline stress (Sengupta and Majumder 2009; Krasensky and Jonak 2012). Strong correlation between pinitol accumulation and drought tolerance in response to low water potential has been addressed in several tropical legume species (Ford 1984). Several classes of osmolytes such as amines, amino acids, and carbohydrates having roles in salt and drought tolerance of plants will be covenanted individually in the following part.

2.1 Amines

2.1.1 Polyamines

Polyamines (PAs) are low-molecular-weight polycations found in all living organisms and known to be essential for their growth and development. PA levels can be changed by abiotic stresses, such as drought, salinity, and cold (Ahmad et al. 2012a). In addition, a positive correlation between high PA levels and stress tolerance has been recorded (Kovacs et al. 2010; Quinet et al. 2010; Alcazar et al. 2011).

Putrescine (Put), spermidine (Spd), and spermine (Spm) are the most common PAs in higher plants (Ahmad et al. 2012a). PAs are synthesized from arginine and ornithine by arginine decarboxylase (ADC) and ornithine decarboxylase (ODC). Putrescine is formed by conversion of agmatine, synthesized from arginine. Spermidine and spermine are synthesized from putrescine by the transfer of aminoporply groups from decarboxylated *S*-adenosylmethionine (dSAM) via Spd and Spm synthases. dSAM is formed by conversion of SAM via a reaction catalyzed by SAM decarboxylase. On the other hand, diamine oxidases (DAO) and polyamine oxidases (PAO) are main PA catabolic enzymes. DOA catalyzes the oxidation of Put to 4-aminobutanal, NH_3, and H_2O_2, while PAO oxidize only higher PAs, such as Spd and Spm.

Protection of membranes and alleviation in oxidative stress are the two functions of PAs (Alcazar et al. 2011; Hussain et al. 2011; Ahmad et al. 2012a) but their functions in stress tolerance are not well understood. Positive role of PAs in stress tolerance has been shown by studies in transgenic plants and various mutant varieties. Putrescine levels of *ADC1* or *ADC2*-deficit mutants which are hypersensitive to stress are lower than wild type (Urano et al. 2004; Cuevas et al. 2008), whereas putrescine levels under drought and freezing tolerance enhance by ADC overexpression (Capell et al. 2004; Alcazar et al. 2010; Alet et al. 2011). Similarly, drought, salt, and cold tolerance of *Arabidopsis* plants increase due to enhanced spermidine content resulting from Spd synthase overexpression (Kasukabe et al. 2004).

Furthermore, tolerance of tobacco plants to salt stress and polyamine levels has been increased by introduction of ODC gene from mouse (Kumriaa and Rajam 2002). In addition, plants turn out to be very sensitive to salinity stress because of Spm synthase deficiency (Yamaguchi et al. 2006).

The application of polyamines (PAs) is also an effective approach for enhancing stress tolerance in plants (Shi et al. 2010). Exogenous application of 0.4 M Spm to soybean plants ameliorates osmotic stress effects by increasing catalase, superoxide dismutase, peroxidase, and polyphenol oxidase activities and modulating levels of plant hormones, ABA and jasmonic acid (Radhakrishnan and Lee 2013). Shu et al. (2013) have examined effects of Spm on chlorophyll fluorescence, antioxidant system, and ultrastructure of chloroplasts in *Cucumis sativus* L. under salt stress. They have found that Spm has reversed effects of salt stress on photosynthetic apparatus. In addition, application of Spm significantly increases superoxide dismutase, peroxidase, and ascorbate peroxidase activities in the chloroplasts thriving under saline conditions. Hence, salt stress in *C. sativus* plants has been mitigated by Spm application.

Exogenous spermidine (Spd) applied to tomato (*Solanum lycopersicum*) cultivars decreases growth and induces increase in free amino acids, ammonium (NH_4^+) contents, and NADH-dependent glutamate dehydrogenase (NADH-GDH) activities. They have suggested that exogenous Spd treatment alleviates disturbances in nitrogen metabolism resulted from salinity-alkalinity stress (Zhang et al. 2013).

