

INFLUENCE OF SALT STRESS ON SOME CHARACTERISTICS OF PLANTS

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ABSTRACT

Sodium chloride (NaCl) is one of the most important components of salt and saline soils, which is caused by Na⁺, composing a major part of all the salt affected soils worldwide. Breeding for tolerance to salinity in crops has usually been limited by a lack of reliable traits for selection. Multiple genes seem to act in concert to increase salinity tolerance, and certain proteins involved in salinity stress protection have also been recognized. The reduction in photosynthetic rates in plants under salt stress is mainly due to the reduction in water potential. Photosynthesis is also inhibited when high concentrations of Na⁺ and/or Cl⁻ are accumulated in chloroplasts. Plants tend to cope with salt stress while synthesizing and accumulating osmoprotective compounds such as proline, glycinebetaine, or polyols, which are known as compatible solutes. The increased production of activated oxygen species (ROS) such as superoxide (O²⁻), hydrogen peroxide (H₂O₂), hydroxyl radical (Lehner *et al.*, 2008), and singlet oxygen in chloroplasts of plants under salt stress has been described. However, stability of biological membranes has been taken as an effective screening tool to assess salinity stress effects.

KEYWORDS: ROS, Compatible solutes, Jasmonic acid, Lipid content.

INTRODUCTION

Salinity

Salinity is a major abiotic stress on both irrigated and non-irrigated lands, inhibiting plant growth and crop productivity (Gondim *et al.*, 2012). Throughout the world, more than 800 × 10⁶ ha of lands are salt-affected (Türkan and Demiral, 2009), and, every year, 2 × 10⁶ ha of the world's agricultural lands are disrupted by salinity (Tuteja, 2007). Sodium chloride (NaCl) is one of the most important components of salt and saline soils, which is caused by Na⁺, composing a major part of all the salt affected soils worldwide (Pessarakli and Szabolcs, 1999). This article is review.

Strategies for alleviation of salt stress

Strategies for alleviation of salt stress involve developing salt-resistant cultivars, leaching excess soluble salts from upper to lower soil layers, flushing soils that contain salt crusts at the surface, reducing salt by harvesting salt-accumulating aerial plant parts in areas with negligible irrigation water or rainfall for leaching, and amelioration of saline soils under cropping and leaching (Qadir *et al.*, 2000). Breeding for tolerance to salinity in crops has usually been limited by a lack of reliable traits for selection. Multiple genes seem to act in concert to increase salinity tolerance, and certain proteins involved in salinity stress protection have also been recognized (Murillo- Amador *et al.*, 2006). Therefore, the development of methods and strategies to ameliorate deleterious effects of salt stress on plants has received considerable attention.

Photosynthesis

Photosynthesis, which is one of the primary metabolic processes in plant growth and production, is adversely affected by salinity in various ways, such as the inhibition of CO₂ intake with stomatal closure (Degl'Innocenti *et al.*, 2009), the reduction of photosynthetic pigment amount (Qados, 2011), and damage to photosynthetic structures [photosystems I and II (PSI and PSII), electron transport proteins etc.] (Sudhir *et al.*, 2005). The reduction in photosynthetic rates in plants under salt stress is mainly due to the reduction in water potential. Photosynthesis is also inhibited when high concentrations of Na⁺ and/or Cl⁻ are accumulated in chloroplasts. As photosynthetic electron transport is relatively insensitive to salts, either carbon metabolism or photophosphorylation may be affected due to salt stress (Sudhir and Murthy 2004).

