

Plant Response to Salt Stress

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Abstract

In most crop species, stress usually inhibits seed germination, seedling growth and vigor, flowering and fruit set. Salinity is one of the major environmental factors limiting plant growth and productivity. It is estimated that about one-third of world's cultivated land is affected by salinity. Salt stress has toxic effects on plants and lead to metabolic changes, like loss of chloroplast activity, decreased photosynthetic rate and increased photorespiration rate which then leads to an increased reactive oxygen species (ROS) production. High salinity affects plants in two main ways: high concentrations of salts in the soil disturb the capacity of roots to extract water, and high concentrations of salts within the plant itself can be toxic, resulting in an inhibition of many physiological and biochemical processes such as nutrient uptake and assimilation. This article is review and the aims of plant response to salt stress.

Keywords: Strategies, tolerant, Shoot growth

Introduction

Abiotic stress

Plants are exposed to several abiotic stresses during its growth and development. Among the abiotic stresses, salt stress drastically affects crop growth and poses a major threat to agricultural productivity worldwide (Epstein *et al.*, 1980; Munns, 2002; Flowers, 2004) [27, 9]. In most crop species, stress usually inhibits seed germination, seedling growth and vigor, flowering and fruit set (Zeinali *et al.*, 2002; Sairam and Tyagi, 2004) [42, 37].

Salinity

Salinity is one of the major environmental factors limiting plant growth and productivity. It is estimated that about one-third of world's cultivated land is affected by salinity (Kaya *et al.*, 2002) [19]. In general, high level of salt in soil causes imbalance in osmotic potential; ionic equilibrium and nutrient uptake (Niu *et al.*, 1995; Munns, 2002) [27]. Further, it facilitates severe ion toxicity by depositing high concentration of Na⁺ which causes membrane disorganization, inhibition of cell division and expansion. In addition, it also impairs a wide range of cellular metabolism including photosynthesis, protein synthesis and lipid metabolism (Alia-Mohanty and Saradhi, 1992) [2]. Excess salt in the soil may adversely affect plant growth either through osmotic inhibition of water uptake by roots or specific ion effects. Specific ion effects may cause direct toxicity or, alternatively, the insolubility or competitive absorption of ions may affect plant nutritional balances (Greenway & Munns, 1980) [10]. Salt stress has toxic effects on plants and lead to metabolic changes, like loss of chloroplast activity, decreased photosynthetic rate and increased photorespiration rate which then leads to an increased reactive oxygen species (ROS) production (Parida & Das, 2005) [33, 34].

High salinity affects

High salinity affects plants in two main ways: high concentrations of salts in the soil disturb the capacity of roots to extract water, and high concentrations of salts within the plant itself can be toxic, resulting in an inhibition of many

physiological and biochemical processes such as nutrient uptake and assimilation (Hasegawa, Bressan, Zhu, & Bohnert, 2000; R. Munns, 2002) [12, 27]. Together, these effects reduce plant growth, development and survival. A two-phase model describing the osmotic and ionic effects of salt stress was proposed by Munns (1995) [29].

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) [36]. 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) [30]. Therefore, the development of methods and strategies to ameliorate deleterious effects of salt stress on plants has received considerable attention.

Plants sensitive or tolerant to salinity

Plants sensitive or tolerant to salinity differ in the rate at which salt reaches toxic levels in leaves. Timescale is days or weeks or months, depending on the species and the salinity level. During Phase 1, growth of both type of plants is reduced because of the osmotic effect of the saline solution outside the roots. During Phase 2, old leaves in the sensitive plant die and reduce the photosynthetic capacity of the plant. This exerts an additional effect on growth. In the first, osmotic phase, which starts immediately after the salt concentration around the roots increases to a threshold level making it harder for the roots to extract water, the rate of shoot growth falls significantly. An immediate response to this effect, which also mitigates ion flux to the shoot, is stomatal closure. However, because of the water potential difference between the atmosphere and leaf cells and

the need for carbon fixation, this is an untenable long-term strategy of tolerance (Hasegawa *et al.*, 2000) [12].

