

PHYSIOLOGICAL AND BIOCHEMICAL RESPONSES OF PLANTS TO SALT STRESS

Masoud Torabi*

Natural Resource and Agricultural Research Center of Isfahan, Iran

**Corresponding author's E-mail: masoud.agro.ir@gmail.com*

Abstract:

Salinity affects plant growth and development in various ways through its impact on photosynthesis, water relations and nutrient absorption. Additionally, the biochemical composition of plants is also affected by salinity through changes in the concentration and type of proteins, amino acids, sugars and other carbohydrates. This paper elucidates with examples the changes that occur in the plant's physiological functions and biochemical composition as a result of increased salinity of the plant's environment. It is highlighted that the fundamental mechanism of salinity's effects on plant function is the increase in the osmotic pressure of the plant's environment that inhibits the absorption of water and nutrients. Invariably, salinity inhibits photosynthesis through its effects on stomatal conductance, water and nutrient uptake and decrease in the chlorophyll concentration. Subsequently, higher levels of salinity create an excessive accumulation of salts in plant tissues that causes toxicity. Prolonged salinity will thus reduce plant growth and yield and with increasing severity of salinity, toxic levels of salts that build up in plant tissues will further aggravate the stress. Plants exhibit several mechanisms that can alleviate the deleterious effects of salinity including compartmentalization of ions, synthesis of compatible solutes, induction of plant hormones and alteration of membrane structure.

Key Words: Biochemical response, plant physiology, crops, salinity, stresses

1. Introduction:

Salinity is one of the major abiotic stresses in arid and semi-arid regions but salt-affected soils have been recorded in practically all the climatic regions where more than 800 million hectares of land or over 6% of the world surfaces are salt affected. Sodium chloride is the most soluble, pervasive, and superabundant salt in the world (FAO, 2008; Munns and Tester, 2008). Rapid population growth and subsequent food shortage especially in Asia and Africa and advancing salinity in arable land due to climate change have increased the importance of finding salt tolerant genotypes (Blumwald *et al.*, 2004). In the arid and semiarid regions, high rate of evapotranspiration and lack of inorganic salts leaching from the soil surface layers have given rise to increase salinity and sodicity (Shannon *et al.*, 1994). The greatest cause of salinity may be due to the use of poor quality irrigation water (Sifola and Postiglione, 2002). There is a serious competition for fresh water so that high quality water is often used for industrial or domestic purposes and saline and polluted water is allocated for cultivated lands (Bouwer, 2002). Saline soils can be classified by the electrical conductivity of the soil saturation extract (EC) and by definition, soils with EC's of 4 dS/m or more are accounted as saline soils and soils with EC's exceeding 15 dS/m are considered strongly saline soils (Omami, 2005).

The factors causing salinization are numerous, including salt composition, climate, topography of lands and human activities (Blumwald *et al.*, 2004). In terms of salt composition, various cations and anions are involved in salinization but the most important ion precipitate are Na^+ and Cl^- where Na^+ particularly causes the soil dispersion while Cl^- causes high toxicity and nutrient imbalances in plants (Hasegawa *et al.*, 2000). Excess salt in the soil influences plant activities including physiological, biochemical and molecular processes and crop production is

suppressed by salinity in terms of quality and quantity (Delamor et al., 2001; Mer et al., 2000; Silvera et al., 2001).

Intensity of salinity depends on the amount of salt in irrigation water, chemistry and physics of soils, type of plants, plant growth stages and irrigation schedules (Oster, 1994; Shannon et al., 1994; Vicente et al., 2004). One strategy to overcome the problem of salinity is selecting salt tolerant genotypes. At low intensity of salinity the plant damages are due to osmotic stress, nutritional imbalances and ion toxicity (Carvajal et al., 1999; Grattan and Grieve, 1998; Wahome et al., 2001). At low salt concentration, shoot dehydration is the primary response of plants to osmotic stress (Carvajal et al., 1999) and at moderate up to high salt concentration, nutritional imbalances due to interferences of saline ions and their toxicity caused by accumulating the ions especially Na^+ and Cl^- are the main effects of salinity on physiological and biochemical activities in plants (De-Pascale et al., 2003a; De-Pascale et al., 2003b). Efforts to release salt tolerant cultivars require a proper understanding of the effects of salinity on plants, responses of plants in terms of physiological, biochemical and molecular activities to salinity and recognition of complex mechanisms of salt tolerance in plants (Apse and Blumwald, 2002; Zhu, 2001).

2. Effects of salinity on plant life - an overview:

Many researchers showed that the growth of plants declined under saline condition but the degree of reduction depended on level of salt, environmental conditions, type of plants and stages of growth for sugar beet (Ghoulam et al., 2002), cotton (Ha and Martinez, 2001), tomato (Romero-Aranda et al., 2006; Romero-Aranda et al., 2001), barley and wheat (Pessarakli et al., 1991) and sultana vines (Fisarakis et al., 2001). The initial effect of salinity on plants is reduction or maybe complete halt in plant growth as a result of reduced osmotic potential that inhibits absorption of water and nutrients by roots. High concentration of salt causes accumulation of salt ions in cells that frequently create toxicity and this is manifested in plants by chlorosis and necrosis of the leaf tissues (Hasegawa et al., 2000; Wahome et al., 2001).

The effects of salinity on plants cover a spectrum from mild osmotic effects which are not easily detected, reduction of shoot and root growth that are more obvious and on the other extreme, chlorosis, necrosis and senescence of young and old leaves (Munns, 2002). Some plant species are capable to overcome osmotic stress by accumulating internal solutes at low up to moderate salinity (Ghoulam et al., 2002). At high concentration of salt, the ions may interfere in the membrane functions and affect the internal solute balance and nutrient absorption, causing deficiency of nutrients with symptoms that are exactly like nutrient deficiency (Grattan and Grieve, 1998).

Reduction of plant growth by salinity differs between species and even between varieties and cultivars due to variability of salt tolerance among domestic and wild germplasms (Bolarian et al., 1991; Ghoulam et al., 2002). The environmental factors such as radiation, temperature, humidity and air pollution contribute towards the intensity of debilitation caused by salinity (Shannon et al., 1994).