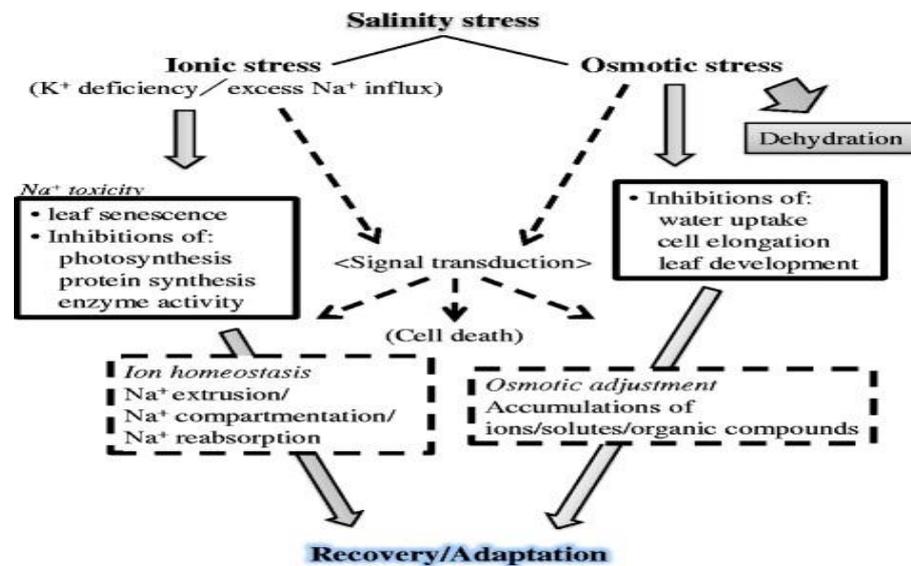


Fig1. Adaptive responses of plants to salt stress (reproduced from).

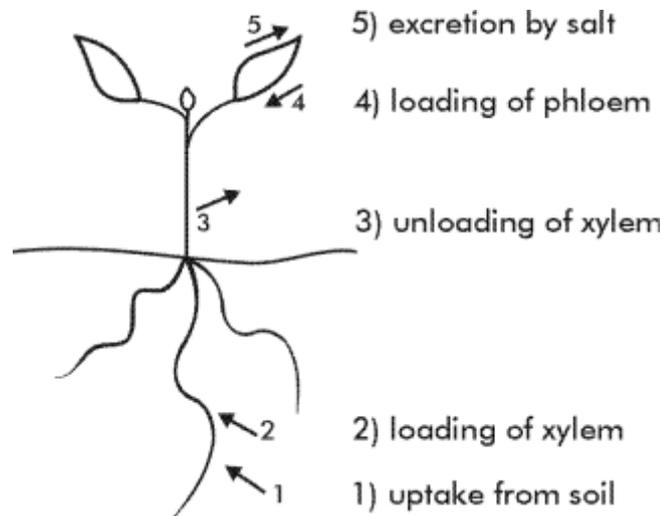


Fig 2. Control points at which salt transport is regulated. These are: 1. selectivity of uptake from the soil solution, 2. loading of the xylem, 3. removal of salt from the xylem in the upper part of the plant, 4. loading of the phloem and 5. excretion through salt glands or bladders. For a salt tolerant plant growing for some time in a soil solution of 100 mM NaCl, the root concentrations of Na⁺ and Cl⁻ are typically about 50 mM, the xylem concentration about 5 mM, and the concentration in the oldest leaf as high as 500 mM (Munns et al., 2002).

A positive correlation between salt stress induced photosynthetic rate and yield has been obtained in different crops (Pettigrew and Meredith 1994 ; Sudhir and Murthy 2004). Fisarakis *et al.* (2001) reported a positive growth inhibition caused by salinity associated with a marked inhibition of photosynthesis. However, there are many reports showing no or little relationship between growth and photosynthetic capacity (Rogers and Noble 1992 ; Hawkins and Lewis 1993).

