Adaptive and Tolerance Mechanism of Plants to Salt Stress

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Abstract: ***Salt tolerance can be expressed as a percentage of biomass produced in saline soil relative to plants growing in non - saline soils over a specific period. Salt stress causes a series of physiological, biochemical, and molecular changes, including the synthesis of specific proteins, free radical scavenging enzymes, SOS signaling pathway, osmolytes intensification, development of specific ion channels, and so on. Plants' tolerance to salt stress is the result of the coordination of multiple stress - responsive genes, which may also interact with other components of stress signal transduction pathways. The search for salt - tolerant germplasm is critical for developing new varieties for secure sustainable agriculture, particularly in semi - arid areas with harsh climatic conditions. In recent decades, conventional breeding has contributed substantially to crop development. Molecular breeding approach can help to reduce time to develop new varieties in much shorter time for this understanding of salt tolerance molecular mechanism is essential. This chapter describes the biochemical response, physiological response, various ion pumps, and signal transduction pathways under salt - stress condition.***

Keywords: Salt stress tolerance, Adaptive mechanism, Salt stress response, Osmolytes.

1. Introduction

The process of increasing the concentration of soluble salts on or near the soil surface is known as salinization, and it is a long - term phenomenon (Szabolcs, 1974). Saline soils are defined as having high concentrations of soluble salt with an electrical conductivity (ECe) more than 4 dSm - 1. The type of irrigation water and its quality determine the salinity and fertility of the soil. The salinization process is found worldwide and is more extensive in arid and semi - arid regions it is a major problem leads to soil degradation with an adverse effect on agricultural production and leads to negative economic and social consequences (De Jong, 1992; Metternicht and Zinck, 1997). Identification of saline soils and estimate of the degree of severity is vital for sustainable agricultural management. Soils are classified into two group's saline and alkali (sodic) based on pH, accumulation of knowledge, characteristics features, physicochemical and biological properties, and geographical and geochemical distribution (Szabolcs, 1974). There are likely to be intermediate attributes in addition to the two mentioned categories (Fig.1).

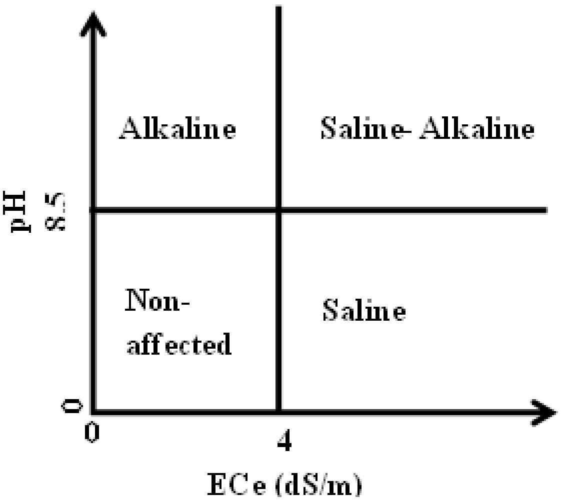

Figure 1: Traditional classification of soil into saline, alkaline, and saline - alkaline soils (Richards, 1554).

Saline and Sodic soils: Excess salts on the soil surface and in the root zone of plants cause the accumulation of sulphates and chlorides of sodium, magnesium and calcium which affects electrical conductivity (EC). If the concentration of salts is high, precipitation of salts occurs, resulting in the formation of salt crystals and salt crusts. The procedure eventually has the effect of raising the concentration of sodium and chloride ions in soils and underground water. On top of the salty soils, deposits of sodium sulphate (Na_2SO_4), calcium chloride ($CaCl_2$), magnesium chloride ($MgCl_2$), or nitrates often have a distinctive fluffy appearance and loose, porous granular structure. The salt - affected areas are classified into non - saline, slightly saline, moderately saline, very saline, and extremely saline based on pH and electrical conductivity (EC) (Table 1).