There are differences between tolerant and sensitive varieties in terms of compartmentalization of salt. The sensitive varieties cannot compartmentalize salt in vacuoles and the salt accumulate very fast in cytoplasm and subsequently the photosynthesis and assimilation is reduced but in tolerant varieties the salt is rapidly compartmentalized in vacuoles and the vital actions change slowly (Munns, 1993; Munns and Tester, 2008). Overall, the factors

that are relevant to degree of salt stress in plants include physiological, biochemical, molecular and morphological characteristics.

2.1. Physiological effects of salt stress on crop plants:

2.1.1. Salinity effects on photosynthesis:

The most dramatic and readily measurable whole plant response to salinity is a decrease in stomatal aperture. Stomatal responses are undoubtedly induced by the osmotic effect of the salt outside the roots (Munns and Tester, 2008). Salinity affects stomatal conductance immediately, firstly and transiently owing to perturbed water relations and shortly afterward owing to the local synthesis of ABA (Munns and Tester, 2008). There is some evidence that the salinity at moderate or high levels interferes with gas exchanges and subsequently decrease photosynthesis rate so that the symptoms are exactly similar to those caused by drought stress (Bongi and Loreto, 1989; Loreto et al., 2003). Decrease in stomatal conductance is followed by reduction of CO₂ assimilation and respiration rate as reported for various species and levels of salinity (Ashraf, 2001; Marler and Zozor, 1996; Romero-Aranda et al., 2001). Previous research showed that rate of reduction in photosynthesis and translocation of assimilates under saline condition depends on species and salt concentrations (Parida et al., 2004). Some evidence showed that at low levels of salinity the photosynthesis rate in some species is stimulated and consequently the rate of photosynthesis increased (Parida and Das, 2005).

Rates of photosynthesis per unit leaf area in salt-treated plants are often unchanged, even though stomatal conductance is reduced (James et al., 2002). This paradox is explained by the changes in cell anatomy that give rise to smaller, thicker leaves and result in a higher chloroplast density per unit leaf area. When photosynthesis is expressed on a unit chlorophyll basis, rather than a leaf area basis, a reduction due to salinity can usually be measured. In any case, the reduction in leaf area due to salinity means photosynthesis per plant is always reduced. Parida et al., (2004) showed the photosynthesis rate of *B. parviflora* at low levels of salinity increased and with further increase in salinity the rate of photosynthesis decreased whereas stomatal conductance at low levels of salinity remained unchanged and at high levels of salinity decreased.

In *A. pseudoalhagi* (a leguminous plant), the leaf CO₂ assimilation rate increases at low salinity (5 dS/m NaCl) but is not affected significantly at 10 dS/m NaCl, whereas it is reduced to about 60% of the control in 20 dS/m NaCl. Also, stomatal conductance behaves similarly with the CO₂ assimilation rate and intercellular CO₂ concentration is lower in the NaCl-treated plants than in control (Kurban et al., 1999). Agastian et al., (2000) showed that in mulberry, stomatal conductance, CO₂ assimilation and respiration rate decreased in response to salinity while concentration of intercellular CO₂ increased with salinity. Khavari-Nejad and Chaparzadeh (1998) found that in alfalfa, chlorophyll content and net photosynthetic rate decreased under NaCl stress whereas respiration rate increased. They showed that there were no changes in the carotenoid content. There is some evidence that salt stress inhibits the apparent quantum efficiency of photosynthesis and suppressed photosystem II(PSII) activity whereas photosystem I (PSI) activity was stimulated by salt stress (Lu and Vonshak, 1999a). Two cultivar of wheat under saline condition exhibited two phases of photosynthetic inhibition so that in the first phase, photosynthetic reduction was gradual and in the second phase was rapid and accompanied by a decline of energy conversion efficiency in photosystem II (Muranaka et al., 2002).

Iyengar and Reddy (1996) noted that decreases in photosynthetic rate in saline condition resulted from a number of factors including:

- High osmotic potential and reduced water availability to plants result in cell membrane dehydration and reduction the permeability of CO₂ and consequently photosynthetic electron transport decreases via shrinkage of intercellular spaces.
- Due to toxicity of NaCl ions, the Cl⁻ ion inhibits photosynthetic rate through its inhibition of NO₃-N uptake by the roots, consequently reduced NO₃-N uptake combined with osmotic stress may explain the inhibitory effect of salinity on photosynthesis (Fisarakis et al., 2001).
- Stomata closure causes reduction in CO₂ supply so that the availability of CO₂ for carboxylation reactions restricted.
- Advancing senescence induced by salinity.
- Changes in cytoplasmic structure enzyme activities.
- Reduction in sink activities as a result of negative feedback.

Some evidence showed that growth is reduced more rapidly at lower concentrations of sodium in the leaf than in photosynthesis. This means that plants can withstand a certain loss in photosynthetic rate without any effect on growth (Alarc et al., 1993).

2.1.2. Salinity effects on photosynthetic pigments:

Several researchers showed that generally the chlorophyll and total carotenoid contents of leaves decrease under salinity where the chlorosis start from oldest leaves during the salt stress (Agastian et al., 2000; Gadallah, 1999; Hernandez et al., 1995). Conversely, Wang and Nil (2000) indicated that salinity caused chlorophyll content increases in *Amaranthus*.

Kennedy and De Filippis (1999) showed that concentration of protochlorophyll, chlorophylls, and carotenoids declined in *Grevilleai licifolia* and the reduction of protochlorophyll was greater than Chl-A and carotenoids and further, anthocyanin pigments significantly increased in this case by salinity. In a study of NaCl effects on photosynthetic pigments, chloroplast ultrastructure in leaves of tomato cultivars, Khavari-Nejad and Mostofi (1998) indicated that the contents of total chlorophyll carotene decreased with NaCl stress. According to Alamgir and Ali (1999) under salt stress, leaf pigments in nine genotypes of rice were reduced in general, but relatively high pigment levels were found in six genotypes. Lu and Vonshak (1999b) exhibited that carotenoid/chlorophyll ratio in the *Cyanobacterium (Spirulina platensis)* did not change but there was a significant decrease in the phycocyanin/chlorophyll ratio.

