

Review

Fatality of salt stress to plants: Morphological, physiological and biochemical aspects

Khalid Nawaz^{1*}, Khalid Hussain¹, Abdul Majeed¹, Farah Khan², Shahid Afghan³ and Kazim Ali³

¹Department of Botany, University of Gujrat, Gujrat-Pakistan.

²Lahore College Women University-Lahore, Pakistan.

³Shakarganj Sugar Research Institute, Jhang-Pakistan.

Accepted 18 June, 2010

Soil salinity affects various physiological and biochemical processes which result in reduced biomass production. This adverse effect of salt stress appears on whole plant level at almost all growth stages including germination, seedling, vegetative and maturity stages. However, tolerance to salt stress at different plant developmental stages varies from species to species. The plant response to salt stress consists of numerous processes that must function in coordination to alleviate both cellular hyperosmolarity and ion disequilibrium. Salt tolerance and yield stability are complex genetic traits that are difficult to establish in crops since salt stress may occur as a catastrophic episode, be imposed continuously or intermittently and become gradually more severe at any stage during development. The objective of this review is to summarize the morphological, physiological and biochemical aspects of plants under salt stress. It was then concluded that salt stress affects plant physiology at whole plant as well as cellular levels through osmotic and ionic adjustments that result in reduced biomass production. This adverse effect of salt stress appears on whole plant level at almost all growth stages including germination, seedling, vegetative and maturity stages. Despite causing osmotic and ionic stress, salinity causes ionic imbalances that may impair the selectivity of root membranes and induce potassium deficiency.

Key words: Salt stress, ions, osmotic adjustment, morphological, physiological and biochemical.

INTRODUCTION

All plants are subjected to multitude of stresses throughout their life cycle. The major environmental factor that currently reduces plant productivity is salinity (Majeed et al., 2010). The productivity of crops is adversely affected by high salt content in most of the soils (Munns and Termaat, 1986). Approximately, 7% of the world's land area, 20% of the world's cultivated land and nearly half of the irrigated land is affected with high salt contents (Rhoades and Loveday, 1990; Szabolcs, 1994; Zhu, 2001). In view of another projection, 2.1% of the global dry land agriculture is affected by salinity (FAO, 2003). Effects of salinity are more obvious in arid and semi-arid regions where limited rainfall, high evapo-transpiration and high temperature associated with poor water and soil management practices are the major contributing factors (Azevedo Neto et al., 2006).

Earth is a predominantly salty planet, with most of its water containing about 3% NaCl. This concentration of salt has rendered the land very salty. It is projected that about 900 Mha land is affected due to salt which considerably poses a serious threat to agricultural productivity (Flowers and Yeo, 1995; Munns, 2002) because most agricultural crops will not grow under conditions of high salt concentration. Hence, the existing salinity is a great challenge to food security. Accumulation of water-soluble salts, especially sodium-chloride (NaCl), sodium carbonate (Na₂CO₃) and partially calcium chloride (CaCl₂) results in salty soils. Wyn (1981) was of the view that soil salinity develops due to high amount of chloride or sulfate salts of sodium.

Naturally occurring salinisation is primarily caused by capillary water level elevation and subsequent evaporation of saline groundwater. However, man-made salinisation is wide spread. Especially, irrigated land in arid regions is highly susceptible to salinisation. Irrigation practices lead to ground water level elevation and a sub-

*Corresponding author. E-mail: nawazkuog@yahoo.com.

sequent increase in evaporation (Supper, 2003).

High salt levels do not only lead to damaging effects on plants but also increase the pH-level of soil. Most crop plants do not grow well under high pH-levels. Salt stress also leads to deterioration of soil structure and hinders desirable air-water balance essential for biological processes occurring at plant roots. As a result of all the detrimental effects of salinisation, crop yields are decreasing, while arable land is being lost irreversibly (Supper, 2003). Salt stress causes various effects on plant physiology such as increased respiration rate, ion toxicity, changes in plant growth, mineral distribution, and membrane instability resulting from calcium displacement by sodium (Marschner, 1986), membrane permeability (Gupta et al., 2002), and decreased photosynthetic rate (Hasegawa et al., 2000; Munns, 2002; Ashraf and Shahbaz, 2003; Kao et al., 2003; Sayed, 2003). Salt stress affects plant physiology at whole plant as well as cellular levels through osmotic and ionic stress (Hasegawa et al., 2000; Muranaka et al., 2002a; Ranjbarfordoei et al., 2002; Murphy and Durako, 2003). Despite causing osmotic and ionic stress, salinity causes ionic imbalances that may impair the selectivity of root membranes and induce potassium deficiency (Gadallah, 2000).

