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Plant Salt Tolerance: Metabolites as Key Regulators of Stress Defence

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The plateau in genetic gain in crop productivity suggests that traditional methods of crop improvement may have reached their maximum potential. Therefore, it is crucial to enhance the productivity of less productive lands, including salt-affected areas, in addition to increasing crop yields. Globally the total area of saline soil is 397 million ha and 434 million ha of sodic soil. Of the 230 million irrigated fields, 45 million ha (19.5%) are salt-affected and almost 1500 million ha of arable agriculture, 32 million (2.1%) are salt-affected. Of the world's salt-affected land, an estimated 6.73 million ha are in India. Extreme events, climatic aberrations and anthropogenic interventions are likely to further aggravate the extent of these degraded soils. Despite the importance of salinity on crop production worldwide, and the abundance of knowledge gathered on genes/mechanisms involved in salinity tolerance, there has been surprisingly little effort to breed for improved salinity tolerance. Developing salt tolerant crop varieties is critical because the increased water scarcity will demand alternate sources like those having salinity and residual alkalinity.

Developing salt-tolerant crop varieties is critical because the increased water scarcity will demand alternate sources like those having salinity and residual alkalinity. Plant adaptation or tolerance to salinity stress involves complex physiological traits, metabolic pathways, and molecular networks. A comprehensive understanding of how plants respond to salinity stress at different levels and an integrated approach of combining physiological and biochemical techniques are imperative for the development of salt-tolerant varieties of plants in salt-affected areas. Recent research has identified various adaptive responses to salinity stress at cellular, metabolic, and physiological levels, although mechanisms underlying salinity tolerance are far from being completely understood. This article provides a comprehensive study on metabolites that regulate plant adaptation and tolerance to salt stress.

Higher plants have a remarkable ability to synthesize a vast array of metabolites, which are categorized as primary metabolites and secondary metabolites. Primary metabolites are the compounds commonly produced by all plants and are directly used by them for their growth and development. Carbohydrates, proteins, nucleic acids, and lipids are considered the main primary metabolites. The functions of primary metabolic compounds are:

- Polysaccharides are mainly used in providing support for plants and also store energy for their later use.
- Proteins build the remaining biomass of living plant cells. A protein consists of polypeptides, which are made up of amino acids. Plants synthesize amino acids from the products of photosynthesis by using large amounts of energy in the form of ATP and NADPH.
- Proteins store energy in seeds and are used as a source of nutrition in the early development of seedlings. For example, corn produces a storage protein called ZEIN.

Secondary metabolites are compounds that are not required for normal growth and the development of plant cells. The products of secondary metabolism are morphine, caffeine, nicotine, menthol, and rubber. The products of secondary metabolism are the metabolism of chemicals, which are very rarely found in plants and do not have any specific role in plant functioning. Few toxic compounds are produced from secondary metabolism like nicotine, which helps the plant protect itself from plant-eating animals (herbivores) and also from microbes.

Primary metabolites differ in chemical complexity and biological functions playing an indispensable role in stress alleviation (Saito and Matsuda, 2010; Dixon and Strack, 2003). Examples of plant metabolites that are involved in salt tolerance include amino acids such as proline, polyols such as mannitol and sorbitol, dimethylsulfonium compounds, glycine betaine, sugars such as sucrose, trehalose, and fructans, etc. that serve as an osmolyte or osmoprotectant (Shulaev et al., 2008). Plants, when subjected to salt stress, show

an increase in the concentration of these osmolytes, thus playing a significant role in stress mitigation.