According to FAO (1988), soil alkalinization process is defined as hydrolysis of exchangeable cations or salts such as Na_2CO_3, $MgCO_3$ and $CaCO_3$. Sodic soils also termed 'Alkali' in older literature and are characterized by the presence of sodium carbonate and bicarbonates in soils, leading to high pH values between 8.5 and 10 and capable of alkaline hydrolysis, mainly Na_2CO_3 (FAO, 1988). As exchangeable sodium concentrations rise, the physical characteristics of the soils deteriorate due to increased soil dispersion, which results in decreased infiltration, hydraulic conductivity, and surface crusting.

Table 1: Soil salinity classes in terms of ECe (Richards, 1954).

Salinity class	ECe (dS/m)	Salinity effects on crops
Non - saline	<2	Salinity effects are negligible
Slightly	2 - 4	Yields of very sensitive crops may be restricted
Moderately saline	4 - 8	Yields of many crops restricted
Very saline	8 - 16	Only tolerant crops yield satisfactory
Extremely saline	>16	Only a few very tolerant crops yield satisfactory

Effect of salinization on plant growth: Abiotic stress inhibits cell growth, root growth, and shoot growth, as well as inhibiting cell expansion and reducing cell wall synthesis. It also has an impact on the light reactions,, energy charge, proton pumping and carbon - reduction cycle all of which result in the formation of toxic molecules (Chaitanya, 2003). Any crop species or variety's ability to tolerate salt may change depending on the environmental circumstances as well as at different stages of the plant's growth, such as seedling, flowering, maturity, etc. (Munns, 1993). Compared to any other developmental stage, the majority of crops are more vulnerable to salinity during germination. High salt concentrations in the soil have negative impacts on plant growth as well as the microbial population's activity. Due to salts' harmful effects on rhizobia, symbiotic nitrogen fixation was decreased. The negative impact of salts on the microbial population is because of loss of nitrogen as NO_3^- which further reduces the nitrification rates. The majority of crops, especially in developing nations where traditional agriculture is practiced, are susceptible to salinity and are frequently expensive for farmers. Crop yields were not greatly affected by salinity until a certain point, beyond which they declined relatively linearly as salinity increased above the threshold point. The biomass of pea cv. Lincoln was reduced at 70 mM and another cultivar Puget was relatively tolerant to 70 mM, whereas these two cultivars' growth was not affected at 50 mM NaCl (Hernandez et al., 2001). Instead of focusing selection at one specific growth stage, it is crucial to have adequate knowledge about the degree of salt resistance at all developmental phases of crop species. To find the salt - tolerant genotypes, substantial efforts have been made and identify salt tolerance germplasm at the varietal level. Reduced growth rate together with a reduction in the number of leaves and leaf area are the main defining characteristics of saline toxicity to plants. Hussain et al., (2002) investigated the effect of salinity on Trifolium alexandrinum and discovered that total green and dry weight decreased sequentially as salt concentration increased. In various experiments, it has been found that root growth is typically less impacted than shoot growth and that having a greater root: shoot ratio at lower salinity levels. Other experiments revealed that, only at higher salinity levels, root growth appeared to be more responsive to salinity than shoot growth. Data on crop tolerance regarding growth stage was examined by Maas and Hoffman (1977) and Maas (1984) who noted that tolerance pattern of barley, wheat, and maize was remarkably similar to that of rice.

According to Lauter et al. (1981), chickpea shoot growth was negatively impacted more than root growth. A similar pattern was shown in chickpeas under salt stress, and shoot dry weight decline was reported to be greater than that of the roots (Dua, 1998). Cordovilla et al. (1996 & 1994) discovered that the presence of salt stress significantly inhibited faba bean growth. At 16 dS m^{-1} EC of saline water, three chickpea varieties, BG - 256, PUSA - 939 and PUSA - 1053 showed a more than 50% reduction in number of leaves, dry weight and lateral branches growth rate of shoots, roots, and leaves; additionally, plants showed delayed flowering, fewer flowers, decreased pod setting, and eventually produced fewer seeds (Mudgal, 2009).