The accumulation of high amounts of toxic salts in the leaf apoplast leads to dehydration and turgor loss, and eventually death of leaf cells and tissues (Marschner, 1995). As a result of these changes, the activities of various enzymes and plant metabolism are affected (Lacerda et al., 2003). At high rates of transpiration, the xylem of all species contains much lower chloride and sodium concentrations than those in the external saline medium. Salt stress enhances the accumulation of NaCl in chloroplasts of higher plants, affects growth rate, and is often associated with decrease in photosynthetic electron transport activities (Kirst, 1989). In higher plants, salt stress inhibits photosystem (PS)-II activity (Kao et al., 2003; Parida et al., 2003), although some studies showed contrary results (Brugnoli and Björkman, 1992; Morales et al., 1992). The reduction of plant growth and dry-matter accumulation under saline conditions has been reported in several important grain legumes (Tejera et al., 2006).

PLANT GROWTH UNDER SALT STRESS

Salt stress causes reduction in plant growth because plant may suffer four types of stresses (Greenway and Munns, 1980)

- (1) Osmotically induced water stress
- (2) Specific ion toxicity due to high concentration of sodium and chloride
- (3) Nutrient ion imbalance, due to high level of Na^+ and Cl^- which reduce the uptake of K^+ , NO_3^- , PO_4^{3-} etc.
- (4) Increased production of reactive oxygen species which damage the macromolecules.

OSMOTIC ADJUSTMENT

Salt stress reduces the plant's ability to take up water, and this leads to reduction in growth. This is the osmotic or water-deficit effect of salt stress. Both cellular and metabolic processes involved in osmotic stress due to salinity are common to drought. The rate at which new leaves are produced depends largely on the water potential of the soil solution, in the same way as for a drought-stressed plant. Salts themselves do not build up in the growing tissues at concentrations that inhibit growth, as the rapidly elongating cells can accommodate the salt that arrives in the xylem within their expanding vacuoles. So, the salt taken up by the plant does not directly inhibit the growth of new leaves (Munns, 2005).

Reductions in the rate of leaf and root growth are probably due to factors associated with water stress rather than a salt-specific effect (Munns, 2002). This is supported by the evidence that Na^+ and Cl^- are below toxic concentrations in the growing cells themselves. For example, in wheat growing in 120 mM NaCl, Na^+ in the growing tissues of leaves was at most only 20 mM, and only 10 mM in the rapidly expanding zones, and Cl^- only about 50 mM (Hu et al., 2005). Similarly, Neves-Piestun and Bernstein (2005) found that Na^+ and Cl^- were only 40 mM in the most rapidly growing tissues, and that the degree of inhibition by salt stress of either the elongation rate or the total volume expansion rate did not correlate with the Na^+ or Cl^- in the tissues of maize growing in 80 mM NaCl. Fricke et al. (2004) found only 38 and 49 mM Na^+ in mesophyll and epidermal cells, respectively, in the growing cells of barley after 24 h of exposure to 100 mM NaCl. This Na^+ was not inhibitory to growth, but was probably beneficial as it might be taken up into the expanding vacuole for osmotic adjustment as indicated by the fact that the growth rate increased with time over 24 h (after a temporary decline when the salt was applied) while the cellular Na^+ increased. The rapid expansion of the growing cells would help to keep the salt from building up to high concentrations. Results of experimental manipulation of shoot water relations suggest that hormonal signals, probably induced by the osmotic effect of the salt outside the roots are controlling the rate of cell elongation growth (Munns et al., 2000). Inhibition of plant growth due to salt stress largely depends on the severity of the stress. Mild osmotic stress leads rapidly to growth inhibition of leaves and stems, whereas roots may continue to grow and elongate (Hsiao and Xu, 2000). The degree of growth inhibition due to osmotic stress depends on the time scale of the response, for the particular tissue and species in question, and whether the stress treatments are imposed abruptly or slowly (Ashraf, 1994; Munns et al., 2000).

SPECIFIC ION TOXICITY

Toxicity occurs as a result of uptake and accumulation of

certain toxic ions from the irrigation water within a crop itself. These toxic constituents include mainly sodium, chloride and sulphate. They can reduce crop productivity and eventually cause crop failures. Not all crops are equally affected but most crops and woody perennial plants are sensitive (Abrol et al., 1988).

The salt taken up by plant concentrates in the old leaves; continued transport of salt into transpiring leaves over a long period of time eventually results in very high Na^+ and Cl^- concentrations, and the leaves die. The cause of the injury is probably due to the salt load exceeding the ability of the cells to compartmentalize salts in the vacuole. Salts then would rapidly build up in the cytoplasm and inhibit enzyme activity. Alternatively, they might build up in the cell walls and dehydrate the cell (Munns, 2005) but Mühling and Läuchli (2002) found no evidence for this in maize cultivars that differed in salt tolerance.