1. Osmolytes accumulation and plant protection

Osmolytes are a diverse group of organic compounds that are soluble, polar, and uncharged. They don't interfere with cellular metabolism even at high concentrations. Some common osmolytes include proline, glycine betaine, sugar, and polyols. Different plant species synthesize and accumulate osmolytes in varying amounts. The cell maintains the concentration of these compatible solutes either by synthesizing them irreversibly or by a combination of synthesis and degradation. Because the accumulation of osmolytes is proportional to the external osmolarity, their primary function is to protect the cell structure and maintain osmotic balance by allowing continuous water influx (Hasegawa et al., 2000). The different osmolytes and their role are discussed as under:

1.1 Amino acids

Amino acids such as cysteine, arginine, and methionine, which constitute about 55% of total free amino acids, decrease when exposed to salinity stress, whereas proline concentration rises in response to salinity stress (El-Shintinawy and El-Shourbagy, 2001). Intracellular proline which is accumulated during salinity stress not only provides tolerance towards stress but also serves as an organic nitrogen reserve during stress recovery. Proline is synthesised either from glutamate or ornithine. In osmotically stressed cells glutamate functions as the primary precursor. The biosynthetic pathway comprises two major enzymes, pyrroline carboxylic acid synthetase and pyrroline carboxylic acid reductase. Both these regulatory steps are used to overproduce proline in plants (Sairam and Tyagi, 2004). It functions as an O2 quencher thereby revealing its antioxidant capability. It has been reported that proline improves salt tolerance in Nicotiana tabacum by increasing the activity of enzymes involved in the antioxidant defence system (Hoque et al. 2008). Deivanai et al. (2011) also demonstrated that rice seedlings from seeds pre-treated with 1 mM proline exhibited improvement in growth during salt stress.

1.2 Glycine betaine

Glycine betaine is an amphoteric quaternary ammonium compound ubiquitously found in microorganisms, higher plants and animals, and is electrically neutral over a wide range of pH. Glycine betaine is a nontoxic cellular osmolyte that raises the osmolarity of the cell during stress periods; thus it plays an important function in stress mitigation. Glycine betaine also protects the cell by osmotic adjustment, stabilizes proteins and protects the photosynthetic apparatus from stress damage and reduction of reactive oxygen species (ROS) (Saxena et al., 2013; Ahmad et al., 2013).

Accumulation of glycine betaine is found in a wide variety of plants belonging to different taxonomical backgrounds. Glycine betaine is synthesised within the cell from either choline or glycine. Synthesis of glycine betaine from choline is a 2-step reaction involving two or more enzymes. In the first step choline is oxidised to betaine aldehyde which is then again oxidised in the next step to form glycine betaine. In higher plants the first conversion is carried out by the enzyme choline mono-oxygenase, whereas the next step is catalysed by betaine aldehyde dehydrogenase (Ahmad et al., 2013). Another pathway that is observed in some plants, mainly halophytic, demonstrates the synthesis of glycine betaine from glycine. Here glycine betaine is synthesized by three successive N-methylation and the reactions are catalysed by two S-adenosyl methionine dependent methyl transferases, glycine sarcosine N-methyl transferase, and sarcosine dimethylglycine N-methyl transferase. These two enzymes have overlapping functions as glycine sarcosine N-methyl transferase catalyses the first and the second step while sarcosine dimethylglycine N-methyl transferase catalyses the second and third steps (Ahmad et al., 2013). Under stressed conditions (150 mM NaCl) the ultrastructures of the seedling shows several damages such as swelling of thylakoids, the disintegration of grana and inter granal lamellae, and disruption of mitochondria. However, these damages were largely prevented when seedlings were pre-treated with glycine betaine. When glycine betaine is applied as a foliar spray in a plant subjected to stress, it led to pigment stabilization and an increase in photosynthetic rate and growth (Ahmad et al., 2013).

1.3 Polyols

Polyols are compounds with multiple hydroxyl functional groups available for organic reactions. Sugar alcohols are a class of polyols functioning as compatible solutes, as low molecular weight chaperones, and as ROS-scavenging compounds (Saxena et al., 2013). They can be classified into two major types, cyclic (e.g., pinitol) and acyclic (e.g., mannitol). Mannitol synthesis is induced in plants during the stressed period via action of NADPH-dependent mannose-6-phosphate reductase. These compatible solutes function as a protector or stabilizer of enzymes or membrane structures that are sensitive to dehydration or ionically induced damage.

