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REGULATION OF ION HOMEOSTASIS IN PLANS AND DIFFERENTIAL EXPRESSION AND FUNCTION OF ARABIDOPSIS THALIANA NHX Na+/H+ ANTIPORTERS IN THE SALT STRESS RESPONSE

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ABSTRACT

Salinity is a major abiotic stress that limits the growth and the productivity of the plants in so many areas of the world mainly due to irrigation with poor quality of water. Plant adaptation and tolerance to salinity stress involves complex physiological traits, metabolic pathways and molecular networks. Recent research has identified various adaptive responses to salinity stress at molecular, cellular, metabolic and physiological levels, although mechanisms underlying salinity tolerance are far from being completely understood. A comprehensive understanding of how plants respond to salinity stress at different levels is an integrated approach of combining molecular tools with physiological and biochemical techniques are imperative for the development of salt-tolerant varieties of plants in salt-affected areas This review provides a comprehensive review of major research advances on biochemical, physiological, and molecular mechanisms regulating plant adaptation and tolerance to salinity stress.

INTRODUCTION

All the plants that grow under natural environmental conditions come across various types of stresses in their life cycle (fig).The response of the plant to these stresses mostly depends on the plant species and the kind of stress the plant face. Any unfavorable condition or substance that affects or may blocks the plant metabolism, growth, development is regarded as stress or in the other words we can say that when some factors of the environment interfere with the complete expression of genotype potential is called stress.

In plants stress is mainly of two types

1. Biotic stress
2. Abiotic stress

Biotic stress causes the damage to the plants by living organism like fungi, bacteria, insects and weeds. Abiotic stress is a physical (eg light, temperature) or any chemical insult that the environment may impose on the plant. When the threshold limit of stress is reached the plant eventually dies. For example plant diseases and pests decrease the crop yields by less than 10 percent but on the other hand abiotic environmental factors on the other hand can severely affect the crop yield upto 65% of the total crop productivity (Serrano, 1999).In the crop plants there are two vital environmental factors that dramatically reduce crop productivity these are drought and salinity (Zhang *et al*., 2000; Bray *et al*., 2002).These factors mainly cause water stress.

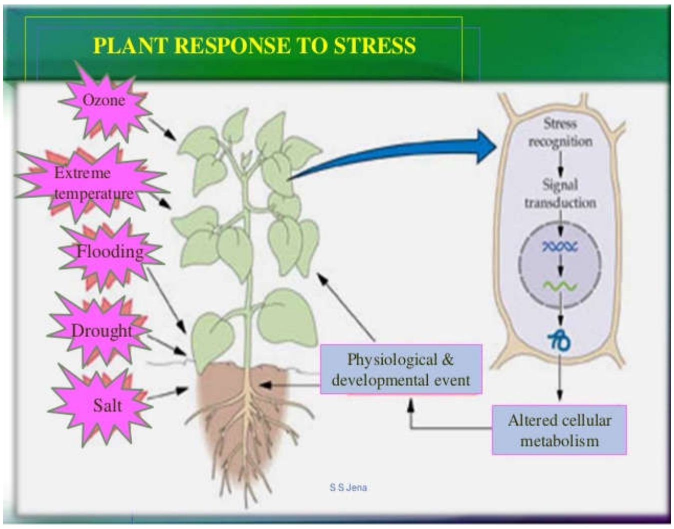

Figure 1 Stresses affecting the yield of agricultural crops under field conditions

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Salinization is a global phenomenon because it affects the farmable lands. The world population is increasing exponentially and it is expected that in the next 20 years the population of world would increase by 1.5 billion. So, it is important to increase the crop yield under salinity stress conditions by applying various genetic and genomic approaches (Blumwald and Grover, 2006; Ismail *et al*., 2007).

Salinity stress: affecting plant productivity and ionic homeostasis in plants

Salt stress is major challenge for the plant. It badly affects the agriculture across the globe mostly on the irrigated farmlands (Rausch, 1996). Large area of the land become saline due to poor irrigation practices. The affect of salinity is becoming more numerous on everyday basis (Winicov, 1998). So; it is an urgent need to improve salt tolerance in plants. There are various factors that mostly contribute to soil salinity and this makes the study of effects of salinity on the plants more complex. Nearly, one third of the irrigated land worldwide is affected by salinity but salinity can also occur in non-irrigated land (Allen *et al*., 1994). Factors such as temperature, light-intensity, irrigation, salinity and soil fertility all alter the effects of soil salinity (Allen *et al*., 1994). As the salt concentration increases the yields are severely affected and move towards zero. The salt level fluctuates seasonally and spatially in the field depending on the circumstances that influence a particular plant. This unevenness makes research much more difficult which is complicated by the fact that each plant species has its own level of salt tolerance.

