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Effect of Environmental Salt Stress on Plants and the Molecular Mechanism of Salt Stress Tolerance

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Abstract

Abiotic environmental stresses can negatively impact plant growth and productivity. Soil salinity is one of the major environment limitations on plant yield and distribution. In this article, we review the damage that environmental salt stress has on plants and how plant tolerates salt stress on the molecular level. We discussed multiple signalling and listed some pathways with certain members identified elements and some of the several common salt tolerance determinants. We examined the effect of salinity stress on plant development by reviewing the intracellular metabolic processes with excessive Na^+ and Cl^-. Salt stress affects every aspect of plant development, inhibits the growth of the plant, reduces the fresh weight and dry weight of root, stem, and leaf, decreases the expansion of leaf and changes the morphology of the leaf. It also suppresses photosynthesis and affects the ion homeostasis in plants, causing an imbalance of metabolism and oxidative stress. We also reviewed the molecular mechanism of plant salt stress tolerance in the form of the regulation of multiple physical and biochemical response, including the salt overly sensitive pathway, MAPK signal pathway, as well as other protein kinase and abscisic acid mediation. All in all, today's research elevates our understanding of plant salt-resistance mechanisms to an unprecedented level. And yet, further studies on more elements of the signalling pathways are needed to fully understand the mechanisms of plant stress tolerance.

Keywords: Plant Stress Tolerance; Abiotic Environment; Salinity; Salt Stress; Salt Overly Sensitive Pathway; Signal Transduction.

Abbreviations: SOS: Salt Overly Sensitive; ABA: Abscisic Acid; MAPK: Mitogen Activated Protein Kinase; MAPKK: Mitogen-Activated Protein Kinase Kinase; MAPKKK: Mitogen Activated Protein Kinase Kinase Kinase; CDPK: Calcium-Dependent Protein Kinase; RPK: Receptor-Like Protein Kinase.

Introduction

The abiotic environment is critical to the proper growth of plants, and abiotic stresses can negatively impact a plant's ability to thrive in a given environment. Salinity is one of the major environment limitations on plant yield and distribution. Saline soils cover about 3.1 percent of the land surface on earth, and this number goes up to 19.5 percent in irrigated land. Salinity in the soil does much damage to the plants and limits the growth and productivity. However, after thousands of millions of years of evolution, plants do not just retreat from these unfavourable environments. They adapted to the environment changes and developed their mechanism to cope with various types of stress.

Effect of Salinity on Plants

The toxic effect of salt stress includes several aspects. Uptake of excessive Na^+ and Cl^- interferences many Intracellular metabolic processes. High salt concentration in the soil causes osmotic stress, which limits water uptake from soil [1]. High concentration of Na^+ nitration inhibits the absorption of nutrient elements. Meanwhile, ion toxicity and osmotic stress will also cause an imbalance of metabolism and oxidative stress [2]. As a whole plant, the toxic effect of salt stress includes the death of the plant or decrease of production capacity. Almost all plants show growth inhibition with salt stress. However, growth repression level and critical death concentration vary a lot among different plants. Salt stress affects almost all aspects of biological processes, including the growth of the plant, photosynthesis, protein synthesis and the metabolism of protein and phospholipid.

Effect of Salt Stress on Plant Development

Salt stress affects every aspect of plant development from germination to vegetative growth to reproductive growth. Sodium is an essential microelement for plant growth. Low concentration of salt stimulates the growth of the plant, increase the biomass of plants. However, the high concentration of plants inhibited the growth of the plant; reduce the fresh weight and dry weight of root, stem, and leaf [3, 4]. Under low salt stress (50 mM NaCl), the fresh weight of *Alhagi pseudoalhagi* increased. However, the fresh weight decreased with a high concentration (100 and 200 mM NaCl). Excessive concentration of NaCl led to decrease in the biomass of cotton root, shot and leaf [5]. Most plants are sensitive to salinity in the soil. Salt stress can repress the growth of plant tissues and organs, shorten the flowering phase, accelerate the aging, death, and fall off of mature leaves [6].

Under high concentration salt stress, the most immediate response was the decrease of the expansion rate of the leaf surface [7]. Salt stress of 100 mM NaCl can shorten the growing region of sorghum leaf and decrease the speed of the cell growth in this region [8]. Salt stress [6] can also shorten the development of wheat main stem by 18 days. Moreover, the generation of the reproductive structure was brought forward. The flowering period was much earlier than untreated wheat, which indicates that salt stress can accelerate the development of the plant. Meanwhile, the number of phyllopodium and leaves decreased [9]. Salt stress can also decrease the deposit of dry materials and slow down the mature of the cell wall [10]. Similarly, salt stress can change the morphology of the leaf. Salt stress increased the thickness of leaf epidermal cells, mesophyll cell and palisade cell [11]. On the contrary, the thickness and intercellular space of leaf epidermal cells decreased due to salt stress caused by NaCl [12]. Potato leaf cells rounded and the cellular space and the number of chloroplasts decreased after salt stress [13]. Salt stress can also lead to the decrease in the surface area of the leaf and the opening of stomata [14].