It was found that the transformation with bacterial mltd gene that encodes for mannitol-1-phosphate

dehydrogenase in both Arabidopsis and tobacco (Nicotiana tabacum) plants confer salt tolerance, thereby maintaining normal growth and development when subjected to high levels of salt stress (Binzel et al., 1988). Pinitol accumulates within the plant cell when the plant is subjected to salinity stress. The biosynthetic pathway consists of two major steps, methylation of myo-inositol which results in the formation of an intermediate compound, inositol, which undergoes epimerization to form pinitol. Inositol methyl transferase enzyme encoded by imt gene plays a major role in the synthesis of pinitol. Transformation of the imt gene in plants shows a result similar to that observed in the case of the mltd gene. Thus it can be said that pinitol also plays a significant role in stress alleviation. Accumulation of polyols, either straight-chain metabolites such as mannitol and sorbitol or cyclic polyols such as myo-inositol or its methylated derivatives, is correlated with tolerance to drought and/or salinity, based on polyol distribution in many species of plants (Bohnert et al., 1995).

1.4 Carbohydrates

Accumulations of carbohydrates such as sugars (e.g., glucose, fructose, fructans, and trehalose) and starch occur under salt stress (Parida et al., 2004). The major role played by these carbohydrates in stress mitigation involves osmoprotection, carbon storage, and scavenging of reactive oxygen species. It was observed that salt stress increases the level of reducing sugars (sucrose and fructans) within the cell in many plants belonging to different species (Kerepesi and Galiba, 2000). Besides being a carbohydrate reserve, trehalose accumulation protects organisms against several physical and chemical stresses including salinity stress. They play an osmoprotective role in physiological responses (Ahmad et al., 2013). Sucrose content was found to increase in tomato (Solanum lycopersicum) under salinity due to increased activity of sucrose phosphate synthase (Gao et al., 1998). Sugar content, during salinity stress, has been reported to both increase and decrease in various rice genotypes. It has been observed that starch content decreased in rice roots in response to salinity while it remained fairly unchanged in the shoot (Alamgir and Yousuf, 1999).

2. Antioxidant in salt tolerance

2.1 Non-enzymatic antioxidant

The reactive oxygen species (Fig. 1) such as superoxide (O2−), hydrogen peroxide (H2O2), hydroxyl radical (•OH), and singlet oxygen (1O2) are produced during normal aerobic metabolism when electrons from the electron transport chains in mitochondria and chloroplasts are leaked and react with O2 in the absence of other acceptors (Thompson et al., 1987). However, plants generally can eliminate superoxide with the help of superoxide dismutase (SOD), which catalyzes the dismutation of superoxide into hydrogen peroxide and oxygen, and is important in preventing the reduction of metal ions and hence the synthesis of hydroxyl radicals (Fig.2). Hydrogen peroxide can be eliminated by an ascorbate peroxidase located in the thylakoid membrane (Chen and Asada, 1989).

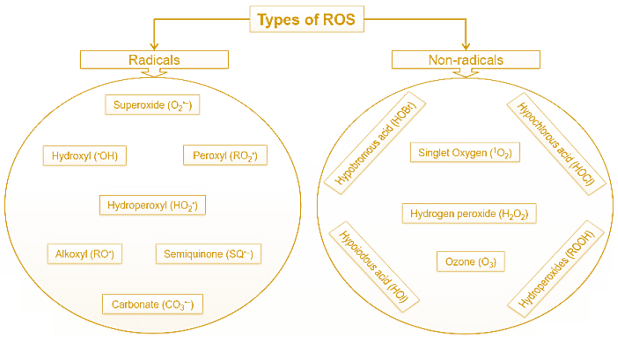

Figure 1. Types of reactive oxygen species in plants (Reproduce from Hasanuzzaman et al., 2020)