2.1.2 Glycine Betaine

Glycine betaine (GB) is the quaternary ammonium compound and methylated derivative of glycine. Along with other quaternary ammonium compounds like -alanine betaine, proline betaine, choline-*O*-sulfate, hydroxyproline betaine, and pipecolate betaine they function as effective compatible osmolytes in halophytes (Ashraf and Harris 2004; Chen and Murata 2008, 2011). Different stress conditions such as osmotic stress (Hanson and Nelsen 1978), salinity (Hanson et al. 1991), and drought (Guo et al. 2009) can induce GB accumulation in plants. The beneficial effects of GB accumulation regarding salt and osmotic stress tolerance have been demonstrated in a number of engineered GB-accumulating plants, including tobacco (Zhang et al. 2008), tomato (Park et al. 2004, 2007), and rice (Chen and Murata 2008). These compounds confer resistance mainly by protecting photosynthetic activity through the maintenance of Rubisco activity and PSII activity (Yang et al. 2008).

Plants are usually very sensitive to environmental stress during reproduction. GB was shown to have a particularly important protective effect on reproductive organs, such as inflorescence apices and flowers during drought and cold stress (Chen and Murata 2008; Sakamoto and Murata 2000). Engineering of GB accumulation has reduced chilling damage on tomato flowers, leading to a 10–30 % increase in fruit production (Park et al. 2004). He et al. (2013) have introduced two genes, glycine sarcosine methyltransferase gene (*ApGSMT2*) and dimethylglycine methyltransferase gene (*ApDMT2*), from the bacterium *Aphanothece halophytica* to maize so that the engineered plants synthesize more GB than control plants. Thus transgenic maize could be drought tolerant by co-expression of *ApGSMT2* and *ApDMT2*. These data confirm that GB is an osmoprotective compound, which can therefore be explored to improve tolerance to salinity and probably to drought and cold stress.

Activation and protection of the ROS detoxification system is another key component of stress tolerance (Moradi and Ismail 2007). Osmoprotective compounds can scavenge ROS directly, or contribute to the protection of the enzymes involved in the antioxidant system. Increase in antioxidant enzymes activities and alleviation of oxidative damages due to abiotic stresses have been reported in different plant species subjected to exogenous applications of GB (Nawaz and Ashraf 2010; Ahmad et al. 2013). For instance, after exogenous GB applications to *Carapa guianensis* plants, ascorbate peroxidase and catalase activities increase whereas lipid peroxidation has been prevented under water stress (Cruz et al. 2013). Foliar application of 50 mM GB to maize plants reduces adverse effects of salt stress by improving proline, Ca^{2+}, and K^{+} levels and maintaining membrane permeability (Kaya et al. 2013).

2.2 Amino Acids

2.2.1 Proline

The imino acid proline, a common denominator of many stress responses, is accumulated during diverse abiotic and biotic stresses (Kavi Kishor et al. 2005; Koca et al. 2007; Ahmad and Sharma 2008; Ahmad et al. 2012b) such as high salinity (Ben Hassine et al. 2008), drought (Choudhary et al. 2005), oxidative stress (Yang et al. 2009), and intense irradiation (Jan et al. 2012a, b). In plants, proline is synthesized from glutamate in the cytosol and probably also in the chloroplast by delta-1-pyrroline-5-carboxylate synthetase (P5CS) and P5C reductase (P5CR). P5CS produces glutamate semialdehyde, which is unstable and is immediately converted to pyrroline-5-carboxylate (P5C). P5CR reduces P5C to proline, a reaction that takes place in the cytosol and according to biochemical data also in the chloroplast (Szabados and Savoure 2010; Koyro et al. 2012).

Proline catabolism occurs in the inner-mitochondrial membrane of all eukaryotes. Proline degradation provides electrons and glutamate for mitochondrial usage. Proline dehydrogenase (ProDH), an FAD enzyme localized to the inner-mitochondrial membrane, catalyzes the first oxidizing step of proline to P5C and meanwhile delivers electrons to the mitochondrial electron transport chain (Kiyosue et al. 1996). P5C is further oxidized to glutamate or transported back to the cytosol for proline re-synthesis by the proline cycle (Deuschle et al. 2004; Miller et al. 2009). Proline accumulation during stress protects cellular structures and stabilizes enzymes owing to its antioxidant potential (Kavi Kishor et al. 2005; Mishra and Dubey 2006; Sharma and Dubey 2005). Proline also maintains redox balance, preserve energy source for the stress recovery and functions as protein precursor (Hoque et al. 2008; Islam et al. 2009; Szekely et al. 2008). In addition, proline synthesis in the chloroplast may allow an efficient oxidation of photosynthetically produced NADPH, which is required for quenching free electrons and nascent oxygen that could otherwise lead to ROS generation (Hare and Cress 1997; Szabados and Savoure 2010).