ultimately reduce the growth and yield of the crop (Rozeff 1995). This reduction in NO_3^- uptake is associated with Cl^- antagonism (Bar et al. 1997) or reduced water uptake under saline conditions (Lea-Cox and Syvertsen 1993). The availability of P was reduced in saline soils due to (a) ionic strength effects that reduced the activity of PO_4^{3-} , (b) phosphate concentrations in soil solution was tightly controlled by sorption processes and (c) low solubility of Ca-P minerals. Hence, it is noteworthy that phosphate concentration in field grown agronomic crops decreased as salinity increased (Qadir and Schubert 2002). Different plant studies indicated that high level of external Na^+ caused a decrease in both K^+ and Ca^{2+} concentrations in plant tissues of many plant species (Hu and Schmidhalter 1997, 2005; Asch et al. 2000). This reduction in K^+ concentration in plant tissue might be due to the antagonism of Na^+ and K^+ at uptake sites in the roots, the influence of Na^+ on the K^+ transport into xylem or the inhibition of uptake processes (Suhayda et al. 1990). In another study, Hu and Schmidhalter (1997) also stated that Mg^{2+} concentration decreased due to salinity in *T. aestivum* leaves.

Reactive oxygen species (ROS)

One of the biochemical changes possibly occurring when plants are subjected to harmful stress conditions is the production of reactive oxygen species (ROS) (Dionisio-Sese and Tobita, 1998). The chloroplasts and mitochondria of plant cells are important intracellular generators of activated oxygen species (Hu et al., 2012). Oxidative damage of lipids, proteins and nucleic acids and alteration of normal cellular metabolism are important impacts of ROS (Munns, 2002; Tammam et al., 2008). Stressors like drought, salt, UV radiation, ozone, chilling, heat shock, and pathogen attack increase the production of ROS in plants (Koca et al., 2007). Depending on their natural and genetic capacity, plants have developed enzymatic and non-enzymatic defense systems against ROS (Keles and Oncel, 2002). Osmotic and ionic stresses caused by salinity promote oxidative stress and plants with high constitutive and induced antioxidant levels have better resistance to damage (Spsychalla and Desborough, 1990; Parida and Das, 2005). However, plants have a number of antioxidant enzymes protecting themselves against the deleterious effects of activated oxygen species. Superoxide dismutase (SOD; EC 1.15.1.1) is a major scavenger of O_2^- and its enzymatic action results in the formation of H_2O_2 and O_2 . Then, the produced hydrogen peroxide is scavenged (Rios-Gonzalez et al., 2002; Tuna et al., 2008) by various enzymes like peroxidase (POX), ascorbate peroxidase (APX), catalase (CAT) and glutathione (GR) (Asada, 1992; Noctor and Foyer, 1998).

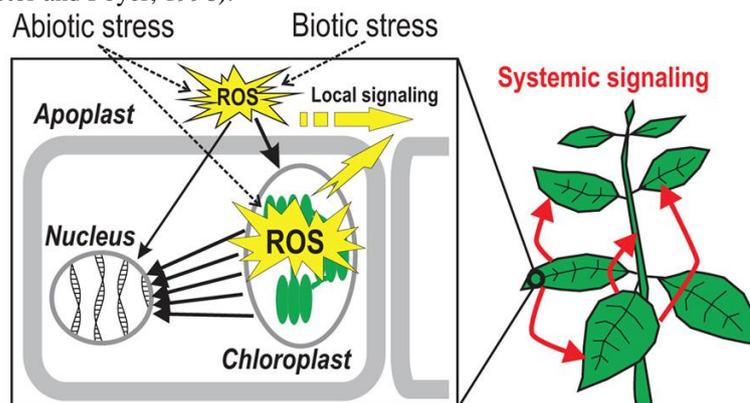


Fig 4. Reactive oxygen species (ROS)-talk in plant cells. Biotic and abiotic stimuli lead to the generation of ROS in the apoplast which is subsequently communicated to the inside of the cell where the signal leads to an increase in chloroplastic ROS production. The chloroplast can further amplify the signal and transmit it to the nucleus via various cytosolic signaling networks. Apoplastic ROS signaling can also reach the nucleus through cytosolic pathways directly. Yellow arrows demonstrate intracellular transmission of apoplastic and chloroplastic ROS-induced signals where they connect neighboring cells (local signaling) or participate in long-distance (“systemic”) signaling throughout the plant (red arrows) (Alexey et al., 2012).