2.1.3. Salinity effects on chlorophyll fluorescence:

During the assimilation process, light absorption by chlorophyll molecules within the photosynthetic membranes is the initial process after which the absorbed energy is transferred to photosynthetic system for chemical reactions (Strasser et al., 2000). Less than one percent of absorbed solar radiation is used for photosynthesis while the rest is discharged as heat (Nobel, 1999). There are several competing processes during de-excitation of excited chlorophyll molecules in PSII and fluorescence is one of the effective processes in PSII. When the chlorophyll exposed to darkness for several minutes and subsequently brightly illuminated, fluorescence rapidly rises to a peak and then it decreases to stable state value (Maxwell and Johnson, 2000; Nobel, 1999). Researchers have used fluorescence induction kinetics as indicator of stress for detecting stress in salinity, chilling, freezing, drought, and air pollution stresses (Pospil and Dau, 2000). Chlorophyll fluorescence measurement in leaves is rapid, reproducible, non-destructive and allowing periodic and repetitive sampling (Percival and Fraser, 2001). The variable component of chlorophyll fluorescence (FV) is the difference between the maximum fluorescence signal (Fm) and the background level signal (Fo). The Fv/Fm ratio represents the

maximum quantum yield of PSII, in turn, is highly correlated with the quantum yield of net photosynthesis (Maxwell and Johnson, 2000; Nikoleudi, 2003).

Some research showed that salinity caused a decrease in Fv/Fm e.g. in olive (Bongi and Loreto, 1989), in *Ruppia maritima* (Murphy et al., 2003), and in celery (Everard et al., 1994). The results of some research showed that salt stress alone does not affect Fv/Fm ratio (Jimenez et al., 1997). The results of study on effects of salinity on chlorophyll fluorescence in naked oat showed that up to 150 mM NaCl the Fv/Fm ratio did not change but when salinity concentration increased to 200 mM or higher a sharp reduction of Fv/Fm ratio was observed (Zhao et al., 2007). There is some evidence in sorghum plant that PSII relative to Fv/Fm ratio is highly resistant to salinity stress but when the plants were faced with both salinity and high temperature, higher value of Fv/Fm ratio were observed (Lu and Zhang, 1998; Lu et al., 2003). Other researchers showed that the chlorophyll fluorescence in spinach is not affected by salinity directly whereas salt stress reduces photosynthesis initially due to reduction of CO₂ diffusion to chloroplast, both by stomatal closure and changes in mesophyll structure (Delfine et al., 1998; Delfine et al., 1999).

2.1.4. Salinity effects on water relations:

Water status is the major reason of growth reduction in plants under salt stress. Increasing salt in root zone reduces the water potential of leaf and subsequently, absorption of water and nutrients by plants are difficult or impossible (Romero-Aranda et al., 2001; Sohan et al., 1999). At low to moderate salinity and higher soil water potential the plants able to adjust water status through the accumulation of compatible solutes and maintenance of influx of water and nutrient by a potential gradient (Koyro, 2006; Shannon, 1997).

Many researchers showed that osmotic potential and water potential became more negative by increasing salt, whereas turgor pressure increased (Ghoulam et al., 2002; Gulzar et al., 2003; Romero-Aranda et al., 2001). Lu et al. (2002) in a study on *Suaeda salsa* known as a halophyte plant indicated that leaf water potential and evaporation rates declined by increasing salt concentration. The same results were shown for *Brassica* genus in which increased salinity caused decreases in leaf water potential, however there were some significant differences between *Brassica* species. *B. campestris* and *B. carinata* maintained significantly higher leaf water potentials than the other species at 200 mM of NaCl so that they were considered more salt tolerant than the others (Ashraf, 2001). In sunflower water potential became more negative by increasing salt concentration (Sohan et al., 1999).

According to Song et al. (2005) as a result of osmotic and ionic toxicity there were a reduction in germination of halophyte *Sueda* and when salinity alleviated, germination improved. However, water loss must be limited either by regulation of transpiration or adjusting osmotic potential. According to Ghoulam et al. (2002) relative water content (RWC) decreased due to salt application in sugar beet varieties. Katerji et al. (1997) indicated a decrease in RWC and a loss of turgor resulted in limited water availability for cell extension processes. Based on the results of these researchers it seems there are two issues:

- In high salt concentration, plants accumulate more Na⁺ and Cl⁻ in the tissues of the leaves than normal situation. Subsequently, by increasing Na⁺ and Cl⁻ within the leaf tissues lower osmotic potentials occurs and resulted in more negative water potentials.
- Root hydraulic conductance reduction decreases the amount of water flow from the roots to the leaves, thus, causing water stress in the leaf tissues.

2.1.5. Salinity effects on ion levels and nutrient contents:

In saline conditions, absorption of Na^+ and Cl^- competes with up taking nutritional elements such as K^+ , N, P, and Ca^{2+} by plants, which create nutritional disorders result in yield quantity and quality reduction (Grattan and Grieve, 1998). Several researchers indicated that increased NaCl concentration in root zone of plants causes accumulation of Na^+ and Cl^- in shoot tissues and decline Ca^{2+} , K^+ and Mg^{2+} levels in a number of plants (Bayuelo-Jimenez et al., 2003; Khan et al., 2000a; Perez-Alfocea et al., 1996). The movement of cations and anions from soil solution to the cytoplasm is controlled by permeability of cell membranes which contain protein transporters that facilitate the passage of ions (Jiménez-Casas, 2009).

Transportation of Na^+ across the cell membrane is inactive and needs membrane proteins to make possible the passageway down the electrochemical slope. Studies on roots of monocot plants subjected to high Na^+ concentrations exhibited that Na^+ influx into roots may be mediated by voltage-independent protein channels or non-selective cation protein channels (Davenport and Tester, 2000; Tester and Davenport, 2003). The net delivery of Na^+ to the xylem can be divided into four distinct components (Tester and Davenport, 2003):

- Influx into cells in the outer half of the root;
- Efflux back out from these cells to the soil solution;
- Efflux from cells in the inner half of the root to the xylem; and
- Influx back into these cells from the xylem before the transpiration stream delivers the Na^+ to the leaf blades.