Mechanisms for tolerance of the salt-specific effects of salinity are of two main types: those minimizing the entry of salt into the plant and those minimizing the concentration of salt in the cytoplasm. Root cytosolic Na^+ concentrations are probably in the order of 10 - 30 mM (Tester and Davenport, 2003). Leaf Na^+ cytosolic concentrations are unknown, but are considered to be much less than 100 mM (Wyn Jones and Gorham, 2002). The concentration at which Cl^- becomes toxic is even less defined. Roots must exclude most of the Na^+ and Cl^- dissolved in the soil solution, or the salt in the shoot will gradually build up with time to toxic levels. Plants transpire about 50 times more water than they retain in their leaves (Munns, 2005).

Husain et al. (2003) used two durum wheat genotypes with contrasting rates of Na^+ transport to leaves to assess the effects of the Na^+ exclusion trait on preventing leaf injury and enhancing yield. They found that older leaves of the high- Na^+ lines lost chlorophyll more rapidly and died earlier than the low- Na^+ lines. The low- Na^+ trait improved yield by greater than 20% in saline soil at moderate salinity. However, yield was not improved at high salinity. This indicates that traits other than Na^+ exclusion are important at high salinity, where the osmotic effect of the NaCl outweighs its salt-specific effect on growth and yield. Na^+ increment inside plants had toxic effects on seed germination, mainly by affecting the plant water relations or through displacement of Ca^{2+} by Na^+ from critical cell wall binding sites, which could disrupt cell wall synthesis and hence inhibit plant growth (Xue et al., 2004).

According to Loreto and Bonghi (1987), Cl^- concentration more than 80mM in total tissue water alters plant morphology, stomata become less responsive to environmental changes and leaf thickness is reduced. Chloride is not adsorbed by soils but moves readily with the soil water. It is taken up by roots and moves upward to accumulate in the leaves. The toxic level of chloride causes leaf burn or drying of leaf tissues, which occurs

first at extreme leaf then tips of older leaves and progresses back along the edges as severity increases. Marschner (1995) found that extreme leaf burn due to toxic level of chloride leading to early leaf drop, of which finally, the whole plant became defoliated.

NUTRITIONAL IMBALANCE

Excessive amount of soluble salts in the root environment causes osmotic stress, which may result in the disturbance of the plant water relations in the uptake and utilization of essential nutrients, and also in toxic ion accumulation. As a result of these changes, the activities of various enzymes and the plant metabolism are affected (Munns, 2002; Lacerda et al., 2003). The interactions of salts with mineral nutrients may result in considerable nutrient imbalances and deficiencies (McCue and Hanson, 1990). Ionic imbalance occurs in the cells due to excessive accumulation of Na^+ and Cl^- and reduces uptake of other mineral nutrients, such as K^+ , Ca^{2+} , and Mn^{2+} (Karimi et al., 2005). High sodium to potassium ratio due to accumulation of high amounts of sodium ions inactivates enzymes and affects metabolic processes in plants (Booth and Beardall, 1991).

Excess Na^+ and Cl^- inhibits the uptake of K^+ and leads to the appearance of symptoms like those in K^+ deficiency. The deficiency of K^+ initially leads to chlorosis and then necrosis (Gopa and Dube, 2003). The role of K^+ is necessary for osmoregulation and protein synthesis, maintaining cell turgor and stimulating photosynthesis (Freitas et al., 2001; Ashraf, 2004). Both K^+ and Ca^{2+} are required to maintain the integrity and functioning of cell membranes (Wenxue et al., 2003). Maintenance of adequate K^+ in plant tissue under salt stress seems to be dependent upon selective K^+ uptake and selective cellular K^+ and Na^+ compartmentation and distribution in the shoots (Munns et al., 2000; Carden et al., 2003). The maintenance of calcium acquisition and transport under salt stress is an important determinant of salinity tolerance (Soussi et al., 2001; Unno et al., 2002).

Salt stress decreases the $\text{Ca}^{2+}/\text{Na}^+$ ratio in the root zone, which affects membrane properties, due to displacement of membrane-associated Ca^{2+} by Na^+ , leading to dissolution of membrane integrity and selectivity (Kinraide, 1998). The increased levels of Na^+ inside the cells change enzyme activity resulting in cell metabolic alteration, disturbance in K^+ uptake and partitioning in the cells and throughout the plant that may even affect stomatal opening, thus diminishing the ability of the plant to grow. Externally supplied Ca^{2+} has been shown to ameliorate the adverse effects of salinity on plants, presumably by facilitating higher K^+/Na^+ selectivity (Hasegawa et al., 2000). Another key role attributed to supplemental Ca^{2+} addition is its help in osmotic adjustment and growth via the enhancement of compatible organic solutes accumulation (Girija et al., 2002).