Strategies adapted by plants to salinity: Salinity stress adaptation is a complex phenomenon, and plants have developed numerous strategies to deal with salt stress, including the accumulation of compatible solutes, increased antioxidant levels, and the reduction of energy - consuming pathways. The effects of salinity on plants have been schematically presented in Figure 2. Salts inhibit plant growth in two ways: osmotic or water - deficit effect and salt - specific or ion - excess effect. Plant exhibit first and second phases of adaptation in response to salt stress. In the first phase, the salt outside the roots causes a rapid decrease in plant growth rate, which creates the water stress or osmotic phase. Low uptake of sodium ions had a higher survival rate and the rate of growth reduction depends on the species/varieties of plant. The second phase adaptation takes time to develop and it is due to internal injury. Continuous transport of salts in the plants eventually results in accumulation of Na^+ and Cl^- ions and enhances the senescence of old leaves and the rate of old leaf senescence is essential for the survival of the plant. If the rate at which new leaves are produced exceeds the rate at which old leaves die, the plant may survive. Excessive salts enter the plant transpiration stream and can be toxic, causing cell damage (Munns, 2002). Salinity impacts the availability, transport, and partitioning of minerals including Mg^{2+}, NO^3, Ca^{2+} and K^+, that are essential for plant growth because Na^+ and Cl^- ion compete with the uptake of nutrients (Hasegawa et al 2000; Hu and Schmidhalter, 2005).

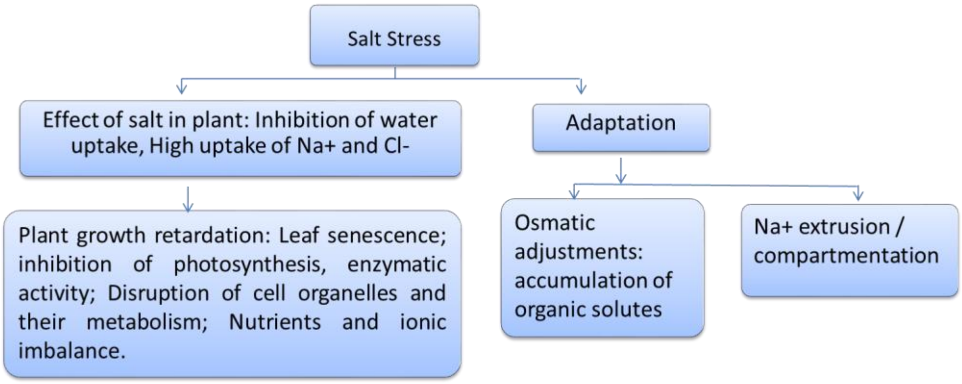

Figure 2: Effect of salinity and adaptation pathway established by plants.

Salt tolerance mechanism: Plants can survive in saline conditions as long as they continuously take up water and expel a significant portion of the salts. Depending on tolerance to salt stress, plants are classified into halophytes and glycophytes groups. Halophytes can withstand salt shocks and can grow at salt concentrations of 200 mM or higher, while glycophytes cannot survive in these conditions (Flowers and Colmer, 2008). In some species, higher salt concentrations of even more than 200 mM are noticed in leaves while still functioning properly; this is attributable to a vacuole sequestering salts and keeping the salt out of the cytoplasm. Enzymatic reactions were inhibited and seriously affected in vitro at concentrations of 200 mM Na$^+$ in glycophytes (Munns, 2002). Salt - tolerant plants use several adaptive strategies, including osmotic stress tolerance, ion exclusion, and ion inclusion (Munns and Tester, 2008). Significant progress has been made in identifying the genes, proteins, and transporters that are responsible for salt stress. Ion toxicity is typically associated with an excess of Na$^+$, Cl$^-$, and other ions, which causes nutritional imbalance. Plants develop various strategies to maintain the K$^+$/Na$^+$ ratio under salt stress conditions, such as restricting excess salts in the vacuole in different tissues to facilitate normal biological functions known as ion compartmentalization (Zhu, 2003). Ion movement into the vacuole may occur directly from the apoplast to the vacuole via membrane (Hasegawa et al., 2000). Salinity and drought stress cause similar biochemical responses, such as osmolyte accumulation and an increase in reactive oxygen species (ROS) levels (Fig.2) (Zhu et al., 2001; Sivakumar et al 2020). Plants must maintain a high cytosolic K$^{+:}$ Na$^+$ ratio to survive in salt - stress conditions (Sivakumar et al 2020). When plants are exposed to salt stress, they undergo osmotic adjustment. To balance the osmotic pressure, organic solutes such as glycine betaine, soluble sugars, free amino acids and proline accumulate in the cytoplasm (Ashraf and McNeilly, 2004; Sivakumar et al 2019).