Increase in the activities of these enzymes closely relates the salt tolerance of many plants as reported in various researches (Zeng et al., 2003a; Lehner et al., 2008; Liu et al., 2011). Evidence suggests that membranes are the primary sites of salinity injury to cells and organelles because ROS can react with unsaturated fatty acids to cause peroxidation of essential membrane lipids in plasmalema or intracellular organelles (Esfandiari et al., 2007). Cell membrane stability has long been taken as an indicator of stress tolerance (Ashraf and Ali, 2008). This attribute has recently been used as

an effective selection criterion for salinity tolerance in plant species such as *Brassica napus* (Ashraf and Ali, 2008) and wheat (Sairam *et al.*, 2002; Farooq and Azam, 2006).

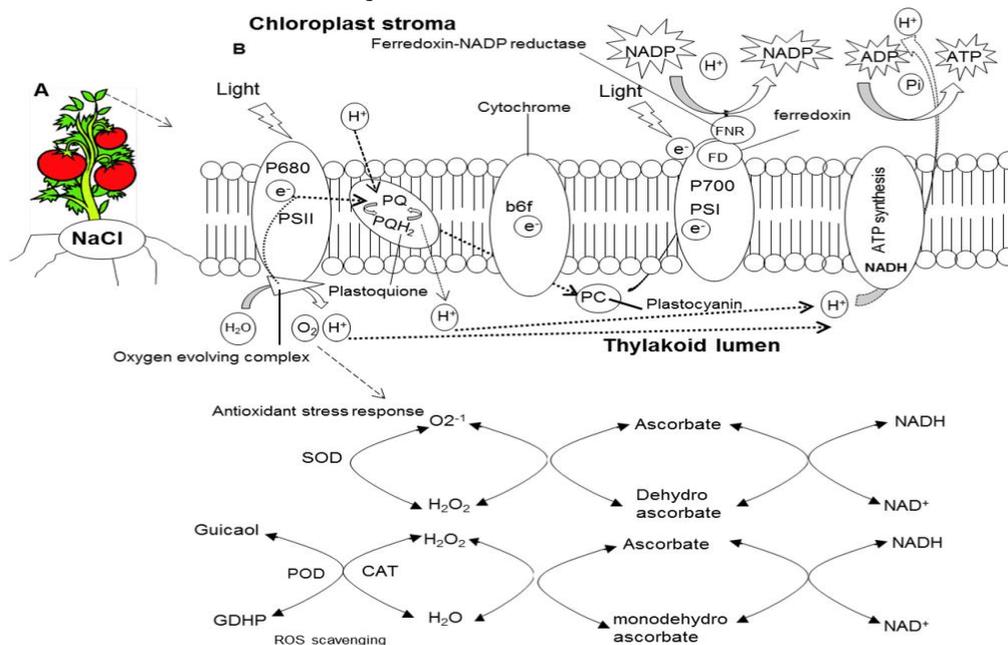


Fig 5. Schematic representation of a mechanism for production of oxidative damage in chloroplasts and its mitigation by the supplement of silicon (Si) (A) tomato plants exposed to salt stress (NaCl) (B) production of reactive oxygen species and defense mechanism in chloroplasts (Sowbiya *et al.*, 2014).

Compatible solutes

Plants tend to cope with salt stress while synthesizing and accumulating osmoprotective compounds such as proline, glycinebetaine, or polyols, which are known as compatible solutes (Hussain *et al.*, 2008). These compatible solutes protect plants from stress in different ways, including cellular osmotic adjustment, detoxification of ROS, protection of membrane integrity, and stabilization of enzymes/proteins (Vijayan, 2009).