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) [6]. The chloroplasts and mitochondria of plant cells are important intracellular generators of activated oxygen species (Hu *et al.*, 2012) [15]. 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) [27]. Stressors like drought, salt, UV radiation, ozone, chilling, heat shock, and pathogen attack increase the production of ROS in plants (Koca *et al.*, 2007) [21]. Depending on their natural and genetic capacity, plants have developed enzymatic and non-enzymatic defense systems against ROS (Keles and Oncel, 2002) [20]. 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) [40, 33, 34]. 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 O₂⁻ and its enzymatic action results in the formation of H₂O₂ and O₂. 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 reductase (GR) (Asada, 1992; Noctor and Foyer, 1998) [31]. Increase in the activities of these enzymes closely relates to the salt tolerance of many plants as reported in various researches (Zeng *et al.*, 2003a; Lehner *et al.*, 2008; Liu *et al.*, 2011) [43, 22, 23]. 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 plasmalemma or intracellular organelles (Esfandiari *et al.*, 2007) [7]. Cell membrane stability has long been taken as an indicator of stress tolerance (Ashraf and Ali, 2008) [4]. 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) [4] and wheat (Sairam *et al.*, 2002; Farooq and Azam, 2006) [38, 8].

Proline accumulation

Proline accumulation might be used as an indicator in selection for withstanding saline stress through the participation in osmoregulation (Ueda *et al.*, 2007; Tammam *et al.*, 2008). Expression of one or more additional genes for proline accumulation can be induced by stress (Misra and Saxena, 2009) [25]. Moreover, proline accumulation under stress conditions may be caused by induction of proline biosynthesis enzymes, reduction the rate of proline oxidation conversion to glutamate, decline utilization of proline in proteins synthesis and enhancing proteins turnover (Tammam *et al.*, 2008).

Shoot growth

Shoot growth is more sensitive than root growth to salt-induced osmotic stress probably because a reduction in the leaf area development relative to root growth would decrease the water use by the plant, thus allowing it to conserve soil moisture and prevent salt concentration in the soil (R Munns & Tester, 2008) [28]. Reduction in shoot growth due to salinity is commonly expressed by a reduced leaf area and stunted shoots (A. Läubli & Epstein, 1990). The growth inhibition of leaves sensitive to salt stress appears to be also a consequence of inhibition by salt of symplastic xylem loading of Ca²⁺ in the root (A. Lauchli & Grattan, 2007). Final leaf size depends on both cell division and cell elongation. Leaf initiation, which is governed by cell division, was shown to be unaffected by salt stress in sugar beet, but leaf extension was found to be a salt-sensitive process (Papp, Ball, & Terry, 1983) [32], depending on Ca²⁺ status.