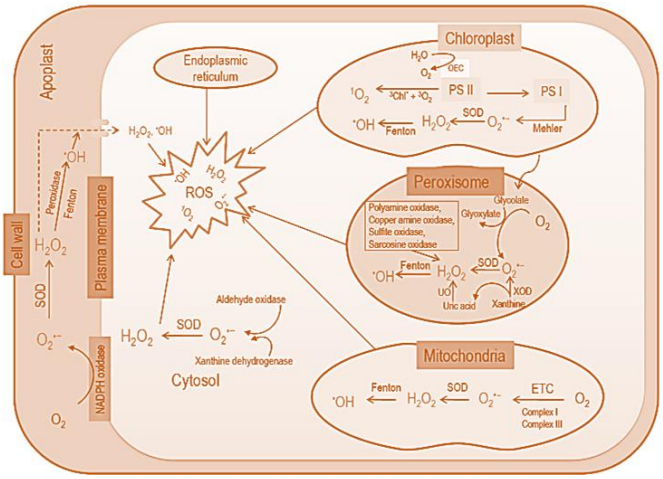

Figure 2. Localization and processes for the generation of ROS in plant cells. (ROS, reactive oxygen species; H2O2, hydrogen peroxide; O2•−, superoxide anion; 1O2, singlet oxygen; •OH, hydroxyl radical; SOD, superoxide dismutase; UO, urate oxidase; XOD, xanthine oxidase; ETC, electron transport chain; PS I, photosystem I; PS II, photosystem II; NADPH, nicotinamide adenine dinucleotide phosphate). Activation of O2 occurs by two different mechanisms. Stepwise monovalent reduction of O2 leads to the formation of O2•−, H2O2, and •OH, whereas energy transfer to O2 leads to the formation of 1O2. O2•− is easily dismutated to H2O2 either non-enzymatically or by superoxide dismutase (SOD) catalyzed reaction to H2O2. H2O2 is converted to H2O by catalase (CAT), guaiacol peroxidase (GPX), and ascorbate peroxidase (APX). (Reproduce from Hasanuzzaman et al., 2020).

There is conclusive evidence that the production of activated oxygen species is enhanced in plants in response to different environmental stresses such as salinity, drought, waterlogging, temperature extremes, high light intensity, herbicide treatment or mineral nutrient deficiency (Wise and Naylor, 1987; Gossett et al., 1994). Plants containing high

concentrations of antioxidants show considerable resistance to the oxidative damage caused by the activated oxygen species (Garratt et al., 2002). Comparing the mechanisms of antioxidant production in salt tolerant and salt sensitive plants, Dionisiosese and Tobita (1998) reported a decline in SOD activity and an increase in peroxidase activity in the salt sensitive rice varieties, Hitomebore and IR28, in response to salt stress. These salt sensitive varieties also showed an increase in lipid peroxidation and electrolyte leakage as well as Na+ accumulation in the leaves under saline conditions. In contrast, two salt tolerant rice varieties, Pokkali and Bankat, showed differing protective mechanisms against activated oxygen species under salt stress. Cv. Pokkali showed only a slight increase in SOD but a slight decrease in peroxidase activity, and almost unchanged lipid peroxidation, electrolyte leakage and Na+ accumulation under saline conditions. In contrast, cv. Bankat showed Na+ accumulation in leaves and symptoms of oxidative damage similar to the salt sensitive cultivars.

2.2 Enzymatic antioxidant

Enzymatic antioxidant (catalase, peroxidase, and polyphenol oxidase) responses were more pronounced in control plants than in Si-treated plants under salinity stress. Anthocyanin is a flavonoid whose accumulation in plants exposed to salt stress has been largely documented. Ascorbate is one of the major antioxidants present within the cell. Pea plants grown under saline (150 mM NaCl) stress showed an enhancement of both ascorbate peroxidase (APX) activity and S-nitrosylated APX, as well as an increase of H_2O_2, NO, and S-nitrosothiol content that can justify the induction of the APX activity. Exogenous application of ascorbate mitigates the adverse effects of salinity stress in various plant species and promotes plant recovery from the stress (Agarwal and Shaheen, 2007; Munir and Aftab, 2011).