Studies about mutants and transgenic plants have showed the protective function of proline. Hypersensitive mutant of *Arabidopsis thaliana* with *p5cs1* insertion has confirmed importance of proline in stress tolerance. Proline content of *Arabidopsis* mutant is 90 % lower than the wild type and produces more ROS and lipid peroxidation products (Szekely et al. 2008). However, proline accumulation increases salt and drought tolerance in *P5CS*-overexpressed tobacco, rice, and soybean (Kishor et al. 1995; De Ronde et al. 2004; Kumar et al. 2010). Similarly, *Swingle citrumelo* plants have been transformed with *Vigna aconitifolia P5CS* gene (*VaP5CSF129A*) that improved proline levels and lead to differential expression levels of antioxidant enzymes (de Carvalho et al. 2013). Transgenic plants exhibit improved mRNA levels of ascorbate peroxidase, superoxide dismutase, and glutathione reductase isoenzymes that produce high proline level than non-transgenic plants. de Carvalho et al. (2013) have claimed that high proline level might have a regulatory role on antioxidant enzymes.

Exogenous proline is also effective in stress liberation of plants. Leaves of wild almond (*Prunus* spp.) species exposed to H_2O_2-mediated oxidative stress displayed high levels of proline (Sorkheh et al. 2012). Improved proline levels have decreased lipid peroxidation, membrane electrolyte leakage, and endogenous H_2O_2 content by modulating antioxidant enzymes such as peroxidase, ascorbate peroxidase, and non-enzymatic antioxidant like ascorbic acid that prevented almond species from oxidative stress injury. Similarly, exogenous proline treatment has alleviated salt stress effects by inducing catalase and ascorbate peroxide activities and decreasing endogenous H_2O_2 content in salt-stressed rice plants (Nounjan and Theerakulpisut 2012).

2.2.2 GABA

Adverse environmental conditions cause rapid accumulation of the non-protein amino acid like γ-aminobutyric acid (GABA) to high levels (Kaplan and Guy 2004; Kempa et al. 2008; Renault et al. 2010). Glutamate decarboxylase (GAD) convert glutamate to GABA in the cytosol, then GABA is transported to the mitochondria. Succinate is formed by GABA transaminase (GABA-T) and succinic semialdehyde dehydrogenase (SSADH) and involved in the TCA cycle (Shelp et al. 1999; Fait et al. 2008). GABA is closely related with ROS scavenging and carbon–nitrogen balance (Bouche and Fromm 2004; Song et al. 2010; Liu et al. 2011). Enzymes having role in GABA metabolism are induced by salt stress (Renault et al. 2010). Adverse effects of ionic stress increase in GABA-T-deficient *Arabidopsis* mutants. Levels of amino acids (including GABA) increased, while carbohydrate levels have been decreased in these mutants (Renault et al. 2010). Expression levels of genes, which are related to sucrose and starch catabolism increase under salt stress conditions with simultaneous loss of GABA-T function. Furthermore, compared with wild type, sugar concentration is twofold reduced in *gaba-t/pop2-1* mutant roots. Based on this information, Renault et al. (2013) provide evidence for the implication of GABA in central carbon metabolism regulation in roots under salt stress conditions.

2.3 Carbohydrates

2.3.1 Fructans

When energy demands increase and energy supplies are reduced, plants accumulate carbohydrates as storage substances. These substances are preferred to be rapidly mobilized sugars such as starch and fructans. Main storage carbohydrate of the most plant species is starch, while fructans can be accumulated by several angiosperms grown in the areas with dry periods and seasonal cold (Hendry 1993; Valluru and Van den Ende 2008). High water solubility, resistance to crystallization under freezing temperatures, and fructan synthesis at low temperatures add compensation in accumulation of fructans (Vijn and Smeekens 1999; Livingston et al. 2009). In addition, during freezing and dehydration, fructans can contribute to osmotic adjustment (Spollen and Nelson 1994; Olien and Clark 1995) and stabilize membranes (Valluru and Van den Ende 2008).

Transferring fructose from sucrose to growing fructan chain, fructosyltransferases, 1-SST, and 6-SFT synthesize fructans in vacuole (Vijn and Smeekens 1999; Livingston et al. 2009). Increased fructosyltransferases in transgenic tobacco and rice plants improve levels of fructans that enhance tolerance to drought and low-temperature stress (Pilonsmits et al. 1995; Li et al. 2007; Kawakami et al. 2008). In addition, increases in 1-fructosyltransferase (1-FFT) and fructan 1-exohydrolase (1-FEH) activity in water-stressed *Vernonia herbacea* (Vell.) Rusby plants accumulate about 80 % of fructans in the underground reserve organs, depicting the potential of fructans in maintenance of water content and drought tolerance by osmotic adjustment (Garcia et al. 2011).