Ca^{2+} has also been implicated in stress protection by stabilizing membranes and reducing oxidative damage (Larkindale and Knight, 2002). High K^+/Na^+ ratio was observed due to abscissic acid (ABA) treatment given to common bean plant that seems to limit sodium translocation to shoot (Khadri et al., 2007).

REACTIVE OXYGEN SPECIES

Exposure of plants to salt stress can up-regulate the production of reactive oxygen species (ROS) such as H_2O_2 (hydrogen peroxide), O_2^- (superoxide), $^1\text{O}_2$ (singlet oxygen) and $\cdot\text{OH}$ (hydroxyl radical). Excess ROS causes phytotoxic reactions such as lipid peroxidation, protein degradation and DNA mutation (McCord, 2000; Wang et al., 2003; Vinocur and Altman, 2005; Pitzschke et al., 2006). In plant cells, ROS, mainly H_2O_2 , superoxide anion (O_2^-), and hydroxyl radical ($\cdot\text{OH}$) are generated in the cytosol, chloroplasts, mitochondria, and the apoplastic space (Bowler and Fluhr, 2000; Mittler, 2002), while ROS have the potential to cause oxidative damage to cells during environmental stress. Recent studies have shown that ROS play a key role in plants as signal transduction molecules involved in mediating responses to pathogen infection, environmental stresses, programmed cell death and developmental stimuli (Mittler et al., 2004; Torres and Dangl, 2005).

Membrane injury induced by salt stress is related to an enhanced production of highly toxic ROS (Shalata et al., 2001). A rise in ROS production may result from stomatal closure, causing a decrease in CO_2 concentration inside the chloroplasts. This in turn causes a decrease in NADP^+ concentration with the concomitant generation of ROS (Foyer and Noctor, 2003). The increased concentration of ROS damages the D1 protein of PS II leading to photoinhibition. Stress enhanced photorespiration and NADPH activity also contributes to increase in H_2O_2 accumulation, which may inactivate enzymes by oxidizing their thiol groups. This toxicity of H_2O_2 is not due to its reactivity alone, but requires the presence of a metal reductant to form the highly reactive hydroxyl radical ($\cdot\text{OH}$), which has the ability to react with all biological molecules (Halliwell and Gutteridge, 1989). Salinity-associated reductions in elongation in the expansion zone of maize leaves are associated with reduced ROS levels and could be alleviated by the addition of ROS (Rodriguez et al., 2004).

PHYSIOLOGICAL AND BIOCHEMICAL PROCESSES

Soil salinity affects various physiological and biochemical processes which result in reduced biomass production. This adverse effect of salt stress appears on whole plant level at almost all growth stages including germination, seedling, vegetative and reproductive stages. However,

tolerance to salt stress at different plant developmental stages varies from species to species. For example, it has been observed that the degree of salt tolerance at different developmental growth stages varies in rice (Akbar and Yabuno, 1977), barley (Norlyn, 1980) and wheat (Ashraf and Khanum, 1997). In contrast, salt tolerance in some other crops such as *Medicago sativa*, *Trifolium alexandranium* and *Trifolium pratense* examined at the seedling stage was also confirmed at the later growth stages (Ashraf et al., 1986). Similarly, while working with safflower, Ashraf and Fatima (1995) also found that salt tolerance does not vary at different plant growth stages in these plants.

Different scientists have reported that variation in salt tolerance in a number of crop species depends on the extent of Na^+ exclusion at root level or ability to compartmentalize salts in the vacuole (Munns, 2002, 2005; Ashraf, 2004). For example, Wyn Jones et al. (1984) found that the higher salt tolerance of *Agropyron junceum* to that of *Agropyron intermedium* was related to its efficient exclusion of both Na^+ and Cl^- . In another study, Carden et al. (2003) found that the salt tolerant variety maintained a 10-fold lower cytosolic Na^+ in the root cortical cells than the more sensitive variety. It is well established that high accumulation of Na^+ in shoots inhibits enzyme activity, and other metabolic processes such as protein synthesis and photosynthesis (Ashraf, 2004; Munns, 2005) thereby reducing leaf growth or causing leaf death. Thus, in most plant species, particularly glycophytes, Na^+ exclusion from the shoot and retention in the root is a general trend and hence an important component of salt tolerance (Ashraf, 2004). However, Mansour et al. (2005) found that salt induced increase in Na^+ accumulation compared with a decrease in K^+ and Ca^{2+} was higher in salt tolerant maize cultivar Giza 2 compared with that in salt sensitive Trihybrid 321. Furthermore, it was found that high accumulation of proline and glycinebetaine was associated with salt tolerance in maize. Although accumulation of toxic ions in the leaves can cause toxicity, variation in specific ion toxicity at inter-specific or intra-specific level could be due to some adaptations to tolerant high levels of toxic ions.