Another antioxidant in stress mitigation is glutathione, which can react with superoxide radicals, hydroxyl radicals, and hydrogen peroxide, thereby functioning as a free radical scavenger. It can also participate in the regeneration of ascorbate via the ascorbate-glutathione cycle. When applied exogenously glutathione helped to maintain plasma membrane permeability and cell viability during salinity stress in Allium cepa (Aly-Salama and Al-Mutawa, 2009). Application of glutathione and ascorbate was found to be effective in increasing the height of the plant, branch number, fresh and dry weight and the content of carbohydrates, phenols, xanthophylls pigment, and mineral ion content when subjected to saline conditions (Rawia Eid et al., 2011). Differences in antioxidant activity between genotypes may be due to genotypic differences in degrees of stomatal closure or in other responses that alter the rate of CO_2 fixation and differences that bring into play the processes that avoid photo-inhibition and for which the plant has abundant capacity. Recently it has been argued that there are three main traits in plants, which help them in their adaptation to salinity stress: ion exclusion, tissue tolerance, and salinity tolerance (Roy et al., 2014). It seems that antioxidants have some role in tissue and salinity tolerance mechanisms.

3. Polyamines in salt tolerance

Polyamines are small, low molecular weight, ubiquitous, polycationic aliphatic molecules widely distributed throughout the plant kingdom. Polyamines play a variety of roles in normal growth and development such as regulation of cell proliferation, somatic embryogenesis, differentiation and morphogenesis, dormancy breaking of tubers and seed germination, development of flowers and fruit, and senescence (Gupta al., 2013). It also plays a crucial role in abiotic stress tolerance including salinity and increases in the level of polyamines are correlated with stress tolerance in plants (Groppa and Benavides, 2008). The most common polyamines that are found within the plant system are diamine putrescine, triamine spermidine, and tetra-amine spermine. The polyamines biosynthetic pathway has been thoroughly investigated in many organisms including plants and has been reviewed in detail (Kusano et al., 2007; Martin-Tanguy, 2001). Diamine putrescine is the smallest polyamine and is synthesised from either ornithine or arginine by the action of enzymes ornithine decarboxylase and arginine decarboxylase, respectively. N-carbamoyl-putrescine is converted to diamine putrescine by the enzyme N-carbamoyl-putrescine aminohydrolase. The diamine putrescine thus formed functions as a primary substrate for higher polyamines such as triamine spermidine, and tetra-amine spermine biosynthesis, which are synthesized by successive addition of aminopropyl group to diamine putrescine and triamine spermidine, respectively, by the enzymes spermidine synthase and spermine synthase (Hasanuzzaman et al., 2014; Alcazar et al., 2006).

An increase in endogenous polyamine levels has been reported when the plant is exposed to salinity stress. Intracellular polyamine level is regulated by polyamine catabolism. Application of exogenous polyamine has been found to increase the level of endogenous polyamine during stress; the positive effects of polyamines have been associated with the maintenance of membrane integrity, regulation of gene expression for the synthesis of osmotically

active solutes, reduction in ROS production, and controlling accumulation of Na+ and Cl− ion in different organs. Overproduction of diamine putrescine, triamine spermidine, and tetra-amine spermine in rice, tobacco, and Arabidopsis enhances salt tolerance (Roy and Wu, 2002). It has been reported that exogenous application of polyamines could alleviate salt-induced reduction in photosynthetic efficiency, but this effect depends on polyamine concentration and types and levels of stress. Li et al. (2013) also reported that the regulation of the Calvin cycle, protein folding assembly, and the inhibition of protein proteolysis by triamine spermidine might play important roles in salt tolerance.

Conclusion

Plant breeders have been successful in improving the salinity tolerance of certain crops over the past few decades through conventional selection and breeding techniques. However, this was achieved without a full understanding of the underlying biochemical mechanisms, relying solely on the phenotypic characteristics of the plants. Scientists agree that selection is easier when distinctive indicators of salt tolerance are present, whether at the whole plant, tissue, or cellular level. Therefore, there is a need to identify cellular mechanisms to provide meaningful advice to plant breeders. Despite many studies on the subject, we still don't fully understand the metabolic sites where salt stress damages plants, nor the adaptive components of salt tolerance. This means there are no well-defined plant indicators for salinity tolerance that can be practically used by plant breeders to improve salinity tolerance in several crops.

It would be more valuable if biochemical indicators were identified for individual species, rather than generalized for all species. Among the many biochemical indicators, antioxidants and organic solutes such as glycine-betaine and proline have gained popularity in recent years. Studies show that plants with high concentrations of these compounds exhibit significant resistance to salinity and other abiotic stresses.

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