Ion compartmentation and Ion exclusion: Ion compartmentation is another mechanism developed in many plants to tolerate the high salt concentration (Munns and Tester, 2008). Plants can reduce or delay the harmful effects of higher ion concentrations by compartmentalising salts inside the vacuoles of mesophyll cells. The Na$^+$ was excluded from the cytoplasm into vacuoles, and this key mechanism allows for the maintenance of optimal K$^+$, Ca^{++}, and Na$^+$ concentrations in the cytosol (Tester and Davenport, 2003). Those species that lack salt compartmentalization in vacuoles eventually result in an excessive salt build - up in the cell, which leads to death via dehydration or poisoning of metabolic systems such as photosynthesis or respiration. Thus, controlling the rate at which salts enter the leaves and compartmentalization is critical for controlling the senescence of old leaves. According to current knowledge of ion compartmentation, higher levels of sodium accumulate in older leaves.

Because the ionic radius of Na$^+$ and K$^+$ is similar and it is difficult to distinguish the transporters, Na$^+$ enters the cell and causes cytoplasmic toxicity (Munns and Tester, 2008). The Na$^+$/H$^+$ antiporters, Na and K transporters, ion channels, ABC - type transporters, plasma membrane, and vacuolar ATPases transport proteins involved in ion homeostasis and essential for salt tolerance in compartmentalization and Na$^+$ exclusion under salt stress (Apse et al., 2003). The expression and activity of Na$^+$/H$^+$ antiporters, V - type H$^+$ - ATPase and H$^+$ - PPase, determine Na$^+$ compartmentation into the vacuole. These phosphatases generate the proton gradient required for the activity of Na$^+$/H$^+$ antiporters. The production of salt - tolerant germplasm with a greater K$^+$/Na$^+$ ratio may be the goal of manipulating the Salt Overly Sensitive (SOS) pathway, which is involved in ion homeostasis. The accumulation of Na$^+$ in the vacuole not only lowers the concentration of Na$^+$ in the cytoplasm but also contributes to osmotic adjustment in order to maintain water uptake from saline solutions. Plastids and mitochondria may also store some Na$^+$ and hence contribute to the overall subcellular compartmentation of Na$^+$. Ion exclusion is an important salt tolerant mechanism in some plant species, in which plant roots exclude most of the ions such as sodium and chlorides dissolved in soil solution and escape from salt accumulation in shoots at toxic levels (Munns and Tester, 2008).

Ionic interaction under salt stress: Pectins and phospholipids in cell membranes have a higher affinity for Ca^{++} ions than for Na+ ions, but an excess of Na$^+$ ions in the cells disrupts the ionic interaction of Ca^{++} with these substances. Due to the considerable physiochemical similarities between K$_+$ and Na$^+$ ions, excess Na+ prefers to bind to the active site of enzymes. This leads to having a negative impact on cellular biochemistry, such as high - affinity K$^+$ transporters of the KUP family and NO3$^-$ transporters (Maathuis, 2006; Santa - Maria et al., 1997). In four grain legumes, higher K$^+$ levels were found in the root than in the shoot, and higher Na$^+$ content was found in both the shoot and the roots of common bean (Phaseolus vulgaris L.), soybean (Glycine max L.), pea (Pisum sativum L.) and faba bean (Vicia faba L.), (Cordovilla et al., 1995a and b). While tissue Cl - and Na+ ion concentrations significantly increased in four wild and two cultivated Phaseolus species in response to salt treatment, and noted K+ concentrations decreased (Bayuelo - Jiménez et al., 2003).