SYMPTOMS OF Na⁺ ACCUMULATION

Salt stress creates both ionic as well as osmotic stress on plants. These stresses can be distinguished at several levels (Tester and Davenport 2003). The root and shoot growth reduces abruptly in salt sensitive plants and this effect does not appear to depend on salt concentration in the growing tissues, it is rather a response to the osmolarity of the external solution (Munns 2002). Na⁺-specific damage is associated with accumulation of Na⁺ in leaf tissues and results in necrosis of older leaves. The time scale over which specific damage is manifested depends on the rate of accumulation of Na⁺ in leaves, and on the effectiveness of Na⁺ compartmentation within leaf tissues and cells. The Na⁺-specific effects are superimposed on the osmotic effects of NaCl (Tester and Davenport 2003), and importantly, show greater variation within species than osmotic effect (Munns 2002). Deficiency of other nutrients in the soil is due to the high concentration of Na⁺ that interacts with other environmental factors, such as drought, which exacerbate the problem (Silberbush and Ben-Asher 2001). Besides, high Na⁺ hampers the uptake of other nutrients by: (1) Na⁺ interfering with transporters in the root plasma membrane, such as K⁺-selective ion channels, and (2) reduction of root growth by high Na⁺ concentration (Tester and Davenport 2003). Thus the uptake of water, growth limiting nutrients (such as P, Fe or Zn) and the growth of soil microorganisms, such as mycorrhizal fungi can be inhibited. Leaves are more vulnerable than roots to Na⁺ simply because Na⁺ and Cl⁻ accumulate to higher levels in shoots than in roots (Tester and Davenport 2003). Though Na⁺ is transported to shoots through the rapidly moving transpiration stream in the xylem, it can only return to roots via the phloem. There is limited evidence of extensive recirculation of shoot Na⁺ to root, suggesting that Na⁺ transport is largely unidirectional and results in progressive accumulation of Na⁺ as leaves age (Tester and Davenport 2003). The high levels of Na⁺ or Na⁺:K⁺ ratio can disrupt various enzymatic processes in the cytoplasm. K⁺ activates more than 50 enzymes and is an essential element in protein synthesis as it binds tRNA to the

ribosomes (Blaha et al. 2000). The disruption in protein synthesis appears to be an important cause of damage by Na⁺ (Tester and Davenport 2003). Several studies suggest that the plasma membrane may be the primary site of salt injury (Mansour 1997). Nonelectrolytes and water permeability get altered markedly upon salt exposure. Osmotic damage (i.e. osmotically driven removal of water from cells) could occur as a result of buildup of high concentrations (possibly several hundred mmol) of Na⁺ in the leaf apoplast, since Na⁺ enters leaves in the xylem stream and is left behind as water evaporates (Flowers et al. 1991).

Jasmonic acid

The adaptive response of salt-stressed plants is controlled by chemical signals that will compensate adjustment of growth and development in response to such unfavorable conditions. It should be noted that some of these signals play a dual role if controlled in space and time, they can act as signals triggering adaptation, if developing unconstrained, they accompany stress-related damage (for a review, see Ismail et al., 2014b). Central players among these stress signals are jasmonic acid (JA), its biologically active precursor 12-oxophytodienoic acid (OPDA), and its derivatives such as methyl jasmonate (MeJA) or the amino acid-conjugated jasmonate, JA-isoleucine (JA-Ile), in the following collectively termed as jasmonates (JAs). JAs have been reported to accumulate in response to salinity stress (tomato, Pedranzani et al., 2003; rice, Moons et al., 1997). Whether this accumulation is a signal triggering adaptation or just a by-product or consequence of adaptation is not very clear. However, the fact that a salt tolerant cultivar of rice shows higher endogenous JA contents as compared with a salt-sensitive cultivar, as well as the observation that exogenous MeJA can reduce the uptake of sodium in this salt-tolerant cultivar (Kang et al., 2005), indicates a function for JAs in salt adaptation. Overexpression of a wheat AOC (ALLENE OXIDE CYCLASE) gene in wheat and *Arabidopsis* resulted in an improved salt tolerance of these species (Zhao et al., 2014). However, it is not possible to draw a general connection between high levels of JA and adaptation; during a comparison of two grapevine cell lines differing in their salinity tolerance, the accumulation of JA and JA-Ile was more pronounced in the sensitive *Vitis riparia* rather than in the salt-tolerant *Vitis rupestris* (Ismail et al., 2014a). These discrepancies underscore that it is not the presence or absence of JAs that decides the salinity response, but rather the right timing and control (for a review, see Ismail et al., 2014b). The complexity in the relationship between JAs and salinity adaptation is further accentuated by the recent finding that the precursor OPDA (but not JA itself) was significantly induced in drought-stressed *Arabidopsis* leaves (Savchenko et al., 2014). Moreover, in rice roots, JA biosynthesis was reported to be strongly induced by drought stress, but only marginally by salt stress, indicating that the two components of salinity stress might differ in their transduction events (Takeuchi et al., 2011).