A number of studies have shown that photosynthetic capacity of different species is reduced due to salinity (Ashraf, 2004; Dubey, 2005). It is evident that higher photosynthetic capacity causes increased plant growth under normal or stress conditions as has earlier been observed in a number of plant spp, e.g., in cotton (Pettigrew and Meredith, 1994), Zea mays (Crosbie and Pearce, 1982), Brassica spp. (Nazir et al., 2001) and wheat (Raza et al., 2007). Furthermore, salt-induced reduction in photosynthesis could be due to stomatal and non-stomatal limitations or combination of both. High accumulation of Na^+ and Cl^- in the leaves also reduces photosynthetic capacity and Na^+ content in the leaves of rice (Yeo, 1998), and wheat (James et al., 2002), while high Cl^- contents in the citrus (Walker et al., 1981) and in

the chloroplast of *Phaseolous vulgaris* (Seemann and Critchley, 1985) were found to be detrimental to photosynthesis. In view of all these reports, it can be concluded that growth inhibition may occur due to both osmotic and toxic effects. However, osmotically induced reduction in growth occurs at early growth stages under salt stress. Furthermore, photosynthesis is also one of the main contributing factors in salt-induced reduction in plant growth and yield. Tolerance of photosynthetic system to salinity depends on how effectively plant excludes or compartmentalizes the toxic ions. However, the extent of the adverse effects of salt stress on photosynthesizing tissue or on growth varies with the type of species, level of stress and duration of stress.

CONCLUSION

It is concluded from the above studies that salt stress affects plant physiology at whole plant as well as at cellular levels through osmotic and ionic adjustments that result in reduced biomass production. The adverse effect of salt stress appears on whole plant level at almost all growth stages including germination, seedling, vegetative and maturity stages. Despite causing osmotic and ionic stress, salinity causes ionic imbalances that may impair the selectivity of root membranes and induce potassium deficiency.