White and Broadley (2001) showed that Cl^- influx across cell membrane may be mediated by both active and passive processes, whereas depending on the external Cl^- concentration, and facilitated by non-selective channels and carriers of other ions. Active Cl^- transport across the plasma membrane dominates Cl^- influx to root cells at low Cl^- concentrations in the soil solution. The participation of a $\text{Cl}^-/2\text{H}^+$ symporter in the Cl^- active transport was confirmed by electrophysiological studies of root-hair cells, where these Cl^- channels mediated either influx or efflux of Cl^- across the plasma membrane (Munns and Tester, 2008). With increasing NaCl and accumulation of Na^+ and Cl^- , the K^+ content of leaves declines but level of K^+ in root does not change in sugar beet (Ghoulam et al., 2002). Parida et al. (2004) indicated that there was an increase in Na^+ and Cl^- in mangrove (*B. parviflora*) exposed to salinity but the content of K^+ and Fe^{2+} in leaves did not change.

Several researchers showed that absorption of nitrogen is affected by saline condition so that salinity caused reduced N accumulation in plants (Feigin et al., 1991; Pardossi et al., 1999; Silvera et al., 2001). In eggplant, accumulation of Cl^- in leaves was accompanied with decreased concentration of NO_3^- . (Savvas and Lenz, 2000).

Based on plant species, growth stages, compositions and levels of salinity, the content of phosphorus will change in saline condition. In most of the plants salinity increasing correlated with P concentration decreasing in plant tissues (Kaya et al., 2001; Sonneveld and De Kreij, 1999).

2.1.6. Salinity effects on leaf and root growth:

There is some evidence that with increasing salinity, the leaves of plant change anatomically, for example, in *Atriplex sp.*, cotton and bean increase of spongy cell diameter, palisade diameter, palisade cell length, mesophyll thickness and epidermal thickness occurred (Longstreth and Nobel, 1979).

Adversely, Parida et al. (2004) noted that by increasing salinity both epidermal and mesophyll thickness and intercellular spaces in leaves of *Brugueira parviflora* decreased, also

Delfine et al. (1998) showed that intercellular spaces in leaves of spinach declined with increasing the salinity. Romero-Aranda et al. (2001) in a study on salinity effects on tomato indicated that in the face of salinity a reduction in stomatal density was observed.

In a study of salt effects on sweet potato Mitsuya et al. (2000) found that salt stress caused:

- Vacuolation development and partial swelling of endoplasmic reticulum.
- Decreasing in mitochondrial cristase and swelling of mitochondria, with an increase of the vesicles released from the Golgi stacks.
- Vesiculation and fragmentation of tonoplast.
- Degradation of cytoplasm by the mixture of cytoplasmic and vacuolar matrices in leaves of sweet potato.

The root is the first organ of plant affected by salinity. Waisel and Breckle (1987) and Munns (1993) showed that root influences on ion accumulation and leaf growth, they noted it can be one of the mechanisms of salt tolerance.

Vaughan et al. (2002) investigated effects of salinity on different alfalfa rooting (low- and high-fibrous rooting characteristics) of populations under increasing salinity condition and found that root production in high-fibrous root types was stimulated more than low-fibrous root types at low and medium salinity. They noted across salinity treatments, final root length density (cm root length per cm³ soil volume) was 24% higher for high-fibrous root types, and herbage yield of high- fibrous root types was 14% higher than low-fibrous root types. High fibrous rooting in alfalfa is a trait with potential usefulness as a salinity stress avoidance mechanism. Root growth has been used as a standard for screening of alfalfa salinity tolerance (Vaughan et al., 2002).

2.3. Biochemical effects of salt stress on crops:

2.3.1. Salinity effects on protein:

Accumulation of protein under salt condition may play a major role in terms of plants salt tolerance, where the proteins may serve as a reservoir of energy or may be adjuster of osmotic potential in plants subjected to salinity (Ingram and Bartels, 1996; Mansour, 2000; Pessarakli and Tucker, 1985; Pessarakli and Huber, 1991). They may be synthesized *de novo* in response to salt stress or may be present constitutively at low concentration (Parvaiz and Satyawati, 2008). It has been concluded that a number of proteins induced by salinity are cytoplasmic which can cause alterations in cytoplasmic viscosity of the cells (Hasegawa et al., 2000; Pessarakli and Tucker, 1985).

Ashraf and Harris (2004) noted that in salt tolerant cultivars of barley, sunflower finger millet, and rice there were a high content of soluble proteins. Several researches showed that soluble protein contents of leaves decreased in response to salinity (Agastian et al., 2000; Alamgir and Ali, 1999; Gadallah, 1999; Muthukumarasamy et al., 2000; Parida et al., 2002; Pessarakli and Tucker, 1988a; Pessarakli and Tucker, 1988b; Wang and Nil, 2000). Soluble protein increased at low up to moderate salt stress (Agastian et al., 2000). However the soluble protein did not change in sensitive accessions of safflower compared to tolerant accessions (Ashraf and Fatima, 1995).

2.3.2. Salinity effects on amino acids:

According to Mansour (2000) many amino acids including proline, alanine, arginine, glycine, serine, leucine, and valine and the non-protein amino acids (citrulline and ornithine) and amides (glutamine and asparagines) accumulate in plants exposed to salt stress. On the other hand Ashraf and Tufail (1995) reported that total free amino acids in the leaves were higher in

salt tolerant than in salt sensitive lines of sunflower , safflower (Ashraf and Fatima, 1995), *Eruca sativa* (Ashraf, 1994a) and *Lens culinaris* (Hurkman et al., 1991).

Proline is a major amino acid that accumulates in plant at a higher rate than other amino acids (Torabi et. al. 2010; Abraham et al., 2003). Ketchum et al. (1991) showed that accumulation of proline occurred in the cytosol and accomplished osmotic adjustment. Proline accumulation affects membrane maintenance and also alleviated the effects of NaCl on cell membrane interruption (Mansour, 1998). Maggio et al. (2002) noted proline as a signaling/regulatory molecule able to activate multiple responses that are components of the adaptation process.

There are different reports in terms of effects of salinity on proline in tolerant and sensitive genotypes among species. Torabi et al. (2010) and Petrusa and Winicov (1997) noted that salt tolerant alfalfa lines had two times more free proline content in root than sensitive lines and also increasing the proline in tolerant lines were more rapid than sensitive lines. Fougère et al. (1991) found the same results in alfalfa but Aziz et al. (1998) and Parida et al. (2004) demonstrated different and negative results in tomato and *Aegiceras corniculatum* respectively. Kaymakanova et al. (2008) indicated that with increasing salinity the amount of proline increased in bean (*Phaseolus vulgaris* L.).