Lipid Content

The increased production of activated oxygen species (ROS) such as superoxide (O₂⁻), hydrogen peroxide (H₂O₂), hydroxyl radical (Lehner et al., 2008), and singlet oxygen in chloroplasts of plants under salt stress has been described. However, stability of biological membranes has been taken as an effective screening tool to assess salinity stress effects (Abdul Jaleel et al., 2007). For example, Farooq and Azam (2006) reported an increase in cell membrane injury under salt stress in different wheat varieties. It has been suggested that decrease in membrane stability reflects the extent of lipid peroxidation caused by ROS (Heidari and Jamshidi, 2011).

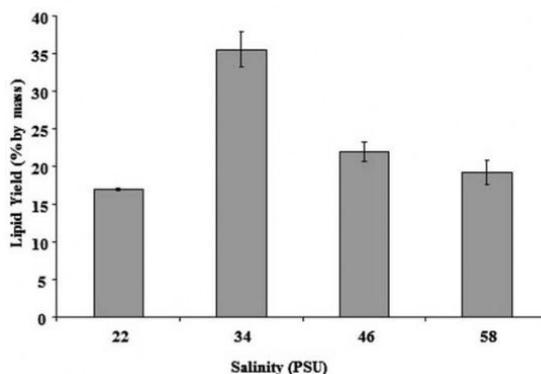


Fig 6. effect of salinity on lipid yield (Meridith et al., 2013)

Lipids and proteins are major components in membrane which has main role in plant cell resistance in proportional to environmental stress. Environmental stress due to disordering in cohesions of membrane lipids and proteins (Yordanov et al, 2003). Lipids are among the most prominent constituents of cell membrane which play a fundamental role in cell permeability (Baybordi et al, 2010). Under condition of stress main change will happen in lipids metabolism (Kesri, 2002). Total lipids content in Canola (*Brassica napus* L.) with increasing NaCl levels was decreased (Baybordi et al, 2010). Increasing soil salinity levels strongly influence the essential lipids biosynthesis (Solinas and Deiana, 1996). In other hand, lipid peroxidation was synchronized with increased of the salinity level which had a relation with plants such as Wheat (Hala et al, 2005), Tomato (Neumann, 2001) and Purslane (Yazici et al, 2007; Rahdari et al, 2012) was reported. Mono galactosyl diglyceride (MGDG) is main glycerol lipid in leaf was effect of intensive stress imposing, was reduced that is express of chloroplast membrane destructions (Rahdari et al, 2012). Low unsaturation lipids degree limited the membrane fluidity band restricted permeability to Na and Cl ions (Konova et al, 2009). Phosphatidic acid (PA) is a common phospholipids that is a major constituent of cell membranes. PA is the smallest of the phospholipids. They have long been recognized as of importance during germination and senescence, and they appear to have a role in response to stress damage and pathogen attack (Bartels and Sunkar, 2005). PA is lipid signals in plants that normally PA only constitutes a minor proportion of the cellular lipid pool but in responses to stress PA levels can increase significantly (Darwish et al, 2009). PA has been implicated in intracellular signaling that formed in response to salt stress has been suggested to function as a signaling molecule guiding the plants accumulation responses to salt stress. PA can bind and affect the activity of various signaling proteins, including protein kinases and phosphatases (Wang, 2005). Also, PA has been suggested to regulate the activity of vacuolar pump upon high salt treatment which may help maintain the protein gradient (Zhang et al, 2006).

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