REFERENCES

- Abrol IP, Yadov JSP, Massiud FI (1988). Salt affected soils and their management. Soil Resour. Manage. Conserv. Ser. FAO Land and water Dev. Div. Bul. p. 39.
- Akbar M, Yabuno T (1977). Breeding saline-resistant varieties of rice. IV. Inheritance of delayed type panicle sterility induced by salinity. Jpn. J. Breed, 27: 237-240.
- Ashraf M (1994). Breeding for salinity tolerance in plants. Crit. Rev. Plant Sci. 13: 17-42.
- Ashraf M (2004). Some important physiological selection criteria for salt tolerance in plants. Flora, 199: 361-376.
- Ashraf M, Fatima H (1995). Responses of some salt tolerant and salt sensitive lines of safflower (*Carthamus tinctorius* L.). Acta Physiol. Plant, 17: 61-71.
- Ashraf M, Khanum A (1997). Relationship between ion accumulation and growth in two spring wheat lines differing in salt tolerance at different growth stages. J. Agron. Crop Sci. 178: 39-51.
- Ashraf M, McNeilly T, Bradshaw AD (1986). Response and ion uptake of selected salt tolerant and unselected lines of three legume species. New Phytol. 104: 463-472.
- Ashraf M, Shahbaz M (2003). Assessment of genotypic variation in salt tolerance of early CIMMYT hexaploid wheat germplasm using photosynthetic capacity and water relations as selection criteria. Photosynthetica, 41: 273-280.
- Azevedo Neto, AD, Prisco JT, Eneas-Filho J, Abreu CEB, Filho, E G (2006). Effect of salt stress on antioxidative enzymes and lipid peroxidation in leaves and roots of salt-tolerant and salt-sensitive maize genotypes. Environ. Exp. Bot. 56: 87-94.
- Booth WA, Beardall J (1991). Effect of salinity on inorganic carbon utilization and carbonic anhydrase activity in the halotolerant algae *Dunaliella salina* (Chlorophyta). Phycologia, 30: 220-225.
- Bowler C, Fluhr R (2000). The role of calcium and activated oxygen as signals for controlling cross-tolerance. Trends Plant Sci. 5: 241-246.
- Brugnoli E, Bjorkman O (1992). Growth of cotton under continuous salinity stress: influence on allocation pattern, stomatal and non stomatal components and dissipation of excess light energy. Planta, 187: 335-347.
- Carden DE, Walker DJ, Flowers TJ, Miller AJ (2003). Single-cell measurements of the contributions of cytosolic Na⁺ and K⁺ to salt tolerance. Plant Physiol. 131: 676-683.
- Crosbie TM, Pearce RB (1982). Effects of recurrent phenotypic selection for high and low photosynthesis on agronomic traits in two maize populations. Crop Sci. 22: 809-813.
- Dubey RS (2005). Photosynthesis in plants under stressful conditions. In: Pessarakli, M. editor. Handbook of photosynthesis. 2nd ed. Florida, CRC Press. pp. 479-497.
- FAO (2003). Global water crisis but May developing countries will face the water scarcity. Rome, Italy: FAO, available at <http://www.fao.org/english/newsroom/nems/2003/15254-en.html>.
- Flowers TJ, Yeo A (1995). Breeding for salinity resistance in crops. Where next? Aust. J. Plant Physiol. 22: 875-884.
- Foyer CH, Noctor G (2003). Redox sensing and signaling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. Physiol. Plant, 119: 355-364.
- Freitas JBS, Chagas RM, Almeida IMR, Cavalcanti FR, Silveira JAG (2001). Expression of physiological traits related to salt tolerance in two contrasting cowpea cultivars. Documentos Embrapa MeioNorte, 56: 115-118.
- Fricke W, Akhilarova G, Veselov D, Kudoyarova G (2004). Rapid and tissue-specific changes in ABA and in growth rate in response to salinity in barley leaves. J. Exp. Bot. 55: 1115-1123.
- Gadallah MAA (2000). Effects of acid mist and ascorbic acid treatment on the growth, stability of leaf membranes, chlorophyll content and some mineral elements of *Carthamus tinctorius*, the safflower. Water Air Soil Pollut. 118: 311-327.
- Girija C, Smith BN, Swamy PM (2002). Interactive effects of sodium chloride and calcium chloride on the accumulation of proline and glycinebetaine in peanut (*Arachis hypogaea* L.). Environ. Exp. Bot. 47: 1-10.
- Gopa R, Dube BK (2003). Influence of variable potassium on barley metabolism. Ann. Agric. Res. 24: 73-77.
- Greenway H, Munns R (1980). Mechanisms of salt tolerance in non halophytes. Ann. Rev. Plant Physiol. 31: 149-190.
- Gupta NK, Meena SK, Gupta S, Khandelwal SK (2002). Gas exchange, membrane permeability, and ion uptake in two species of Indian jujube differing in salt tolerance. Photosynthetica, 40: 535-539.
- Halliwell B, Gutteridge JMC (1989). Free Radicals in Biology and Medicine, Clarendon Press.
- Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000). Plant cellular and molecular response to high salinity. Ann. Rev. Plant Physiol. Plant Mol. Biol. 51: 463-499.
- Hsiao TC, Xu LK (2000). Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. J. Exp. Bot. 25: 1595-1616.
- Hu Y, Fromm J, Schmidhalter U (2005). Effect of salinity on tissue architecture in expanding wheat leaves. Planta, 220: 838-848.
- Husain S, Munns R, Condon AG (2003). Effect of sodium exclusion trait on chlorophyll retention and growth of durum wheat in saline soil. Aust. J. Agric. Res. 54: 589-597.
- James RA, Rivelli AR, Munns R, Caemmerer SV (2002). Factors affecting CO₂ assimilation, leaf injury and growth in salt-stressed durum wheat. Func. Plant Biol. 29: 1393-1403.
- Kao WY, Tsai TT, Shih CN (2003). Photosynthetic gas exchange and chlorophyll a fluorescence of three wild soybean species in response to NaCl treatments. Photosynthetica, 41: 415-419.
- Karimi G, Ghorbanli M, Heidari H, Khavarinejad RA, Assareh MH (2005). The effects of NaCl on growth, water relations, osmolytes and ion content in *Kochia prostrata*. Biol. Plant. 49: 301-304.
- Khadri M, Tejera NA, Lluch C (2007). Sodium chloride-ABA interaction in two common bean (*Phaseolus vulgaris*) cultivars differing in salinity tolerance. Environ. Exp. Bot. 60: 211-218.
- Kinraide TB (1998). Three mechanisms for the calcium alleviations of mineral toxicity. Plant Physiol., 118: 513-520.
- Kirst GO (1989). Salinity tolerance of eukaryotic marine algae. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40: 21-53.
- Lacerda CF, Cambraia J, Cano MAO, Ruiz HA, Prisco JT (2003). Solute

