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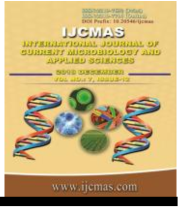

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Biochemical and Molecular Mechanism of Salinity Stress Tolerance in Plants

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ABSTRACT

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Salinity is one of the most aggressive environmental stresses that hamper crop productivity worldwide. Increased salt concentration in soil reduces plants ability to take up water. It also reduces nutrients availability, uptake and transport, and there distribution resulting nutritional imbalance in plant. The Salt Overly Sensitive (SOS) signalling pathway is crucial to mediate cellular signalling and to maintain ion homeostasis under salinity stress. Many HKT family plasma membrane transporters play an essential role in salt tolerance mechanism by regulating Na^+ and K^+ transportation. The nitric oxide (NO) directly or indirectly triggers numerous redox-regulated genes expression. Many genes were induced or repressed in response to salinity stress. Extensive research in the course of metabolic, cellular, and physiological analysis has elucidated that strategies or mechanisms regulating stress signaling, uptake of ions, their transport and osmotic balance, metabolism of hormone, and antioxidant play vital roles in developing plant to mitigate salt stress.

Introduction

Crop production is severely affected by high salt concentrations in soils. Salt level build up in arable soils is generally derived from irrigated water containing sodium chloride (NaCl) and from seawater (Flowers and Yeo, 1995; Tester and Davenport., 2003). Soil salinity, on the basis of the origin of salts, can be classified into two groups; natural/primary salinity and human induced/secondary Salinity. Increased salt concentration in the soil reduces the ability of a plant to take up water. If the excessive amounts of Na^+ and Cl^- taken up in large amounts by roots and accumulated in leaves, then both Na+ and Cl^- ions negatively affect plant growth by impairing metabolic processes and decreasing photosynthetic efficiency. High Na^+ concentration also inhibits uptake of K^+ ions (Hasan *et al*., 2015), which results into poorer productivity and may even lead to death of plant. Thus salinity is one of the most aggressive environmental stresses that hamper crop productivity worldwide (Munns and Tester, 2008). In this review, we have examined the key biochemical and molecular mechanisms that can make plants tolerance to salinity stress.

Biochemical mechanism of salinity stress tolerance

Role of ion homeostasis in salinity stress tolerance

Maintaining the ion homeostasis is crucial for plant growth under normal and salinity stressed condition (Kamyab *et al*., 2016). At high salt concentration, the Na^+ ion entered in the cytoplasm is compartmentalized in to vacuole by Na^+/H^+ antiporter. Increasing evidence confirmed the roles of a Salt Overly Sensitive (SOS) pathway (Figure 1) in ion homeostasis and salt tolerance (Hasegawa *et al*., 2000). The Arabidopsis NADPH oxidases, *AtrbohD* and *AtrbohF* were active in ROS-dependent regulation of Na^+/H^+ ion homeostasis under salinity stress (Ma *et al*., 2012). During salinity stress, due to increased Na^+ ion concentration in the soil, Na^+ ion competes with K^+ ion for the same transport mechanism thereby decreasing the uptake of K^+. The *Arabidopsis* class 1 HKT transporters (HKT1) have been well known to cope salinity stress by preventing excess accumulation of Na^+ in leaves. Similar results were observed in the rice experiment in which HKT1 transporter eliminate excess Na^+ from xylem, thus defending the photosynthetic leaf tissues from the toxic effect of Na^+ (Schroeder *et al*., 2013). In fact more NHX isoforms e.g. LeNHX3 and LeNHX4 from tomato have been identified from different plant species and established their roles in ion (Na+, K+, H+) homeostasis (Galvez *et al*., 2012).

Role of compatible osmolytes in salinity tolerance

Compatible osmolytes (also known as compatible solutes) are a group of chemically diverse organic compounds that are low molecular weight, uncharged, polar, and highly soluble in nature and they do not interfere with the cellular metabolism even at high concentration. The proline accumulated during salt stress is not only provides salt tolerance but also serves as an organic nitrogen reserve during stress recovery. Besides these, proline plays other three major roles during stress, i.e., as a signaling molecule, as antioxidative defense molecule and a metal chelator. Both pyrroline-5-carboxylate synthetase (P5CS) and pyrroline carboxylate (P5C) reductase (P5CR) enzymes are used to overproduce proline in stressed plants cell (Sairam *et al*., 2004). Glycine betaine as well protects the cell by osmotic adjustment, stabilizes proteins, and protects the photosynthetic apparatus from stress induced damages (Saxena *et al*., 2013; Cha-Um *et al*., 2010). The salt stress induced damages were largely prevented when *Oryza sativa* seedlings were pretreated by glycine betaine (Rahman *et al*., 2002).