Plant response to salt stress is rooted in the transcriptional activation of several defense proteins (Chae *et al*., 2010). Osmotic stress and ion toxicity are the consequences of salt stress and decrease in chemical activity that causes cell to lose its turgor (Serrano *et al*., 1999). Since plant cell growth depends on turgor that stretches the cell wall. Plants defense mechanism against salinity requires osmotic adjustment and to a certain level, this can be done through synthesis of intracellular solutes (Shoumskaya *et al*., 2005).Salinity creates ion toxicity and high sodium concentration is not good for cells. High salt concentrations reduce enzyme activity by impending the balance of forces that control the protein structure (Liu *et al*., 2006). Salt toxicity can occur at very low concentration and depending on the plant species. So, homeostasis of sodium is important for the tolerance of plants to salt stress. The stress caused by ion concentrations decreases water gradient thus making it more intricate for water and nutrients to move through the root membrane (Volkmar *et al*., 1998). As a result, water uptake slows down and the osmotic effect spreads from the root membrane to the internal membrane-the ion concentration inside the plant changes the osmotic balances (Volkmar *et al*.,1998). The overall effect of salinity on plants is final reduction of leaf size, which leads to loss of leaf and finally the plant. Salinity also causes reduction in the ATPs and growth regulators which are required for normal functioning of plants (Allen *et al*., 1994).

The ability of plants to grow and survive under saline conditions is known as salt tolerance. Plants adapt various processes and mechanisms to respond to salt stress which in turn is a multigenic response (Nagarajan and Nagarajan, 2010). A fundamental two-phase model explains the overall growth response of plants to salinity. An initial water deficit that lasts for few days or weeks followed by a second phase which starts where the ion toxicity initiates leaf death (Rausch *et al*., 1996). Exclusion of salts from shoot portion of the plant is a prime form of tolerance in non-halophytic plants. In plant system, most of the sodium going from the root to shoot region is via the xylem stream (Robinson *et al*., 1997). The ability of plants to offset stress also depends on the potassium levels available to the plant (Maathius an d Amatmann, 1999).Potassium is an important component of plants which works as balancing charge and is also vital for plants to counter balance the excess salt. On the other hand, sodium is essential only for C4 species where it works as a micronutrient (Maathius and Amtmann, 1999). The sodium ion that competes for the potassium binding sites in the cytoplasm inhibits metabolic processes that largely depend on potassium. Broad range of salinity tolerance among higher plants (Robinson *et al*., 1997) but variation also persists in plants with lower salt tolerance. Sodium to potassium ratio in cell is regulated by transport systems which are present on plasma and vacuolar membranes. There are three processes which are involved in the transportation of these ions. Pumps are transporters fueled by energy and transport across an electrochemical gradient but no pumps are found in higher plants (Carden *et al*., 2003).

Plants possess several mechanisms to deal with salt stress and to adjust to a saline environment. Roots play vital role for short term adaptation to salt tolerance. It is found that morphology of the roots regulate the amount of salt taken into the plant (Maggio *et al*., 2001). Many studies have also shown that salt stress can also alleviated by an increased supply of silica and calcium to the growth medium (Rausch *et al*.,1996;Tuna *et al*.,2008;Ali *et al*.,2009). Sodium and calcium can replace each other from the plasma membrane and calcium might reduce salt toxicity.

Bottleneck for raising stress tolerant plants

Development and growth in the plants involves gene and gene products of large number. In the plants during stress the various biochemical metabolism that function normally in plants are negatively affected that leads low productivity. Salt stress causes up regulation and down regulation of the numerous genes (Kawasaki *et al*.,2001). In order to raise transgenic crops assortment of genes from given gene pool is required which is complex task. In ancient times efforts have specifically been made to understand the components of both the abiotic stress signal recognition and the transduction pathways (Zhu, 2001; Chinnusamy *et al*., 2005) and leads to raise transgenic plants which may show improved stress tolerance.

Efficient and new tools are now accessible to understand better about the genetics of abiotic stress tolerance (Kasuga *et al*.,1999) and to identify the various complications of the stress response that are essential for the production of stress tolerant transgenic plants (Sabharwal *et al*.,2010).