- accumulation and distribution during shoot and leaf development in two sorghum genotypes under salt stress. *Environ. Exp. Bot.* 49: 107-120.
- Larkindale J, Knight MR (2002). Protection against heat stress-induced oxidative damage in *Arabidopsis* involves calcium, abscisic acid, ethylene, and salicylic acid. *Plant Physiol.* 128: 682-695.
- Loreto F, Bonghi G (1987). Control of photosynthesis under salt stress in the olive. International conference on Agrometeorology, Fondazione Cesena Agricoltura, Cesena.
- Majeed A, Nisar MF, Hussain K (2010). Effect of saline culture on the concentration of Na⁺, K⁺ and Cl⁻ in *Agrostis tolonifera*. *Curr. Res. J. Biol. Sci.* 2(1): 76-82.
- Mansour MMF, Salama KHA, Ali FZM, Abou Hadid AF (2005). Cell and plant responses to NaCl in *Zea mays* cultivars differing in salt tolerance. *Gen. Appl. Plant Physiol.* 31: 29-41.
- Marschner H (1986). Mineral Nutrition in Higher Plants. Acad. Press, London. pp. 477-542.
- Marschner H (1995). Mineral nutrition of higher plants. 2nd ed. Acad. Pr., San Diego. Kindly p. 889.
- McCord JM (2000). The evolution of free radicals and oxidative stress. *Am. J. Med.*, 108: 652-659.
- McCue KF, Hanson A D (1990). Salt inducible betaine aldehyde dehydrogenase from sugar beet: cDNA cloning and expression. *Trends Biotechnol.* 8: 358-362.
- Mittler R (2002). Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.* 7: 405-410.
- Mittler R, Vanderauwera S, Gollery M, Breusegem FV (2004). Reactive oxygen gene network of plants. *Trends Plant Sci.*, 9: 490-498.
- Morales F, Abadía A, Gómez-Aparisi J, Abadía J (1992). Effect of combined NaCl and CaCl₂ salinity on photosynthetic parameters of barley grown in nutrient solution. *Physiol. Plant.* 86: 419-426.
- Mühling KM, Läuchli A (2002). Effect of salt stress on growth and cation compartmentation in leaves of two plant species differing in salt tolerance. *J. Plant Physiol.* 159: 137-146.
- Munns R (2002). Comparative physiology of salt and water stress. *Plant Cell Environ.* 25: 239-250.
- Munns R (2005). Genes and salt tolerance: bringing them together. *New Phytol.* 167: 645-663.
- Munns R, Hare RA, James RA, Rebetzke GJ (2000). Genetic variation for salt tolerance of durum wheat. *Aust. J. Agric. Res.*, 51: 69-74.
- Munns R, Termaat A (1986). Whole plant responses to salinity. *Aust. J. Plant Physiol.* 13: 143-160.
- Muranaka S, Shimizu K, Kato M (2002a). Ionic and osmotic effects of salinity on single leaf photosynthesis in two wheat cultivars with different drought tolerance. *Photosynthetica*, 40: 201-207.
- Murphy KST, Durako MJ (2003). Physiological effects of short-term salinity changes on *Ruppia maritima*. *Aquat. Bot.* 75: 293-309.
- Nazir N, Ashraf M, Rasul E (2001). Genomic relationships in oilseed Brassica with respect to salt tolerance-photosynthetic capacity and ion relations. *Pak. J. Bot.* 33: 483-501.
- Neves-Piestun BG, Bernstein N (2005). Salinity-induced changes in the nutritional status of expanding cells may impact leaf growth inhibition in maize. *Func. Plant Biol.* 32: 141-152.
- Norlyn JD (1980). Breeding salt tolerant crop plants. In: Genetic engineering of osmoregulation: Impact on plant productivity for food, chemicals and energy (eds Rains DW, Valentine RC, Hollaender A), Plenum Press, New York. pp. 293-309.
- Parida AK, Das AB, Mitra B (2003). Effects of NaCl stress on the structure, pigment complex composition, and photosynthetic activity of mangrove *Bruguiera parviflora* chloroplasts. *Photosynthetica*, 41: 191-200.
- Pettigrew WT, Meredith WR (1994). Leaf gas exchange parameters vary among cotton genotypes. *Crop Sci.* 34: 700-705.
- Pitzschke A, Forzani C, Hirt H (2006). Reactive oxygen species signaling in plants. *Antioxidants and Redox Signaling*, 8: 1757-1764.
- Ranjbarfordoei A, Samson R, Lemeur R, Damme PV (2002). Effects of osmotic drought stress induced by combination of NaCl and polyethylene glycol on leaf water status, photosynthetic gas exchange, and water use efficiency of *Pistacia khinjuk* and *P. mutica*. *Photosynthetica*, 40: 165-169.