Role of antioxidant in salinity tolerance

Salt stress tolerance is positively correlated with accumulation of both the activity of antioxidant enzymes and the nonenzymatic antioxidant compounds (Abbasi *et al*., 2016). Many helicase proteins like DESD-box helicase and OsSUV3 dual helicase have been reported to improving or maintaining antioxidant machinery under stressed condition (Tuteja *et al*., 2013).

Exogenous application of ascorbate mitigates the adverse effects of salt stress in different plant species and promotes plant revival from the salt stress (Munir and Aftab, 2011). Another antioxidant implicated in stress mitigation is glutathione. It acts as a free radical scavenger. It also participates in the ascorbate regeneration via ascorbate-glutathione cycle. Exogenously applied glutathione helped to maintain membrane permeability and cell viability in onion (*Allium cepa*) during salinity stress.

Roles of polyamines in salinity tolerance

Polyamines (PA) are ubiquitous, low molecular weight, polycationic aliphatic molecules. The putrescine (PUT), spermine (SPM) and spermidine (SPD) are the most common polyamines found within the plant (Shu *et al*., 2012). The PUT, which is the smallest polyamine, synthesised from either ornithine, by the action of ornithine decarboxylase (ODC) enzyme, or from arginine, by arginine decarboxylase (ADC) enzyme (Hasanuzzaman *et al*., 2014). When plant is exposed to salt stress, the increased level of endogenous polyamines was regulated via. Oxidative catabolism by FAD binding polyamine oxidases and copper binding diamine oxidases. Thus these oxidase enzymes play a major role in salt stress tolerance. It was observed that the mutant for polyamine biosynthetic genes, such as deficient in *ADC1* and *ADC2*, is hypersensitive to salt stress (Hussain *et al*., 2011). Over expression of genes encoding PUT, SPD, and SPM enzymes in plants like in rice, tobacco, and *Arabidopsis* marks increased in polyamines level that enhanced salt tolerance in plants. SPM and SPD acts as effective inducers of Nitric oxide (NO), which is one more important signalling molecule involved in salinity tolerance

Roles of nitric oxide in salinity tolerance

Nitric oxide (NO) is an essential endogenous signaling molecule. The application of exogenous NO has been found to play important roles in stress mitigation (Sung *et al*., 2010). In other study it was found that the exogenous application of sodium nitroprusside, which is a NO donor, on *Lupinus luteus* seedlings subjected to salt stress improved seed germination and root growth. Improved plant growth under salt stress by exogenous application of NO was linked with increases in contents of the antioxidant enzymes such as SOD, APX, CAT, GPX, and GR, and decrease in malondialdehyde (MDA) production or lipid peroxidation (Nalousi *et al*., 2012).