An overview on SOS pathway

Sensing and responding to various ecological perturbations are significant for all living organisms. Plant maintains the ion homeostasis by keeping the toxic ion concentrations below the threshold limit. So many molecular mechanisms are involved when plants responds to adverse environments such as soil salinity and drought besides others. For cytosolic enzymes to function properly intracellular K^+ and Na^+ homeostasis is crucial as excess of Na ions pose toxicity for cellular metabolism (Amtmann and Leigh, 2010). Potassium plays important roles in so many processes including metabolism, growth and stress adaptation. So, the K and Na ion homeostasis becomes more under salt stress conditions. Any disturbance in the Na ion due to salt stress leads disastrous pathologies and badly affects cell survival, growth and division. As a result the concentration of Na is to be kept low in the cytosol. The JK Zhu laboratory at university of California, U.S.A. recently pioneered the identification of salt tolerance determinants using forward genetics in the plant model Arabidopsis (Hasegawa *et al*.,2000a; Sanders,2000;Zhu,2000). This effort has identified three complementation groups of ion hypersensitive (SOS) mutants. Physiological and genetic data indicate that SOS3, SOS2 and SOS1 are components of signal pathway that regulates ion homeostasis and salt tolerance and their functions are calcium dependent.SOS1 encodes the putative plasma membrane Na/H antiporter and SOS2 encodes the Suc non-fermenting like (SNF) kinase and SOS3 encodes a Ca 2+ binding protein with sequence similarity to the regulatory subunit of calcineurin and neuronal Ca^{2+} sensors (Liu and Zhu, 1998; Liu *et al*., 2000; Shi *et al*., 2000).Molecular analysis indicate that SOS3 is required for the activation of SOS2 that regulates the SOS1 transcription (Halfter *et al*.,2000;Shi *et al*.,2000). Signal pathway is SOS3-SOS2-SOS1 (Hasegawa *et al*., 2000a; Sanders, 2000; Zhu, 2002).

Plant growth under stress and normal conditions are mediated by chemicals like calcium ions (Ca^{2+}) that function as secondary messenger molecule (Boudsocq and Sheen, 2010). Membrane receptors are first perceives the extracellular stress signal which activate complex signaling cascade intracellular such as generation of calcium ions. Than these calcium ions begins the stress signaling pathway for stress tolerance. It is recently discovered that calcium sensor calcineurin B like proteins (CBLs) and their interacting partners CBL- interacting protein kinases (CIPKs) have appeared to be play very important role to the calcium and stress signallig.CIPK starts phosphorylation cascade that again regulate down- stream components for stress tolerance.

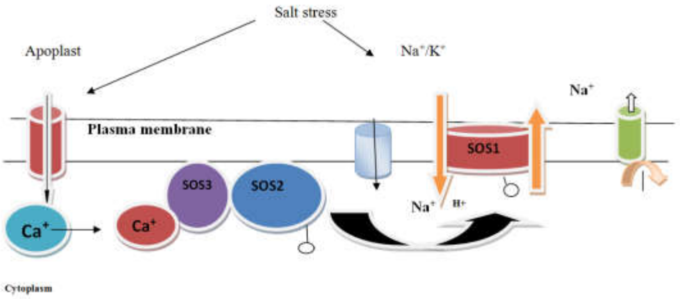
SOS 1: plasma membrane Na^+/H^+ antiporter

SOS 1 is plasma membrane Na^+/H^+ antiporter in Arabidopsis is salt tolerant determinant used for maintenance of ion homeostasis in saline stress conditions. In normal conditions SOS1 mRNA is unstable but its stability is increased under salt stress and other ionic dehydration stresses (Zhu *et al*., 2008).Comparison of the ORF with genomic sequence has disclosed that SOS1 is composed of 22 introns and 23 exons. Further analysis with computational approach revealed that SOS1 encodes the polypeptide of 1146 amino acid residues with the molecular mass of 127 kDa. C-terminal region of SOS1 is highly hydrophilic in nature. C terminal hydrophilic tail makes SOS1 the largest known Na^+/H^+ antiporter sequence. Phylogenetic analysis has revealed that SOS1 is closely associated with the plasma membrane antiporters such as SOD2 (Superoxide dismutase), NHA1 NHaA and NhaP.NHA 1 functions in the plasma membrane and mediates Na^+ and K^+ efflux (Banuelos *et al*., 1998).With the help of hydrophobic plot analysis it is revealed that N terminal region has hydrophobic nature and has 12 predicted transmembrane domains.

SOS1 has also been isolated from Populus euphratica growing in semi-arid saline areas.PeSOS1 showed 64% sequence identity with AtSOS1 (Ding *et al*., 2007).Recent study on the model plant Arabidopsis thaliana suggested the roles of the SOS 1 protein with its function as a Na^+/H^+ antiporter whose disruption affected membrane traffic and vacuolar functions possibly by controlling pH homeostasis in the root cells (Oh *et al*., 2009).

SOS2: Ser/Thr protein kinase

Jian-kang Zhu and his coworkers in 1997 first isolated the SOS2 gene by using positional cloning method. This gene was found crucial for sodium and potassium ion homeostasis and salt tolerance (Liu *et al*., 1997).Phosphorylation with the help of protein kinase is considered most important regulatory mechanism.PKSs and CIPKs are large family of 25 protein kinases in Arabidopsis thaliana are like SOS2 protein kinase (Guo *et al*.,2001;Luan *et al*.,2002;Mahajan *et al*.,2006).