It is also known that, as in plants, both ornithine and glutamate are precursors of proline biosynthesis in microorganisms and mammals (Parvaiz and Satyawati, 2008). In proline biosynthetic route pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR) play major roles (Delauney et al., 1993). Hong et al. (2000) demonstrated that by genetic manipulation of tobacco plant, the proline content increased and subsequently the tolerance to salinity increased. Some results showed that accumulation of proline in some plants was a consequence of salt injury and not a prerequisite for salt tolerance as shown in rice (De Lacerda et al., 2003). Also Lutts et al. (1999) exhibited that concentration of proline in sensitive rice cultivars was higher than tolerant genotypes.

2.3.3. Salinity effects on carbohydrates:

The accumulation of soluble carbohydrates in plants has been widely reported as a response to salinity or drought, despite a significant decrease in net CO₂ assimilation rate (Murakezy et al., 2003). When glycophytes are exposed to high salinity, the increase in soluble sugars contributes up to 50% increase in osmotic potential (Parvaiz and Satyawati, 2008). Parida et al. (2002) reported that carbohydrates such as mono and disaccharides (glucose, fructose, sucrose, fructans) and polysaccharides like starch accumulate under salt stress and play a major role in osmoprotection, osmotic adjustment, carbon storage, and radical scavenging. Parida et al. (2002) found that salinity reduced starch and increased reducing and non-reducing sugars in leaves of *Bruguiera parviflora*. In corroboration, Khavari-Nejad and Mostofi (1998) indicated that the contents of soluble sugars and total saccharides are increased significantly, but the starch content was not affected in leaves of tomato.

Some evidence showed that there are differences between accessions and cultivars in terms of amount of sugar in salinity conditions, as shown by Ashraf and Tufail (1995). Singer and Lindquist (1998) in a study on abiotic stresses found that trehalose as a disaccharide accumulates in various abiotic stresses and protects membranes and proteins in cells exposed to stress caused by water deficit and reduced aggregation of denatured proteins. Also trehalose inhibit apoptotic cell death and there are some proofs that trehalose is present in trace amounts in vascular plants, but some roles of trehalose are still unknown (Yamada et al., 2003).

3. SALT TOLERANCE IN PLANTS:

Salt tolerance has been defined as an inherent ability of plants to withstand the effects of high salt concentrations in the root zone or in the leaves without a significant adverse effect. Shannon and Grieve (1998) and Sacher and Staples (1985) defined salt tolerance as the ability of a plant to grow and complete its life cycle on a substrate that contains high concentrations of soluble salt. Shannon et al. (1994) and Levitt (1980) have classified plants into halophytes and glycophytes depending on their sensitivity to salinity. Plants that can survive on high concentrations of salt in the rhizosphere and grow well are called halophytes (Parida and Das, 2005). Depending on their salt-tolerating capacity, halophytes are either obligate or characterized by low morphological and taxonomical diversity with relative growth rates increasing up to 50% sea water or facultative and found in less saline habitats along the border between saline and non-saline upland and characterized by broader physiological diversity which enables them to cope with saline and nonsaline conditions (Parida and Das, 2005). Almost all major crop species as well as most wild species are glycophytes. Although individual responses to high salinity may differ, several lines of evidence suggest that all plants use the same general salt tolerance regulatory mechanisms, and differences between halophytic and glycophytic species are a quantitative rather than qualitative nature (Omami, 2005; Zhu, 2001).

3.1. Salt tolerance interactions with environment factors:

Interaction between salt and other environmental factors such as soil, water, and climatic conditions affect salt tolerance in plant (Shannon, 1985; Shannon et al., 1994). Hoffman et al. (1983) suggested plants grown under high temperature and water deficit conditions exhibit low salt tolerance in comparison with plants grown in cool and humid conditions. Under hot and dry conditions yield will decrease more rapidly with increasing salinity compared to yield reduction under cool and humid conditions. This is mainly due to decreased ion accumulation and/or improved plant water relations in the latter conditions (Shannon, 1985). A clear understanding of these interactions is necessary for a precise assessment of salt tolerance (Omami, 2005).

3.2. Genotype diversity in salt tolerance:

Plant growth generally decreases with increasing salinity but the rate of decrease vary with genotypes (threshold concentration). There are differences between genus, species and even cultivars since some cultivars or ecotypes can tolerate much higher salt concentrations than normal populations (Torabi et al., 2011; Hester et al., 1996; Hester et al., 1998; Hester et al., 2001).

Chen et al. (2005) screened some genotypes for salt tolerance by measuring K^+ flux and indicated that there is very strong negative correlation between the magnitude of K^+ efflux from the root and salt tolerance of a particular cultivar of barley. Bayuelo-Jimenez et al. (2002) in a study on *Phaseolus* showed that there are intraspecific and interspecific variations in salinity tolerance. The potential of improving the salt tolerance of white clover (*Trifolium repens L.*) was evaluated by Rogers et al. (1997). They showed that there are correlation between chloride ion exclusion and heritability and resulting in high variation of salt tolerance among the white clover cultivars, also they proposed that it is possible to increase levels of salt tolerance in white clover by selecting for low shoot Cl^- concentrations under saline conditions and this criterion can be used at very early stages of exposure to NaCl. Smethurst et al. (2009) used excised leaves to screen alfalfa for salt tolerance and reported that by using excised leaves exposed to salinity it may enhance PSII and allow the use of Fv/Fm measurements as an efficient screening tool for salt tolerance. Sabir and Ashraf (2007) screened local accessions of *Panicum maliaceum L.* for salt tolerance at seedling stage by using biomass production and ion accumulation and reported a

great magnitude of variations for salt tolerance observed in this set of germplasms. Saadallah et al. (2001) in a study on genotypic variability for tolerance to salinity of N₂-fixing common bean (*Phaseolus vulgaris*) noted that a genotypic variation in tolerance to salt was found, estimation parameters of growth and symbiotic nitrogen fixation showed that some lines which exhibited vigorous growth under the control treatment were greatly affected by salt treatment; the relative tolerance of some lines to salt seems to depend on the ability to maintain an adequate leaf area and to develop an abundant and efficient nodular system.