2.3.2 Starch, Mono and Disaccharides

Starch, a glucose polymer, serves as a source of soluble sugars and main carbohydrate storage for most of the plants. Environmental changes easily affect starch metabolism. Starch levels are very sensitive to salt and drought stress generally. These stresses cause decrease in starch content and lead to enhancement in soluble sugars in leaves (Todaka et al. 2000; Kaplan and Guy 2004; Basu et al. 2007; Kempa et al. 2008). Under stress conditions, sugars accumulate and function as osmolytes to maintain cell turgour, protect membranes and proteins from stress injury (Madden et al. 1985; Kaplan and Guy 2004). Starch degradation is included by glucan-water dikinase (GWD) and phosphoglucan-water dikinase (PWD), which catalyze phosphorylation of starch granules. Maltose synthesized from glucans by β-amylases is converted to glucose followed by formation of fructose and sucrose in cytosol (Tetlow et al. 2004; Kotting et al. 2010).

Starch hydrolysis in the leaves under stressed conditions may be related to β-amolytic pathway of starch hydrolysis under normal growth conditions. Decrease in the freeze tolerance of *Arabidopsis sex1* (starch excess 1) mutants, disable to show GWD activity, is an evidence for the relation between β-amolytic pathway of starch hydrolysis and stress conditions (Yano et al. 2005). In addition, during osmotic stress total β-amylase activity has increased, while it has reduced in light-stimulated starch accumulation in wild-type *Arabidopsis*. On the other hand, *Arabidopsis* β-amylase mutant *bam1* (*bmy7*) is hypersensitive to osmotic stress (Valerio et al. 2011). Similarly, a reduction in low stress tolerance of photosystem II has been shown in BMY8 (BAM3) antisense plants, which accumulate high starch levels, have not induced maltose, glucose, fructose, and sucrose accumulation (Kaplan and Guy 2005). Zeeman et al. (2004) have suggested a role of the phosphorolytic starch degradation pathway during stress. After salt and low air humidity exposures to *Arabidopsis* plants deficient in plastidial α-glucan phosphorylase, lesions formation increase in the regions surrounded by cells with high starch levels.

2.3.3 Trehalose

Some desiccation tolerant plants, for example, *Myrothamnus flabellifolius* can accumulate trehalose, the non-reducing disaccharide to high amounts (Bianchi et al. 1993; Drennan et al. 1993). Later, trehalose accumulation has been detected in numerous other plants under different stress conditions such as drought, cold, and high salinity (Pramanik and Imai 2005; Lopez et al. 2008). Stabilization of proteins and membranes can be done by trehalose, which can function as an osmoprotective compound at sufficient levels (Paul et al. 2008). However, trehalose levels of most angiosperms can be increased by abiotic stresses but to moderate level only (Rizhsky et al. 2004; Guy et al. 2008; Kempa et al. 2008).

Trehalose biosynthesis is a two-step pathway in which trehalose-6-phosphate is produced from UDP glucose and glucose-6-phosphate by trehalose phosphate synthase, which is converted to trehalose by the enzyme trehalose phosphate phosphatase (Vogel et al. 1998, 2001). Trehalose is catabolized by trehalase, which converts it to glucose (Goddijn et al. 1997; Brodmann et al. 2002). The importance of trehalose in stress responses has been demonstrated by engineering the trehalose biosynthetic pathway in transgenic plants. Trehalose level has been enhanced by overexpression of bacterial trehalose biosynthetic genes like *otsA* and *otsB* in rice which improve its salt and drought tolerance (Garg et al. 2002). Several other transgenic plants that accumulate trehalose at high levels have been produced. The idea about regulation of stress tolerance can be done by inducing trehalose metabolism and has been proven via studies on genetically modified plants (Ge et al. 2008; Stiller et al. 2008). On the other hand, in another study, modification of trehalase which is responsible for conversion of trehalose to glucose has showed that trehalase plays a role in the regulation of stomatal closure in plants under drought stress. During water-deficit stress, *AtTRE1* overexpression in *A. thaliana* plants that have low level of trehalose exhibits better resistance to water deficit than *Attre1* mutants that has elevated trehalose contents. High sensitivity of *AtTRE1* stomata to ABA maintains leaf water content by closing more stomata than the mutants (Van Houtte et al. 2013). Exogenous applications of trehalose provide plants with improved tolerance to drought and salt stresses. Trehalose treatments cause increases in transcription of antioxidant enzyme genes such as superoxide dismutase, ascorbate peroxidase, peroxidase, and catalase in salt-stressed rice plants. Trehalose-treated plants recover immediately compared to non-treated plants (Nounjan et al. 2012).