Interaction of SOS2 with other factors in response to salt stress

Both the SOS pathway and SOS2 is point of cross talk between salt stress and other stress signals and stress response (Chinnusamy *et al*., 2005; Pardo *et al*., 2006, Zhu, 2003).The SOS2 kinase has been considered as an one of the important regulatory component through its interaction with other signaling proteins. Being a vital part of the SOS signaling pathway, the regulatory region of SOS2 has been shown to interact with SOS3 (Halfter *et al*., 2000).SOS2 also interacts with the ABA insensitive 2 protein phosphatase 2C with the help specific protein phosphatase interaction domain (ohta *et al*., 2003).It has been found that SnRK3s or CIPK interact with ABI 1or ABI2 but not with the both. So finding of other proteins that interact with the SOS2 remains a potential approach towards better understanding of the stress signaling. The interaction of SOS2 with ABI2 suggests correlation to the other aspects of stress signaling (Ohta *et al*., 2003).Other SnRK3 kinases also involved in the signaling mechanisms controlling responses to the environment and hormone response mainly ABA signal transduction (Guo *et al*., 2002). SOS2 has been also found to be associated with catalase 2 (CAT2) and CAT3 and that further associates SOS2 to H_2O_2 metabolism and signaling. So the interaction of SOS2 with both the NDPK2 and CATs reveals a point of cross talk between salt stress response to other signaling factors including H_2O_2 (Verslues *et al*.,2007).

Biochemical characterization of SOS2

The mechanism of regulation and the biochemical characteristics of SOS2 and its kinase activity are not fully understood. Regulation of the protein kinases can be achieved by different mechanisms which includes protein phosphorylation by many other kinases (Elion, 1998), autophosphorylation (Cooper and MacAuley, 1988; Sato *et al*., 1996). The key feature of regulation in protein kinases is thought to be the phosphorylation of many residues within the activation loop of the catalytic subunit (Vertommen *et al*., 2000;McCartney and Schmidt,2001). The unphosphorylated activation loop can block access of substrate to the active site but the phosphorylation can cause an outward rotation of the activation loop and makes substrate accessible to the active site residues for catalysis (Jeffrey *et al*.,1995;Sicheri and Kuriyan, 1997; Xu *et al*.,1999). It is found that SOS2 protein produced in bacteria exhibits no substrate phosphorylation activity in the absence of SOS3, although it has autophosphorylation activity (Halfter *et al*., 2000).

Structural domains of SOS2

As the level of salt stress increases inside the cell the level of intracellular calcium get increases which is sensed by the calcium binding protein SOS3. After binding with calcium the confirmation changes takes place in SOS3 and it interacts with the SOS2. This interaction is further supported by the sos2sos3 double mutant analysis which shows that these two genes function in same pathway (Halfter *et.al*.,2000). In case of Arabidopsis,SOS 2 encodes ser/thr protein kinase with an N-terminal catalytic domain which is similar to SNF/AMPK and novel C-terminal regulatory domain (Liu *et.al*.,2000).In order to make SOS2 functional both the catalytic and regulatory domains are necessary. It is studied that 37 amino acid domain of SOS2 which is designated as the protein phosphatase interaction motif and it is important for interaction with ABI2 (Ohta *et.al*. 2003).

SOS 3: Calcium binding protein

SOS3/CBL4 is a small myristoylated protein that seems to have no enzymatic activity by itself so the binding of calcium and myristoylation are required for SOS3 function in the salt tolerance (Ishitani *et al*., 2000). SOS3 senses the change in the calcium ion concentrations and it transduces the signal downstream. The binding of calcium with SOS3 is very low as compared to the other calcium sensors (Ishitani *et al*., 2000).SOS 3 encodes a noval EF hand Ca $^{2+}$ sensor and it is also called as CBL4 (Liu and Zhu,1998).SOS3 shares the sequence similarity with the regulatory calcineurin B subunit from the yeast (Saccharomyces cerevisiae) and the neuronal Ca^{2+} sensors from animals (Klee *et al*.,1988).SOS3 is myristoylated which may help to target SOS3 and its interacting proteins(e.g.,SOS2) to membranes where their target transporters are located (SOS1).

Soil salinity is the one of the major abiotic stress that decreases the plant growth and productivity. It was reported recently that plants over expressing AtNHX1 or SOS1 have significantly increased salt tolerance. From the research it is found that transgenic plants which ;over express the SOS3 exhibit the increased salt tolerance that is similar to the plants over expressing SOS1.

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