Osmolytes, Ionic channels and various factors involved in Salt stress response: The initial step in a plant's response to salt stress is the perception of the signal by cell receptors like histidine kinase, G - protein - coupled receptors, and ion channels. The generation of various secondary signal molecules, including calcium, glycine betaine, proline, ROS, inositol phosphate, and ABA, is triggered by receptors' sensing of salts in the root zone. The expression of early or delayed stress - responsive genes is transduced once the plant detects the signal. Several transcription factors that express within a few minutes and often transiently can activate the expression of delayed stress - responsive genes. The salt stress signal activates the SOS pathway, which aids in the regulation/activation of various mechanisms/ pumps/ channels. Histidine kinases, Na^+/H^+ antiporters (SOS1), Nonspecific cation channels (NSCC), K^+ outward - rectifying channel (KOR) and K^+ inward - rectifying channel (KIRC) are among the various mechanisms/pumps/channels (KORC). Finally, the plant responds to salt stress in one of three ways: adaptation to salt, growth inhibition, or cell death, depending on the plant genotype.

The presence of an excess of soluble salts in the root environment limits the availability of water and decreases water potential is responsible for osmotic potential, which causes water stress in plants. A major category of organic osmatic solutes such as quaternary amino acid derivatives (glycine betaine, proline), simple sugars (glucose and fructose), sugar alcohols (trehalose, raffinose and fructans), sulfonium compounds (dimethyl sulfonium propionate) and tertiary amines (1, 4, 5, 6 - tetrahydro - 2 - methyl - 4 - carboxy pyrimidine) protects the cells from salt stress (Zhifang and Loescher 2003).

Glycine betaine (N, N, N - trimethylglycine betaine) is one of the most extensively researched compatible major osmolytes, assisting plants' protective mechanisms in response to stress by maintaining osmatic status and stabilizing macromolecules (Rontein et al., 2002). The enzymes choline monooxygenase and betaine aldehyde dehydrogenase act on choline to produce glycine betaine. The expression of the Arthrobacter globiformis choline dehydrogenase gene (codA) in rice and the N - methyl transferase gene in cyanobacteria and Arabidopsis improved salinity tolerance (Vinocur and Altman, 2005). Plants under salt stress treated with glycine betaine exhibited significant Na^+ decrease and increased K^+ concentrations in shoots when compared to untreated plants, implying that it plays a role in signal transduction and ion homeostasis for tolerance.

The important imino acid proline together with other amino acids serine, leucine, alanine, glycine, arginine and valine and non - protein amino acids, citrulline and ornithine have been reported to accumulate in higher plants under salinity stress (Mansour, 2000). Proline is one of the important most widely developed osmolytes and plays an important role in scavenging free radicles, buffering redox potential, up - regulate the activity of several antioxidants under stress conditions and correlating with osmatic adjustment (Vinocur and Altman, 2005). Pyrroline - 5 - carboxylate synthetase (P5CS) and pyrroline - 5 - carboxylate reductase (P5CR) enzymes are responsible for the synthesis of proline in plant. Kishor et al., (1995) reported that overexpression of the P5CS gene in tobacco resulted in improved production of proline, which leads to tolerance towards salinity and drought. The external application of proline helps with osmoprotectant and aided the growth of salinity - stressed plants. Accumulation of carbohydrates such as sucrose, hexoses and sugar alcohols under stress conditions has been observed in various plant species. The sugars stabilize the membrane structure by acting as an osmoprotectant and are assumed to prevent membrane fusion. Several reports are confirming a strong correlation between stress and sugar accumulation (Taji et al., 2002; Bartels and Sunkar, 2005).

Molecular mechanism of salt tolerance:
Calcium plays a very crucial role in signaling of salt tolerance. Plants respond to high salinity, with the accumulation of cytosolic Ca^{++}. The phospholipases - C hydrolyze the phosphatidylinositol biphosphate to inositol trisphosphate and the subsequent release of Ca^{++}. The sensor proteins recognize Ca^{++} levels and transmit the information downstream and initiate a phosphorylation cascade, leading to salt - responsive gene expression. Calcium along with abscisic acid and pholipase - D acts as a negative regulator of proline biosynthesis in *Arabidopsis thaliana* (Thiery et al., 2004).