Trehalose is suggested to function as chemical chaperon and has been shown to stabilize membranes and protect proteins in tissues under drought stress (Crowe et al. 1984; Crowe 2007). Trehalose can act as a signal molecule below 1 mg/g fresh weight instead of being a compatible solute (Garg et al. 2002). Therefore, the signaling function of trehalose and trehalose-6P could be more important than the previously suggested chaperone or osmolyte function, although in some tissues such a protective role cannot be excluded (Fernandez et al. 2010).

2.3.4 Polyols

One other class of osmoprotective compounds is polyols or sugar alcohols, which are chemically, reduced forms of aldose or ketose sugars. Water-like hydroxyl groups of polyols forming a sphere of hydration around macromolecules allow them to act as osmoprotectants under low osmotic potential. Polyols have functions as molecular chaperons stabilizing macromolecules. They also prevent membranes and enzymes from oxidative damage by scavenging ROS (Smirnoff and Cumbes 1989; Shen et al. 1997). Compared to sorbitol and galactitol, mannitol is the most common sugar alcohol and is an important photosynthetic product in a number of plant species (Loescher et al. 1992; Rumpho et al. 1983). In some plant species, there has been a correlation between stress tolerance and accumulation of mannitol and sorbitol (Stoop et al. 1996). Increase in tolerance to salinity or water deficit has been observed in *Arabidopsis*, tobacco, poplar, and wheat, which have been introduced mannitol-1-phosphate dehydrogenase (*mtlD*) from *E. coli*, that converts fructose-6-phosphate to mannitol-1-phosphate (Abebe et al. 2003; Chen et al. 2005; Sengupta et al. 2008). Similarly, targeted expression of *mt1D* in tobacco chloroplasts causes an increase in cytoplasmic mannitol concentration in transgenic tobacco plants, this increase, in turn, results in resistance to methyl viologen-induced oxidative stress (Shen et al. 1997). Overexpression of celery M6PR is an alternative way to enhance mannitol biosynthesis and has been shown to be an efficient way to improve salt tolerance of *Arabidopsis* (Zhifang and Loescher 2003). In a halophyte *Prosopis strombulifera*, leaf mannitol content increases during NaCl stress whereas sorbitol content increases after Na_2SO_4 treatment. According to increase in mannitol content during NaCl stress, it has been concluded that

P. strombulifera prefer mannitol for osmotic adjustment, however, sorbitol synthesis during Na_2SO_4 might be related to problems in carbon metabolism due to toxicity of sulfate (Llanes et al. 2013).

Myo-inositol is an essential polyalcohol in plants and eukaryotes for being an important precursor of some lipid signaling molecules and it has potential role in signaling during stress, cell wall biosynthesis, cell death, and plant hormone synthesis. Biosynthesis of myo-inositol starts from D-glucose-6P, which is converted to myo-inositol-1P by myo-inositol-1P synthase (MIPS) (Johnson and Sussex 1995; Majumder et al. 1997). Myo-inositol is produced from myo-inositol-1P by dephosphorylation and is used for the subsequent biosynthesis of all inositol-containing compounds, including phospholipids. MIPS genes were shown to be salt-induced, leading to accumulation of myo-inositol in the halophyte ice plant, but not in the glycophyte *Arabidopsis* (Ishitani et al. 1996). MIPS genes can be regulated by several environmental stress factors such as drought, heat and cold stress, high light and controlled by ABA signals (Yoshida et al. 1999, 2002; Abreu and Aragao 2007; Wei et al. 2010a, b). Phosphorylated derivatives of myo-inositol are important signaling compounds in responses to biotic and abiotic stresses which are involved in numerous regulatory pathway and control diverse aspects of plant development (Nelson et al. 1999). Improved tolerance to salt stress during germination, seedling growth and development has been observed in *Arabidopsis thaliana* that overexpress myo-inositol 1-phosphate synthase gene (*SaINO1*) in halophytic grass, *Spartina alterniflora* (Joshi et al. 2013).