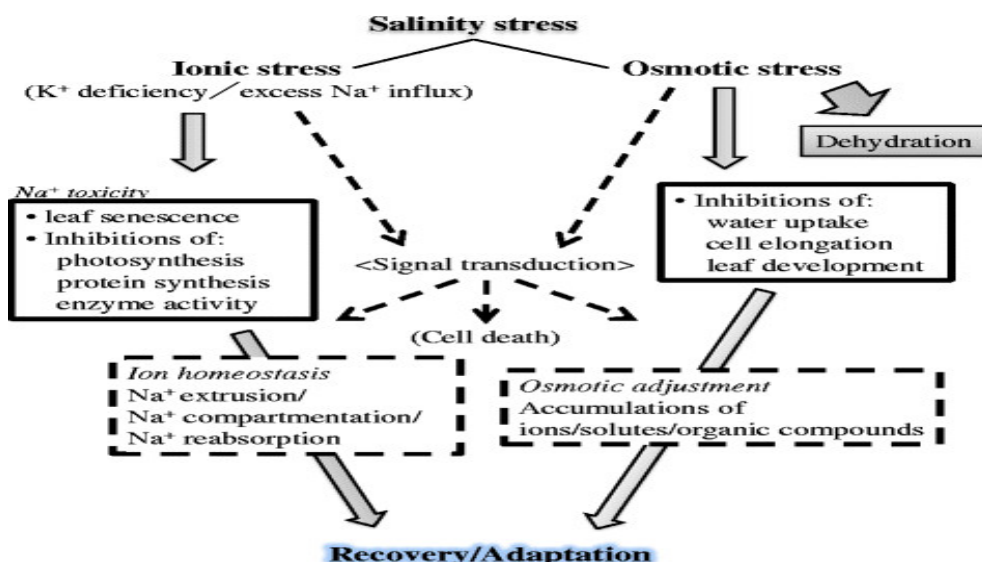


Fig 1: Adaptive responses of plants to salt stress (Horie *et al.*, 2012) [13]

Accumulation of ions

The second phase, ion specific, corresponds to the accumulation of ions, in particular Na⁺, in the leaf blade, where Na⁺ accumulates after being deposited in the transpiration stream,

rather than in the roots (R. Munns, 2002) [27]. Na⁺ accumulation turns out to be toxic especially in old leaves, which are no longer expanding and so no longer diluting the salt arriving in them as young growing leaves do. If the rate at which they die is greater

than the rate at which new leaves are produced, the photosynthetic capacity of the plant will no longer be able to supply the carbohydrate requirement of the young leaves, which further reduces their growth rate (R Munns & Tester, 2008) ^[28]. In photosynthetic tissues, in fact, Na⁺ accumulation affects photosynthetic components such as enzymes, chlorophylls, and carotenoids (Davenport *et al.*, 2005) ^[5].

Salt tolerance

Salt tolerance, in fact, can be usually assessed as the percent biomass production in saline versus control conditions over a prolonged period of time (this usually correlates with yield) or in terms of survival, which is quite appropriate for perennial species (R. Munns, 2002) ^[27]. Salt tolerance may vary considerably with genetic traits. A plant species' tolerance for salinity will be overridden by a sudden exposure to salinity, even if the species is a halophyte (Albert, 1975) ^[1]. Different adaptive mechanisms may be involved in gradual acclimation to salinity in contrast to adjustment to a sudden shock. The sensitivity to salinity of a given species may change during ontogeny. Salinity tolerances may increase or decrease depending on the plant species and/or environmental factors. For some species, salt sensitivity may be greatest at germination, whereas for other species, sensitivity may increase during reproduction (Howat, 2000; Marschner, 1986) ^[14,24]. Plants have evolved several mechanisms to acclimatize to salinity. It is possible to distinguish three types of plant response or tolerance: a) the tolerance to osmotic stress, b) the Na⁺ exclusion from leaf blades and c) tissue tolerance (R Munns & Tester, 2008) ^[28].

Chemical signals

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 (Ismail *et al.*, 2014b) ^[17]. 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) ^[35, 26]. 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) ^[18], 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) ^[44]. 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) ^[16]. 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) ^[17]. 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) ^[39]. 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) ^[41].