3.3. Effect of growth stage on salt tolerance:

Salt tolerance may be influenced by growth stage of plants but there is not enough information about the salt tolerance of crops at different stages of growth. Garg (2008), Omami (2005) and Vicente et al. (2004) noted that reaction to salt stress varies with the stage of plant development so that cultivars may be tolerant at one stage and sensitive at another. Efforts to use the criteria of salt tolerance during germination and emergence to evaluate salt tolerance at later growth stages have not generally been successful; tolerance at one growth stage usually is not related to another (Shannon and Grieve, 1998). The results showed that generally germination and seedling stages are less tolerant than other stages (Maas and Poss, 1989; Vicente et al., 2004). The relation between tolerance at germination and adult stage of growth was determined by Bayuelo-Jimenez et al. (2002), Lovato et al. (1994) and there is some argument that selection for salinity tolerance at germination, seedling stage or early vegetative growth may not produce tolerant adult plants (El-Hendawy et al., 2005; Kingsbury and Epstein, 1984). In some situations, salt tolerance at only one growth stage may have a significant benefit. For instance, improved tolerance during germination in sugar beet could remove a limiting step to tolerance throughout its growth (Shannon and Grieve, 1998). Sometimes salt stress applied at specific growth stages may be used to advantage. Moderate salinity applied during fruit development can change the partitioning of photosynthesis and improve soluble solids in melon and tomato (Shannon and Grieve, 1998).

4. MECHANISMS OF SALT TOLERANCE IN PLANTS:

Plants under salt stress employ biochemical and molecular mechanisms to overcome the stress for growth and development. Biochemical pathways are found in some processes which subsequently produces some compounds that improve salt tolerance ability (Iyengar and Reddy, 1996). The following biochemical strategies have been described by Ashraf and Harris (2004), Flowers et al. (1977) and Yamaguchi and Blumwald (2005):

- Selective accumulation or exclusion of ions
- Control of ions uptake by roots and transport into leaves
- Compartmentalization of ions at the cellular and whole-plant levels
- Synthesis of compatible solutes
- Change in photosynthetic pathways
- Alteration in membrane structure
- Induction of antioxidative enzymes
- Induction of plant hormones

Salt tolerant mechanisms are either low-complexity or high-complexity mechanisms. Low-complexity mechanisms appear to involve changes in many biochemical pathways. High-complexity mechanisms involve changes that protect major processes such as photosynthesis and respiration (Parida and Das, 2005).

4.1. Regulation and compartmentalization of ions:

When the plants are exposed to high levels of salinity the salt concentration increases in leaves gradually up to extreme levels and the salts exert their toxicity in leaves but the mechanisms is still unknown. Salt may accumulate in the apoplast and dehydrate the cell and maybe in cytoplasm and restrict enzymes in carbohydrate metabolism or maybe they accumulate at chloroplast and cause toxic effects on photosynthetic processes (Dajic, 2006). Large amount of salt in cytoplasm for both glycophytes and halophytes is harmful and to overcome the problem plants either restrict the excess salts in the vacuole or compartmentalize the ions in different tissues to facilitate their metabolic functions (Garg, 2008; Iyengar and Reddy, 1996; Reddy et al., 1992; Zhu, 2003). Ions uptake and compartmentalization are crucial not only for normal growth but also for growth under saline conditions (Adams et al., 1992). One of the mechanisms in glycophytes is limiting sodium uptake or movement of sodium to older tissues so that serve as storage compartments which are eventually sacrificed (Cheeseman, 1988). Normally at low up to moderate of salinity levels exclusion of ions is an effective mechanism whereas at high levels of salinity mainly halophytes make use of compartmentalization mechanism (Bohnert et al., 1995; Cheeseman, 1988). The compartmentalization act or Na^+ removal occur in vacuoles by salt-inducible enzyme Na^+/H^+ antiporter (Apse et al., 1999). Two electrogenic H^+ pumps, the vacuolar type H^+ -ATPase (V-ATPase) and the vacuolar pyrophosphatase (VPPase), coexist at membranes of the secretory pathway of plants (Dietz et al., 2001). Due to regulation the expression and activity of K^+ and Na^+ transporters and of H^+ pumps when plants under salt stress they maintain high concentrations of K^+ and low concentrations of Na^+ in the cytosol (Zhu et al., 1993).

One of the important adaptation accepted as osmotic adjustment is inclusion of ions in the cytoplasm (Halperin and Lynch, 2003). Experimental results indicated that Ca^{2+} has special role in salt adaptation so that Ca^{2+} reduces the toxic effects of NaCl, probably by facilitating higher K^+/Na^+ selectivity (Lauchli and Schubert, 1989; Liu and Zhu, 1997). There is some evidence that due to high levels of salt, cytosolic Ca^{2+} increased so that Ca^{2+} are transported from the apoplast intracellular compartments (Knight et al., 1997).

Other mechanisms of salt regulation are salt secretion and selective salt accumulation or exclusion (Dajic, 2006). Salt secretion occurs through development of unique cellular structures called salt glands (Dajic, 2006). These salt glands secrete salt (especially NaCl) from leaves and maintain internal ion concentration at lower level (Marcum and Pessaraki, 2006). Salt exclusion occurs through roots to regulate the salt content of their leaves in many halophytes (Levitt, 1980). Selective accumulation of ions or solutes enables the plants to make osmotic adjustments, which occur through mass action, and results in increasing water retention and/or sodium exclusion (Parida and Das, 2005).

4.2. Induced biosynthesis of compatible solutes:

When plants are exposed to salt stress, the cytoplasm tries to accumulate low molecular mass compounds to adjust the ionic balance in vacuoles. These compounds are called compatible solutes because they do not interfere with normal biochemical reactions (Ashihara et al., 1997; Burg et al., 1997; Ford, 1984; Garg, 2008; Hasegawa et al., 2000; Zhifang and Loescher, 2003). The main compatible solute include proline (Abrahmet. al., 2003; Hong et al., 2000; Kaymakanova et al., 2008; Khatkar and Kuhad, 2000; Maggio et al., 2002; Mansour, 2000; Singh et al., 2000), glycine betaine (Khan et al., 2000b; Rhodes and Hanson, 1993; Wang and Nil, 2000) sugars (Kerepesi and Galiba, 2000; Murakezy et al., 2003; Parida et al., 2002; Pilon-Smits et al., 1995; Yamada et al., 2003), and polyols (Bohnert and Shen, 1998; Bohnert et al., 1995; Dopp et al., 1985; Ford, 1984).