Salt Stress affects Plant Photosynthesis

Salt stress affects plant photosynthesis in the short or long term. The short-term effect happens within a few hours to one or two days when exposed to salt stress. This reaction is crucial. Carbon assimilation stopped entirely during this period. However, the long-term effect happens after a few days when the plant was exposed to salt stress [6]. Due to the accumulation of salt in the leaf, the assimilation of carbon decreased obviously [15]. Many research shows that the photosynthesis was suppressed by salt stress [14,16,17]. However, some research shows that the rate of photosynthesis did not decrease under salt stress. The rate was even a little [14] higher than untreated condition [18]. The assimilation rate of carbon dioxide was slightly higher when *Alhagi pseudoalhagi* was treated with low salt. The assimilation rate was not affected when treated with 100 mM NaCl. However, the assimilation rate of carbon dioxide dropped to 60% of the untreated plant when the salt treatment increased to 200 mM. Similarly, stomatal conductance was consistent with the assimilation rate of carbon dioxide. Moreover, the concentration of carbon dioxide in the intercellular space of plants was lower than the control group [18]. The carbon dioxide assimilation rate of *Bidens parviflora* increased under low concentration salt stress but decreased under high concentration salt stress [12].

Thylakoid structure of chloroplasts was disrupted when the plant was treated with salt treatment. The number and size of pellets of the plastid increased, and the starch content decreased [19,20]. Expansion of chloroplasts thylakoid membrane was observed in salt-treated potato [21]. The chloroplasts were found to be aggregated together in the leaves of salt treated tomato. Moreover, no grana and thylakoid structure were observed in chloroplasts [22]. The ultra-microstructure of salt treated *Eucalyptus microcorys* chloroplasts also changed. This will induce the production of numerous starch granules [23].

Salt Stress affects the Ion Homeostasis in Plant

Uptake of too much NaCl impaired the absorption of other nutrient ions, which will lead to the deficiency of K^+. The increase of NaCl in the soil led to the increase of cellular Na^+ and Cl^- and the decrease of Ca^{2+}, K^+, and Mg^{2+} [24,25]. Salt stress can increase the contents of Na^+, Ca^{2+}, and Cl^- in broad bean and decrease the K^+/Na^+ value [26]. The increase of Na^+ and Cl^- in *U. fasciata* induced the accumulation of proline. It decreased the content of proline dehydrogenase (PDH) and soluble Ca^{2+} [27].

The Molecular Mechanism of Plant Salt Stress Tolerance

Plant salt stress tolerance involves the regulation of multiple physical and biochemical response. Many protein and metabolites are involved. This is a process with complicated gene network interaction. Moreover, different plants have different responses and adaptive mechanisms.

Salt Overly Sensitive Pathway

High level of salt stress can lead to Na^+ toxicity, and cause osmotic and oxidative stress, which will repress the growth and development of plants. Under salt stress, plant cells can efflux toxic Na^+ or isolate Na^+ in the vacuole to build new ion homeostasis. There Salt Overly Sensitive (SOS) gene (SOS1, SOS2, and SOS3) were isolated by using genetic methods. These three genes formed the critical SOS signal transduction pathway [28]. SOS1 is a Na^+/H^+ Channel protein with 10-12 trans membrane domains [29]. SOS1 may also be a Na^+ sensor. SOS2 is a Ser/ Thr protein kinase with a regulation domain at C terminal and a catalytic domain at N terminal [30]. SOS3 is a calcium binding protein Located in the cytoplasm. Salt treatment can transiently induce the Ca in the cytosol and this increase of Ca^{2+} can be perceived by SOS3 [31,32]. Then SOS3 will bind to an active SOS2 [33]. The activated SOS3-SOS2 compound can phosphorylate SOS1 and pump Na^+ out of the cell [34]. Any mutation in this SOS pathway will increase plant sensitivity to salt. Overexpression of SOS1 or activation of SOS2 will improve plant salt tolerance [35,36]. Salt stress may also accumulate ABA in the cell. ABA signal can regulate SOS pathway through SOS2. Yeast two-hybrid found that SOS2 can bind to ABA Insensitive2 (ABI2) but not to ABI2 mutant *abi*2, Seedlings of *abi*2 are more sensitive to salt stress [37].