References

1. Albert R. Salt regulation in halophytes. *Oecologia*, 1975; 21(1):57-71.
2. Alia-Mohanty P, Saradhi PP. Effect of sodium chloride on primary photochemical activities in cotyledonary leaves of *Brassica juncea*. *Biochem Physiol*. 1992; 188:1-12.
3. Allan AC, Fluhr R. Two Distinct Sources of Elicited Reactive Oxygen Species in Tobacco Epidermal Cells. *Plant Cell*, 1997; 9:1559-1572.
4. Ashraf M, Ali Q. Relative membrane permeability and activities of some antioxidant enzymes as the key determinants of salt tolerance in canola (*Brassica napus* L.) *Environmental and Experimental Botany* 2008; 63:266-273.
5. Davenport R, James R, Zakrisson-Plogander A, Tester M, Munns R. Control of Sodium Transport in Durum Wheat. *Plant Physiology*, 2005; 137:807-818.
6. Dionisio-Sese ML, Tobita S. Antioxidant responses of rice seedlings to salinity stress. *Plant Science* 1998, 135:1-9.
7. Esfandiari E, Shekari F, Shekari F, Esfandiari M. The effect of salt stress on antioxidant enzymes' activity and lipid peroxidation on the wheat seedling. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 2007; 35:48-56.
8. Farooq S, Azam F. The use of cell membrane stability (CMS) technique to screen for salt tolerant wheat varieties. *Journal of Plant Physiology* 2006; 163:629-637.
9. Flowers TJ. Improving crop salt tolerance. *J of Expt Botany*. 2004; 55(396):307-319.
10. Greenway H, Munns R. Mechanisms of salt tolerance in nonhalophytes. *Annual Review of Plant Physiology*, 1980; 31:149-190.
11. Hare PD, Cress WA. Metabolic implications of stress-induced proline accumulation in plants. *Plant Growth Regulation*, 1997; 21(2):79-102.
12. Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ. Plant cellular and molecular responses to high salinity. *Annual Review of Plant Physiology and Plant Molecular Biology*, 2000; 51:463-499.
13. Horie T, Karahara I, Katsuhara M. Salinity tolerance mechanisms in glycophytes: An overview with the central focus on rice plants. *The Rice Journal* 2012; 5(1):1-18.
14. Howat D. Acceptable Salinity, Sodicity and pH Values for Boreal Forest Reclamation, 2000. Available at www.gov.ab.ca/env/protenf/landrec/index.html. In E. S. D. Alberta Environment, Edmonton Alberta. Report # ESD/LM/00-2. 191.
15. Hu L, Li H, Pang H, Fu J. Responses of antioxidant gene, protein and enzymes to salinity stress in two genotypes of perennial ryegrass (*Lolium perenne*) differing in salt tolerance. *Journal of Plant Physiology* 2012; 169:146-156.