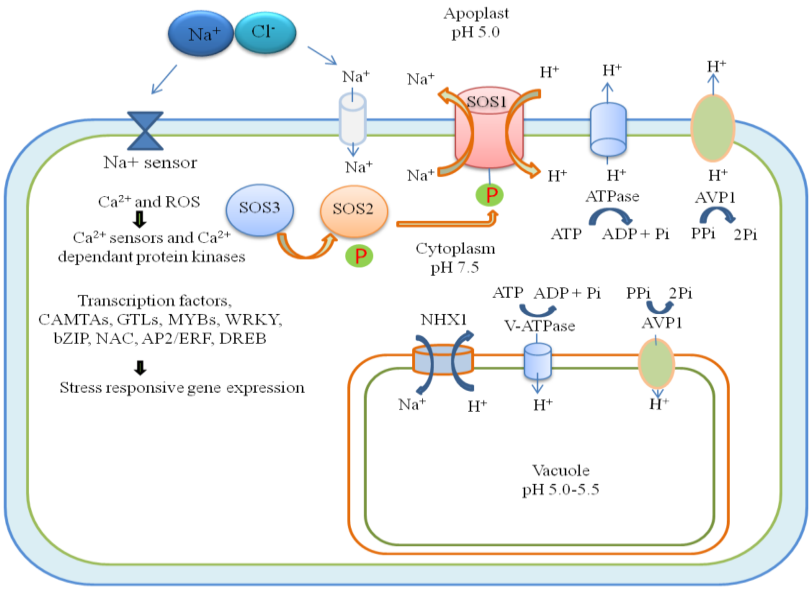
High salt concentration is sensed by Na^+ ion sensors and induces Ca^{2+} and ROS. The Na+ and Ca^{2+} ion is sensed by Ca^{2+} dependent protein kinase (SOS3), which activates SOS2 kinase. Then SOS2 not only enhances ion extrusion into the apoplast by regulating Na^+/H^+ antiporter (SOS1) of plasma membrane but also increase Na^+ ion transport into the vacuole by increasing the activity of Na^+/H^+ antiporter of tonoplast. Many transcriptional factors regulate salinity stress responsive gene expression. In some plant salt content is compartmentalized in vacuole vi NHX 1.

Molecular mechanism of salinity stress tolerance

Transcriptomic analysis is widely used to screen a variety of candidate genes involved in stress responses (Wang *et al*., 2016). Recently, the next-generation RNA-Seq technology used to elucidate the salt-tolerance mechanism in plants like *Gossypium davidsonii* (Zhang *et al*., 2016). In *Arabidopsis*, salt stress moderates the upregulation of AtWRKY8 which directly binds with the *RD29A* promoter, signifying it to be as one of the target genes of AtWRKY8 transcription factor (Hu *et al*., 2013). Wheat cultivar exposed to long-term salinity showed variation in the *bZIP* genes expression. The *bZIP* genes expression was upregulated in salt-sensitive wheat cultivar while it is decreased in salt-tolerant variety. The OsNAC5 and ZFP179 transcription factors may regulate the synthesis and accumulation of sugar, proline, and LEA proteins that consecutively play an integral role in stress tolerance (Rahman *et al*., 2002). A transcription factor in rice (*Oryza sativa*), *SALT-RESPONSIVE ERF1 (SERF1)*, that showed a root specific induction upon salt and H_2O_2 treatments. Loss of *SERF1* damaged the salt inducible expression of genes encoding members MAPK cascade and salt tolerance mediating TFs. Furthermore, they illustrated that SERF1 binds to the promoters of *MAP3K6, MAPK5, ZFP179,* and *DREB2A* in both in vitro and in vivo. The plants having SERF1 deficiency are more sensitive to salt stress compared with the wild type, whereas constitutive over-expression of SERF1 get better salinity tolerance. The *AtMYB12* confer salt and drought tolerance through increasing the levels of flavonoids, ABA, proline, superoxide dismutase (SOD) and peroxidase (POD in transgenic Arabidopsis (Wang *et al*., 2016), thus *AtMYB12* gene has the potential to be used to improve tolerance to salt and other abiotic stresses in plants.

High-throughput sequencing for transcriptome analysis in plant has revealed that alternative splicing affects transcriptome at higher proportion than was previously assumed. A group of Ser/Arg-rich proteins, that acts as a key regulators of alternative splicing, go through alternative splicing themselves in response to salt stress and other abiotic stresses (Staiger and Brown, 2013).

Figure.1 Signal transduction and tolerance mechanisms against salinity stress



Future research perspectives

In conclusion salt stress tolerance involves a complex of responses at physiological, biochemical and molecular levels. Extensive research in the course of physiological, biochemical, molecular, and cellular analysis has elucidated that strategies or mechanisms regulating different processes, such as uptake of ions, their transport and balance, metabolism of plant hormone, antioxidant, and stress signaling, play vital roles in developing plant to mitigate salt stress. In addition, in the face of the significant advancement in the understanding of plants salt stress responses, there is still a huge gap in our understanding of ion transport across membrane, key sensor and receptor in the signaling transduction. Genetic engineering approaches has been proved to be an efficient way to the enlargement of salt stress-tolerant plants.

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