Salt stress can also induce oxidative stress. Research has shown that SOS1 can interact with the protein RCD1 (radical-induced cell death 1). RCD1 is a transcriptional regulator of *Arabidopsis* under oxidative stress. RCD1 is located in nucleus without any stress. However, with salt or oxidative stress, RCD1 is found in both nucleus and cytoplasm. Both sos1 and *rcd*1 mutants are sensitive to oxidative and salt stress [38]. Too much cytosol Na^+ caused by salt stress will inhibit the absorption of potassium. All salt overly sensitive mutants lacked K^+. By screening for the suppressors of sos3 [39], identified AtHKT1, which is a Na^+ transporter. It can transport Na^+ into the cell. The mutant of AtHKT1 can not only compensate the salt-sensitive phenotype of salt overly sensitive mutants. To reduce the cytoplasm sodium, transporting the sodium into the vacuole is a very effective strategy. AtNHX1 is

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a Na^+/H^+ antiporter, which can transport Na^+ into vacuole. The expression of AtNHX1 can be induced by salt stress [40]. AtNHX2 and AtNHX5, which are homologs of AtNHX1, have the similar function in isolating the sodium in the plant vacuole [40-42].

MAPK Signal Pathway

The typical mitogen-activated protein kinase signalling pathway contains three members, which are MAPKKK, MAPKK and MAPK. Plant MAPK involves in development guidance, cell division, plant hormones, biotic and abiotic stress tolerance [43]. Salt stress can active MAPK protein SIMK (salt stress-induced MAPK).SIMKK can activate SIPK. Moreover, the activation can be enhanced by salt stress [44]. Salt stress can induce the expression and kinase activity of many MAPKs. AtMPK6 and AtMPK4 were activated under salt stress [45]. Phosphorylated upstream kinase *AtMKK*2 activated these two MAPKs. The mutant of *mkk2* was sensitive to salt stress [46]. Studies showed that MPK6 could bind to and phosphorylate SOS1. Studies have shown that phosphatidic acid binds to MPK6 after salt treatment [47]. MPK6 immuno precipitated by *Arabidopsis thaliana* under salt stress and increase in phosphatidic acid can increase the phosphorylation of SOS1 [48].

Other Protein Kinase

Protein kinases are essential signal transduction molecules in vivo. In addition to mitogen-activated protein kinases which play a significant role in salt stress signal transduction, many other protein kinases also played critical roles in the signal transduction network under salt stress.

Calcium-dependent protein kinase (CDPK) is a type of signal transduction factor that uses calcium concentration as an upstream signal. CDPK can sense calcium levels by binding to calcium ions and phosphorylate downstream proteins to convert calcium signals to phosphorylated signals. In *Arabidopsis*, AtCDPK1 and AtCDPK2 can be induced by both high salinity stress and drought stress [49]. One of the cloned proteins induced by salt stress, McCDPK, which is located in the nucleus, may be related to transcriptional regulation [50].

There is also a class of proteins located on the cell membrane, which can sense the outside signal and participate in intracellular signalling. These proteins are called receptor-like protein kinase (RPK). RPK1 is a receptor protein kinase located in the cell membrane of *Arabidopsis* that can be induced by high salinity or drought, and there is evidence that it is involved in plant salt [51]. AtGSK1 is also a protein kinase induced by salt stress. It is a glycogen synthase kinase (GSK). Over expression of At GSK1 can enhance the tolerance of *Arabidopsis* to salt stress [52]. Studies have shown that some salt-induced gene expression can be induced by AtGSK1 [53]. GRIK1, upstream kinase of SnRKs can phosphorylate SOS2 in vitro. Moreover, *grik*1 mutants are sensitive to high salt [54].

Abscisic Acid (ABA) Mediated Salt Stress Signal

ABA is a critical plant hormone that plays an important role in many aspects of plant growth and development. It is the best studied in plant drought stress tolerance. ABA also plays an important role in salt stress tolerance. Salt stress can induce the accumulation of ABA in some tissue. Taking corn as an example, the ABA concentration in root with salt stress can be ten times higher than that in leaves [55]. The shrinking of the cells due to osmotic stress also leads to the synthesis and accumulation of ABA, thereby regulating the osmotic stress that caused by over-salinity. ABA controls the cell's water balance by regulating the stomatal switch, and it also regulates the expression of genes that control osmotic synthesis [56,57]. ABA controls the closure of stomatal pore and the expression of downstream genes by modulating Ca^{2+} concentration [58,59].