As an important osmoprotectant, a six-carbon alcohol sorbitol is the most preferable accumulated carbon source in some fruit trees of *Rosaceae* family (Tari et al. 2010; Feng et al. 2011; Li et al. 2012). Sorbitol confers tolerance against abiotic and biotic stresses by participating in osmotic adjustment during stress. Sorbitol is synthetized from hexose phosphates like sucrose. Sorbitol-6-phosphate dehydrogenase (S6PDH) is a regulatory enzyme in sorbitol biosynthesis, which catalyzes conversion of glucose-6-phophate to sorbitol-6-phosphate then in turn, sorbitol-6-phosphate is dephosphorylated to form sorbitol by sorbitol-6-phosphate phosphatase (Kanamaru et al. 2004; Liang et al. 2012).

Sorbitol transporter genes are induced by subjecting plants to stress so that plants can accumulate sorbitol. Sour berry, apple, and *Arabidopsis* plants have been scanned for the transporter genes and the genes have been identified in these plants (Gao et al. 2005; Fan et al. 2009). Differential regulation of sugar regulators is maintained through sugar transporters induced in response to varied abiotic and biotic stress (Wormit et al. 2006). Sorbitol accumulation in salt-stressed *Plantago major* has been detected by Pommerrenig et al. (2007). In addition, up-regulation of three sorbitol transporters in apple plants has improved drought tolerance in vegetative tissues with subsequent increment in sorbitol concentration as confirmed by HPLC analysis of leaves, roots, and phloem tissues (Li et al. 2012).

Pinitol is a methylated inositol, which is synthetized from myo-inositol by inositol-o-methyltransferase (IMT1) and ononitolepimerase (OEP1) (Bohnert et al. 1995; Rammesmayer et al. 1995; Sengupta et al. 2008). Pinitol increase has been correlated with improved tolerance of some plants subjected to drought or heat stress.

Increase in the drought resistance of pine seedlings that accumulate pinitol has been determined. The cultivars that acquire higher pinitol content are resistant to drought stress than the low pinitol-producing cultivars (N'Guyen and Lamant 1988). Many studies confirm sucrose as the well-known low-molecular-weight carbohydrate that is accumulated in soybean plants under stress (Yamada and Fukutoku 1985; Fellows et al. 1987). Ford (1984) has reported inadequate increase in sucrose contents and significant accumulation of pinitol in soybean plants under water-stressed conditions. Pinitol accumulation is a characteristic feature of a number of halophytic plants in saline environment and occurs in several glycophytic plants grown under osmotic stress conditions (N'Guyen and Lamant 1988; Gorham et al. 1981; Popp 1984; Paul and Cockburn 1989; Sengupta et al. 2008). Unlike native rice cultivars, pinitol hyperaccumulation has been found in *Porteresia coarctata*, a halophytic wild relative of rice. This pinitol accumulation is controlled by inositol methyl transferase 1 (*PcIMT1*) gene, an essential metabolic response for salt stress (Sengupta et al. 2008). Increased salt tolerance was shown in transgenic tobacco displaying *P. coarctata*, *MIPS* overexpression, and *M. crystallinum* IMT1 gene insertion. These transgenic tobacco plants accumulate more inositol and pinitol that confer improved growth, higher photosynthetic activity, and lower oxidative damage during salt stress (Patra et al. 2010).

3 Conclusions and Future Perspective

Plants being sessile are subjected to diverse environmental stresses that impede their growth and development. Therefore, metabolic adjustment to cope with environmental stress conditions is important considerably for plants. However, this adjustment is brought at different levels in diverse ways making tolerance mechanism even more complex. As each organism, even its varieties exhibit assorted response to array of external stimuli. For instance, changes in cellular metabolism during development and acclimation under adverse conditions are closely related to the developmental stage of a plant. Therefore, there is great necessity to study state of vulnerability at particular developmental stage and metabolic adjustment in stress conditions.

Osmoprotective compounds like sugars and proline could function as metabolic signals and therefore have broader influence on physiological responses and metabolic adjustment to stress conditions. Despite there are many studies about signaling networks, however there is paucity regarding reports about how a metabolic response is induced by an environmental change and what are the roles of osmolytes in stress signaling. Engineering of crop plants via genetic transformation is a promising tool to study the significance of osmoprotective compounds in stress responses and to improve the performance of crop plants under suboptimal conditions. Enhanced accumulation of a metabolite can be achieved via activation of the biosynthetic pathway or inhibition of the catabolic pathway. Furthermore, novel pathways can be established in plants, by introducing genes from other species. Combining advanced approaches like genomics, proteomics, and metabolomics could increase our understanding of plant stress responses on a global scale and will put forth metabolic bases of adaptation to drought, salinity, or extreme temperatures.

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