Abscisic acid (ABA) is a plant hormone that regulates plant growth and development in addition it plays an important role in environmental stress and plant pathogen including salinity stress (Zhu, 2003; Chinnusamy et al., 2004). Under salt stress conditions, expression of ABA synthesis pathway enzymes such as zeaxanthin oxidase, 9 - cis - epoxy carotenoid dioxygenase, ABA - aldehyde oxidase, and molybdenum cofactor sulfurase up - regulated through a calcium - dependent phosphorylation pathway in plants (Chinnusamy et al., 2004). Kinight et al., (1997) reported that calcium has a role in ABA - dependent induction of the P5CS gene during salinity stress. Accumulation of proline in plants may be mediated by both ABA - dependent and independent signaling pathways (Zhu, 2003).

Reactive oxygen intermediates (ROI) such as singlet oxygen, superoxide radical, hydrogen peroxide, and hydroxyl radical were developed during stress and enhanced production of ROIs becomes a threat to plants. Mitochondria, chloroplast, and microbodies with a very much oxidizing metabolic activity are major sources of ROS production in plant cells. Catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione reductase (GR) and guaiacol peroxidase (GPX) are ROS scavenger enzymes that are present in plants, and make use of complex anti - oxidant system to overcome the salinity induced oxidative stress. The primary request for an anti - oxidant system includes carotenoids, ascorbate (ASC), glutathione (GSH) and tocopherols, and the above - mentioned enzymes. Kukreja et al., (2005) analyzed higher activities of SOD, POX, ascorbate peroxidase (APX), glutathione transferase (GTase), GR, and CAT in the presence of salt stress in roots of *C. arietinum* plants.

K^+ inward - rectifying channels (KIRC) are highly selective for K^+ over Na^+ and they are the first plant ion channels to be identified at a molecular level and present in most plant cell types and involved in many physiological processes (Maathuis and Sanders, 1995). The isolation of *akt1 - 1* mutant revealed the simple division of carrier - mediated K^+ transport with a high affinity. The *akt1 - 1* null mutant and wildtype exhibited comparable salt sensitivity suggesting a negligible role for AKT1 in Na^+ uptake (Hirsch et al., 1998). The key purpose of K^+ outward - rectifying channels **(**KORCs) is assumed to be in relieving the membrane potential or providing K^+ release and influx of Na^+ and these channels open during depolarization of plasma membrane (Maathuis and Sanders, 1995). Probably KORCs could play a role in facilitating the inflow of Na+ into plant cells. Wegner and Raschke (1994) reported KORC channels of barley roots disclosed a high selectivity for K^+ than Na^+. Roberts and Tester (1997) showed that opening of the KORC results in an increasing Ca^{++}, suggesting that the opening of these channels might effect in an increase of cytosolic Ca^{++} with the associated stimulation of other ion channels.

SOS1 is a Na^+/H^+ antiporter, and the sos1 mutant was hypersensitive to salt. Removal of Na+ out of the cytosol takes place by the movement of H+ inside cells and it is powered by the electrochemical gradient generated by H+ - ATPases. Research on Salt Overlay Sensitive mutants in *Arabidopsis* results in identification of SOS1, SOS2, and SOS3 genes (Wu et al.1996). The SOS3 gene encodes the Ca^{+2} binding protein (calcineurin B - like protein, CBL, calcium sensors) and senses the cytosolic Ca^{+2} concentration in the cytosol, and transduces the signal downstream. Loss of function of SOS reduces the Ca^{+2} binding capacity which leads the plant hypersensitive to salt (Zhu, 2002). SOS2 encodes CBL - interacting protein kinase (CIPK), a serine/threonine protein kinase and it is activated by SOS3 in a calcium - dependent manner (Mahajan et al., 2008). The SOS3 - SOS2 kinase complex was found to phosphorylate the SOS1 directly and these three SOS1, SOS2 and SOS3 function in a common pathway of salt tolerance (Zhu, 2002). The SOS pathway also crosses talk or interacts with NHX, and CAX1 systems for Na+ sequestration to maintain cellular ion homeostasis. The AtNHX family of Na^+/H^+ antiporters function in Na^+ compartmentation in Arabidopsis AtNHX1 and AtNHX2 are present in the tonoplast membrane and they levelled upregulated during osmotic stress (Yokoi 2002). The electrochemical gradient created by H^+ - ATPases drives Na^+ elimination from cells, allowing the NHX to couple the passive movement of H^+ inside along the electrochemical gradient and extrusion of Na+ out of the cytosol.

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