16. Ismail A, Seo M, Takebayashi Y, Kamiya Y, Eiche E, Nick P. Salt adaptation requires efficient fine-tuning of jasmonate signaling. *Protoplasma* 2014a; 251:881-898.
17. Ismail A, Takeda S, Nick P. Life and death under salt stress: same players, different timing? *Journal of Experimental Botany*. 2014b; 65:2963-2979.
18. Kang DJ, Seo YJ, Lee JD, Ishii R, Kim KU, Shin DH *et al.* Jasmonic acid differentially affect growth, ion uptake and abscisic acid concentration in salt-tolerant and salt sensitive rice culture. *Journal of Agronomy and Crop Science* 2005; 191:273-282.
19. Kaya C, Kirnak H, Higgs D, Saltati K. Supplementary calcium enhances plant growth and fruit yield in strawberry cultivars grown at high (NaCl) salinity. *Scientia Horticulturae*, 2002; 26:807-820.
20. Keles Y, Oncel I. Response of antioxidative defense system to temperature and water stress combinations in wheat seedlings. *Plant Science* 2002; 163:783-790.
21. Koca H, Bor M, Ozdemir F, Turkan I. The effect of salt stress on lipid peroxidation, antioxidative enzymes and proline content of sesame cultivars. *Environmental and Experimental Botany* 2007; 60:344-351.
22. Lehner A, Mamadou N, Poels P, Côme D, Bailly C, Corbineau F. Changes in soluble carbohydrates, lipid peroxidation and antioxidant enzyme activities in the embryo during ageing in wheat grains. *Journal of Cereal Science* 2008; 47:555-565.
23. Liu H, Xin Z, Zhang Z. Changes in activities of antioxidant-related enzymes in leaves of resistant and susceptible wheat inoculated with *Rhizoctonia cerealis*. *Agricultural Sciences in China* 2011; 10:526-533.
24. Marschner H. *Mineral Nutrition of Higher Plants* Academic Press Inc. London., 1986, 150.
25. Misra N, Saxena P. Effect of salicylic acid on proline metabolism in lentil grown under salinity stress. *Plant Science* 2009; 177:181-189.
26. Moons A, Prinsen E, Bauw G, Montagu MV. Antagonistic effects of abscisic acid and jasmonates on salt stress-inducible transgenic transcripts in rice roots. *The Plant Cell* 1997; 9:2243-2259.
27. Munns R. Comparative physiology of salt and water stress. *Plant, Cell & Environment*, 2002; 25(2):239-250.
28. Munns R, Tester M. Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, 2008; 59:651-681.
29. Munns R, Schachtman D, Condon A. The Significance of a Two-Phase Growth Response to Salinity in Wheat and Barley. *Functional Plant Biology*, 1995; 22(4):561-569.
30. Murillo-Amador B, Jones HG, Kaya C. Effects of foliar application of calcium nitrate on growth and physiological attributes of cowpea (*Vigna unguiculata* L. Walp.) grown under salt stress. *Environmental and Experimental Botany*, 2006; 58:188-196.
31. Noctor G, CH Foyer. Ascorbate and glutathione: keeping active oxygen under control. *Annual Review of Physiology and Molecular Biology of Plants* 1998; 49:249-279.
32. Papp JC, Ball MC, Terry N. A comparative study of the effects of NaCl salinity on respiration, photosynthesis, and leaf extension growth in *Beta vulgaris* L. (sugar beet). *Plant, Cell & Environment*, 1983; 6(8):675-677.
33. Parida AK, Das AB. Salt tolerance and salinity effects on plants: a review. *Ecotoxicology and Environmental Safety* 2005; 60:324-349.
34. Parida AK, Das AB. Salt tolerance and salinity effects on plants: a review. *Ecotoxicology and Environmental Safety*, 2005; 60:324-349.
35. Pedranzani H, Racagni G, Alemano S, Miersch O, Ramirez I, Pena-Cortes H *et al.* Salt tolerant tomato plants show increased levels of jasmonic acid. *Plant Growth Regulation* 2003; 41:149-158.
36. Qad r M, Ghafoor A, Murtaza G. Amelioration strategies for saline soils: a review. *Land Degradation Dev*, 2000; 11:501-521.
37. Sairam RK, Tyagi A. Physiology and molecular biology of salinity stress tolerance in plants. *Current Sci.* 2004; 86(3):407-421.
38. Sairam RK, Veerabhadra Rao K, Srivastava GC. Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration. *Plant Science* 2002; 163:1037-1046.
39. Savchenko T, Kolla VA, Wang CQ, Nasafi Z, Hicks DR, Phadungchob B *et al.* Functional convergence of oxylipin and abscisic acid pathways controls stomatal closure in response to drought. *Plant Physiology* 2014; 164:1151-1160.
40. Spychalla JP, Desborough SL. Superoxide dismutase, catalase, and alfa-tocopherol content of stored potato tubers. *Plant Physiology* 1990; 94:1214-1218.
41. Takeuchi K, Gyohda A, Tominaga M. RSOsPR10 expression in response to environmental stresses is regulated antagonistically by jasmonate/ethylene and salicylic acid signaling pathways in rice roots. *Plant and Cell Physiology* 2011; 52:1686-1696.
42. Zeinali E, Soltani A, Galeshi S. Response of germination component to salinity stress in oilseed rape (*Brassica napus* L.). *Iranian J of Agric Sci.* 2002; 33:137-145.
43. Zeng L, Lesch SM, Grieve CM. Rice growth and yield respond to changes in water depth and salinity stress. *Agricultural Water Management* 2003a; 59:67-75.
44. Zhao Y, Dong W, Zhang N, Ai X, Wang M, Huang Z *et al.* A wheat allene oxide cyclase gene enhances salinity tolerance via jasmonate signaling. *Plant Physiology* 2014; 164:1068-1076.