Polyols as one of the major compatible solutes have other roles including as low-molecular-weight chaperones, and as scavengers of stress-induced oxygen radicals (Bohnert et al., 1995; Smirnov, 1998). Basically, polyols serve two functions, namely osmotic adjustment and osmoprotection. In osmotic adjustment, they act to maintain the osmotic potential of water in the cytoplasm through isolation of sodium to vacuole or apoplast while for osmoprotection they interact with membranes, protein complexes, or enzymes (Crowe et al., 1997). The carbohydrates include sugars (glucose, fructose, sucrose, fructans) and starch as compatible solute accumulated under salt stress (Parida et al., 2002) and their main roles are osmoprotection, osmotic adjustment, carbon storage, and radical scavenging (Kerepesi and Galiba, 2000; Khatkar and Kuhad, 2000; Singh et al., 2000).

When plants are exposed to salinity a few of nitrogen-containing compounds (NCC) accumulate in plants. The NCC that is known to accumulate in plants are amino acids, amides, imino acids, proteins, quaternary ammonium compounds, and polyamines. There are variations among plant species for type and amount of NCC that accumulate in plants under salt stress. The major roles of NCC include osmotic adjustment, protection of cellular macromolecules, storage of nitrogen, maintenance of cellular pH, detoxification of the cells, and scavenging of free radicals under stress conditions (Mansour, 2000). The results obtained from many researchers indicated that when plants are exposed to salinity, NCC accumulates in plant especially free amino acid and glycine betaine (Khan et al., 2000b; Khan et al., 1998; Khan et al., 2000b; Saneoka et al., 1999; Wang and Nil, 2000).

4.3. Ions uptake and transport control by roots:

For normal metabolism plants need ionic balance, hence they need to inhibit uptake and translocation of toxic ions such as Na^+ and Cl^- and on the other hand, accelerate uptake of metabolically required ions such as K^+ by K^+ and Na^+ transporters and H^+ pumps (Ashraf and O'leary, 1996; Noble and Rogers, 1992; Zhu et al., 1993). The thermodynamics of a Na^+/H^+ antiporter is simple because the electroneutral exchange this antiporter catalyzes is unaffected by membrane potential. Thus, the direction of Na^+ movement is determined simply by the differences in free concentrations of Na^+ and H^+ . Carden et al. (2003) in a study on salinity effects on barley indicated that salt tolerant varieties kept up a cytosolic Na^+ ten times lower than sensitive varieties. There are some evidence that some tomato cultivars are able to select and transfer the major nutrients (K^+ , Ca^{2+} , Mg^{2+} and NO_3^-) to young leaves under moderate salinity and when plants are exposed to high levels of salinity they are not able to select and transfer NO_3^- (Perez-Alfocea et al., 1996). Ashraf and Khanum (1997) mentioned that ionic status can be considered to identify salt tolerance and used as a precise tool for breeding the salt tolerant cultivars.

4.4. Changes in photosynthetic pathways:

A reduction in photosynthesis rate under salinity is unavoidable and it can be due to water deficit and reduction in water potential. So the main mechanism to overcome salt stress in this situation is to build up the water use efficiency under salinity.

In this case some plants can be facultative halophyte like *M. crystallinum*, so that they can shift their C_3 mode of photosynthesis to CAM (Cushman et al., 1989; Parida and Das, 2005). There is some evidence that some plants such as *Atriplex lentiformis* when exposed to salt stress will shift from the C_3 to the C_4 pathway in response to salinity (Maricle et al., 2007; Parida and Das, 2005).

4.5. Induction of antioxidative enzymes:

Salinity effects and water deficit are similar as osmotic effects so that the osmotic activities can be due to wide range of environmental stresses (Cheeseman, 1988; Greenway and Munns, 1980; He et al., 2007; Imlay, 2003).

Increasing osmotic potential in cells causes an increase in reactive oxygen species (ROS) such as superoxide, hydrogen peroxide, hydroxyl radical and singlet oxygen (Imlay, 2003). He noted cytotoxic activated oxygen species are seriously able to disrupt normal metabolism through oxidation that is deleterious to lipids, proteins and nucleic acids (Fridovich, 1986; He et al., 2007; Imlay, 2003; Wise and Naylor, 1987).

On other hand the increase in O₂ concentration resulting from photosynthesis that remains in the chloroplasts also creates activated oxygen species (Asada, 1992; Harir and Mittler, 2009; Luhua et al., 2008). In plants exposed to abiotic stress such as high light intensity, temperature extremes, drought, high salinity, herbicide treatment, or mineral deficiencies, generally cause the imbalance between the production of reactive oxygen species and the quenching activity of the antioxidants (Imlay, 2003; Mittova et al., 2004; Spychalla and Desborough, 1990).

Plants have an effective system for scavenging active oxygen species that protect them from harmful oxidative reactions (Foyer et al., 1994; Mittova et al., 2004). Antioxidative enzymes such as catalase, glutathione reductase, superoxide dismutase and glutathione-S-transferase are the main enzymes to protect cells (Garratt et al., 2002; Mittova et al., 2003). Whereas superoxide dismutase, metabolizes oxygen (O₂) radicals to hydrogen peroxide (H₂O₂), then protecting cells from damage and catalase, ascorbate peroxidase, and a variety of peroxidases catalyze the subsequent breakdown of H₂O₂ to water and oxygen (Garratt et al., 2002; Gossett et al., 1994; Mittova et al., 2002; Mittova et al., 2003). Several researchers showed that when plants are exposed to salinity the activity of antioxidant increase, in rice (Fadzilla et al., 1997; Lee et al., 2001), wheat (Meneguzzo et al., 1999) and lentil (Bandeolu et al., 2004). There are some differences between genotypes in terms of oxidative tolerance in plants. Munns and Tester (2008) mentioned genetic differences in salinity tolerance are not necessarily due to differences in the ability of detoxify ROS. They noted that “differences in antioxidant activity between genotypes may be due to genotypic differences in degrees of stomatal closure or in other responses that alter the rate of CO₂ fixation, differences that bring into play the processes that avoid photoinhibition and for which the plant has abundant capacity”

4.6. Induction of plant hormones:

Based on previous research it is clear that with increasing salt stress, content of some hormones such as ABA and cytokinins increase in leaves of plant (Aldesuquy, 1998; Thomas et al., 1992; Vaidyanathan et al., 1999). There are some special roles for ABA when plants are exposed to salt stress such as activate salt-stress-induced genes (De Bruxelles et al., 1996; Gomez-Cadenas et al., 2003) to alleviate the inhibitory effect of NaCl on photosynthesis, growth and translocation of assimilates (Popova et al., 1995) to promote switch from C₃ to crassulacean acid metabolism (CAM) (Thomas et al., 1992) and promote stomata closure by rapidly altering ion fluxes in guard cells. Other hormone called jasmonates also has important roles in salt tolerance when content of jasmonates in salt-tolerant tomato cultivars was higher than salt-sensitive cultivars (Pedranzani et al., 2003). The main role of jasmonates is mediate signaling, such as defense responses, flowering, and senescence (Pedranzani et al., 2003).