- Raza SH, Athar HR, Ashraf M, Hameed A (2007). Glycinebetaine-induced modulation of antioxidant enzymes activities and ion accumulation in two wheat cultivars differing in salt tolerance. *Environ. Exp. Bot.* doi:10.1016/j.envexpbot.2006.12.009.
- Rhoades JD, Loveday J (1990). Salinity in irrigated agriculture. In: Steward BA, Neilsen DR (ed.): *Irrig. Agric. Crops*. pp: 1089-1142.
- Rodriguez AA, Llicia RA, Co rdoba R, Ortega L, Taleisnik E (2004). Decreased reactive oxygen species concentration in the elongation zone contributes to the reduction in maize leaf growth under salinity. *J. Exp. Bot.* 55: 1383-1390.
- Sayed OH (2003). Chlorophyll fluorescence as a tool in cereal crop research. *Photosynthetica*, 41: 321-330.
- Seemann JR, Critchley C (1985). Effects of salt stress on the growth, ion content, stomatal behaviour and photosynthetic capacity of a salt sensitive species. *Phaseolus vulagris* L. *Plant Physiol.* 82: 555-560.
- Shalata A, Mittova V, Volokita M, Guy M, Taj M (2001). Response of cultivated tomato and its wild salt-tolerant relative *Lycopersicon pennellii* to salt-dependent oxidative stress: the root antioxidative system. *Physiol. Plant.* 112: 487-494.
- Soussi M, Santamaria M, Cana A, Lluch C (2001). Effects of salinity on protein and lipopolysaccharide pattern in a salt-tolerant strain of *Mesorhizobium ciceri*. *J. Appl. Microbiol.* 90: 476-481.
- Supper S (2003). Verstecktes Wasser. Sustainable Austria, Nr. 25 December.
- Szabolcs I (1994). Soils and salinization. In *Handbook of plant and Crop Stress*. Ed. Pessarakli, M. Marcel Dekker, New York, pp. 3-11.
- Tejera N, Ortega E, Rodes R, Lluch C (2006). Nitrogen compounds in the apoplastic sap of sugarcane stem: Some implications in the association with endophytes. *J. Plant Physiol.* 163: 80-85.
- Tester M, Davenport R (2003). Na⁺ tolerance and Na⁺ transport in higher plants. *Ann. Bot.* 91: 503-507.
- Torres MA, Dangl JL (2005). Functions of the respiratory burst oxidase in biotic interactions, abiotic stress and development. *Curr. Opin. Plant Biol.* 8: 397-403.
- Unno H, Maeda Y, Yamamoto S, Okamoto M, Takenaga H (2002). Relationships between salt tolerance and Ca²⁺ retention among plant species. *Jpn. J. Soil Sci. Plant Nutr.* 73: 715-718.
- Vinocur B, Altman A (2005). Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. *Curr. Opin. Biotechnol.* 16: 123-132.
- Walker RR, Törökfalvy E, Scott NSS, Kriedemann PE (1981). An analysis of photosynthetic response to salt treatment in *Vitis vinifera*. *Aust. J. Plant Physiol.* 8: 359-374.
- Wang WX, Vinocur B, Altman A (2003). Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta*, 218: 1-14.
- Wenxue W, Bilisborrow PE, Hooley P, Fincham DA, Lombi E, Forster BP (2003). Salinity induced difference in growth, ion distribution and partitioning in barley between the cultivar Maythorpe and its derived mutant Golden Promise. *Plant Soil*, 250: 183-191.
- Wyn Jones RG (1981). Salt tolerance. In: Johnson, C. B. (Ed.): *Physiological processes limiting plant productivity*. Butterworths, London. pp. 271-292.
- Wyn Jones RG, Gorham J (2002). Intra and inter-cellular compartmentation of ions. In: Läuchli, A. and U. Lüttge, eds. *Salinity: Environment – Plants – Molecules*. Dordrecht, the Netherlands: Kluwer. pp. 159-180.
- Wyn Jones RG, Gorham J, McDonnell E (1984). Organic and inorganic solute contents as selection criteria for salt tolerance in the Triticeae. In: Staples R, Toennissen GH (Eds.), *Salinity Tolerance in Plants: Strategies for Crop Improvement*. Wiley and Sons, New York, pp. 189-203.
- Xue ZY, Zhi DY, Xue GP, Zhang H, Zhao YX, Xia GM (2004). Enhanced salt tolerance of transgenic wheat (*Triticum aestivum* L.) expressing a vacuolar Na⁺/H⁺ antiporter gene with improved grain yields in saline soils in the field and a reduced level of leaf Na⁺. *Plant Sci.* 167: 849-859.
- Yeo A (1998). Molecular biology of salt tolerance in the context of whole-plant physiology. *J. Exp. Bot.* 49: 915-929.
- Zhu JK (2001). Plant soil tolerance. *Trends Plant Sci.* 6: 66-71.