Under salt stress, ABA can regulate osmotic stress corresponding gene and ion transporter. ABA activates stress response genes RD29A and KIN2 [60]. ABA can also induce AtPLC1 expression. A study of transgenic plants expressing the antisense strand of AtPLC1 found that At PLC1 expression was required for ABA to induce RD22, RD29A, and KIN2 [61]. Genetic screening of the RD29A::LUC reporter gene accelerated the screening of *Arabidopsis* abiotic stress mutants and ABA signaling pathway mutants [62]. Two of the mutants *los5* and *los*6 attenuated the expression of stress response genes under salt stress, such as RD29A, COR15A, COR47, RD22, and P5CS. However, the expression of RD29A::LUC induced by salt stress in mutants could be restored to a reasonable level by the exogenous addition of ABA. They were found to be alleles of ABA3 and ABA1 respectively after cloning the two genes *LOS*5 and LOS6 [63,64]. ABA-deficient mutants *los5* and *los6* were both more tolerant to salt stress during germination. However, *los5* was hypersensitive to salt stress during vegetative growth [63,65]. These results indicate that the expression of salt stress-responsive genes is mediated by ABA. Salt stress and ABA up-regulate the vacuolar Na^+/H^+ transporter At NHX1, while the expression of AtNHX1 in ABA-deficient mutants *aba2-1* and *aba3-1* decreased but not in salt overly sensitive mutants. Mutant *abi1-1* reduced ABA content and salt-induced AtNHX1 expression, whereas *abi*2-1 did not. AtNHX1 also contains ABRE elements, indicating that up regulation of AtNHX1 transcriptional level under salt stress is partly dependent on ABA synthesis and ABA signalling, a process that cannot be separated from ABI1 [66]. The QTL for salt tolerance in the germination period is very different from that of salt tolerance in the seedling stage, which also indicates that the mechanism of salt tolerance during the seedling stage is different from during germination stage [67,68]. The inhibition of salt stress on seed germination is mainly due to the inhibition of ABA by the stress [28].

Studies on Other Salt Stress-Related Mutants

In addition to studies on the above kinases and their pathways, many other mutants related to salt stress have also been found, yet their specific roles in salt stress tolerance remain unclear. *sos4* and *sos5* are two mutants obtained by screening salt hypersensitive mutants, which both exhibit significantly shorter root length than wild-type plants under salt stress. SOS4 encodes a pyridoxal kinase, which participates in the process of pyridoxal 5-phosphate formation. Pyridoxal 5-phosphate is an essential

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molecular chaperone of many enzymes. SOS4 is possibly involved in plant salt tolerance through producing pyridoxal 5- phosphate [66]. SOS5 encodes a cell surface adhesion protein. Its mutant sos5 is sensitive to salt due to failure to expand normally in the absence SOS5 [69]. Ren et al. used the salt stress sensitivity difference between Landsberg erecta (Ler), a salt and ABA sensitive ecotype of *Arabidopsis* thaliana, and Shakdara (Sha), an ecotype that is not sensitive to salt and ABA, to study salt sensitivity. They cloned a salt stress and ABA-induced gene RAS1 using quantitative trait locus technology (QTL). Overexpression of this protein enhanced plant sensitivity to ABA and salt stress [70]. Salt stress leads to the accumulation of reactive oxygen species (ROS) in plant cells. The plant has to response to neutralize the excessive ROS and many enzymes are involved in this process [71,72]. RSA3 is bi-functional protein, which can bind to and stabilize cytoskeleton to minimize the oxidative damage during salt stress in [73].

Conclusion

Salt is essential to any form of life on earth, be it animals, plants or bacteria. Modern biology suggests that it regulates blood flow and pressure in animals, mediates osmosis in plants and that it serves as critical messengers in cellular signal transduction. However, such vital elements are now known to become detrimental stresses to life if exceeding proper amounts. In fact, salt stress is one of the primary abiotic stresses that affect plant growth and decrease in crop yield. In this review, we discussed the damage that environmental salt stress can do to plants and how plant tolerates salt stress on the molecular level. Today's research elevates our understanding of plant salt-resistance mechanisms to an unprecedented level. We discussed multiple signaling pathways with certain identified elements and several common salt tolerance determinants. They make up part of the salt stress signaling network. However, there are other proteins, signal molecules and other mechanisms involved but not mentioned in this review, such as non-coding RNAs and epigenetics regulation. And yet, further studies on more elements of the signaling pathways are needed to fully understand the mechanisms of plant stress tolerance.

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