5. CONCLUSIONS AND PERSPECTIVES:

The deleterious salt influences on plant can be along with their physiological and biochemical processes in plants. The initial and many dramatic responses of plants when exposed to salt condition is decrease of stomatal conductivity. Stomatal conductance and resistance are reduced by salinity in rhizosphere. Photosynthesis is influenced by salt stress attributable to closure of the stomata and a reduction in carbon assimilation owing to reduction in photosynthetic pigments, chlorophyll fluorescence, and unbalanced in ions and water relation. Usually the chlorophyll content and chlorophyll fluorescence decreases under salt stress in leaves. Chlorophyll fluorescence can monitor the function of the photosynthetic machinery to salt stress. Many studies indicated that osmotic potential and water potential became more negative by increasing salt. The unbalanced in ions is owing to competes ions salt with up taking nutritional elements such as K^+ , N, P, and Ca^{2+} by root plants and accumulation of Na^+ and Cl^- in shoot tissues and decline Ca^{2+} , K^+ and Mg^{2+} levels. The biochemical responses to salt stress can be attributable to accumulation of low molecular weight organic solutes or inorganic ions in cell, whereas each on play major roles to adjust osmotic potential in plant under salt stress. The protein and amino acids accumulate as a reservoir of energy and adjuster of osmotic potential in plants subjected to salinity whereas everyone can create tolerance in plants in face to salt stress. The accumulation of carbohydrates and changing in types of them is another biochemical response of plants to salt stress whereas each on plays a major role in osmoprotection, osmotic adjustment, carbon storage, and radical scavenging. Salt tolerance in plant is an inherent ability of plants to survive the impacts of salt concentrations in the root zone or in the leaves without a significant adverse effect. Nevertheless diversity among genotypes create different levels of salt tolerance but on other hand salt tolerance can be influenced by interaction of plants and environment factors such as soil, water, and climatic conditions. It is concluded that the effects of salinity on plants is complex and multifaceted and further work is required to understand how effects of salinity on crops can be overcome or alleviated. Further work is needed to understand the molecular basis of salinity tolerance of the halophytic plants in order to transfer some of the traits to the important crops that are now faced with the prospect of having to be grown in marginal lands where salinity is one of the major limitations.

References:

- Abraham E., Rig G., Székely G., Nagy R., Koncz C., Szabados L. (2003) Light-dependent induction of proline biosynthesis by abscisic acid and salt stress is inhibited by brassinosteroid in Arabidopsis. *Plant Molecular Biology* 51:363-372.
- Adams P., Thomas J., Vernon D., Bohnert H., Jensen R. (1992) Distinct cellular and organismic responses to salt stress. *Plant and Cell Physiology* 33:1215-1223.
- Agastian P., Kingsley S., Vivekanandan M. (2000) Effect of salinity on photosynthesis and biochemical characteristics in mulberry genotypes. *Photosynthetica* 38:287-290.
- Alamgir A.N.M., Ali M.Y. (1999) Effect of salinity on leaf pigments, sugar and protein concentrations and chloroplast ATPase activity of rice (*Oryza sativa L.*). *Bangladesh J. Botany* 28:145-149.
- Alarc J., Sanchez-Blanco M., Bolar n M., Torrecillas A. (1993) Water relations and osmotic adjustment in *Lycopersicon esculentum* and *L. pennellii* during short-term salt exposure and recovery. *Physiologia Plantarum* 89:441-447.
- Aldesuquy H. (1998) Effect of seawater salinity and gibberellic acid on abscisic acid, amino acids and water-use efficiency by wheat plants. *Agrochimica* 42:147-157.

- Apse M., Blumwald E. (2002) Engineering salt tolerance in plants. *Current Opinion in Biotechnology* 13:146-150.
- Apse M., Aharon G., Snedden W., Blumwald E. (1999) Salt tolerance conferred by over expression of a vacuolar Na⁺/H⁺ antiport in *Arabidopsis*. *Science* 285:1256-1264.
- Asada K. (1992) Ascorbate peroxidase- a hydrogen peroxide-scavenging enzyme in plants. *Physiologia Plantarum* 85:235-241.
- Ashihara H., Adachi K., Otawa M., Yasumoto E., Fukushima Y., Kato M., Sano H., Sasamoto H., Baba S. (1997) Compatible solutes and inorganic ions in the mangrove plant *Avicennia marina* and their effects on the activities of enzymes. *Zeitschrift fur Naturforschung. C. A journal of biosciences* 52:433-440.
- Ashraf M. (1994a) Organic substances responsible for salt tolerance in *Erucasativa*. *Biologia Plantarum* 36:255-259.
- Ashraf M. (1997) Changes in soluble carbohydrates and soluble proteins in three arid-zone grass species under salt stress. *Trop. Agric* 74:234-237.
- Ashra M. (2001) Relationships between growth and gas exchange characteristics in some salt-tolerant *amphidiploid Brassica* species in relation to their diploid parents. *Environmental and Experimental Botany* 45:155-163.
- Ashraf, M., Tufail M. (1995) Variation in salinity tolerance in sunflower (*Helianthus annuus L.*). *Journal of Agronomy and Crop Science* 174:351-362.
- Ashraf M., Fatima H. (1995) Responses of some salt tolerant and salt sensitive lines of safflower (*Carthamustin ctorius L.*). *Acta Physiol. Plant* 17:61-71.
- Ashraf M., O'leary J. (1996) Responses of some newly developed salt-tolerant genotypes of spring wheat to salt stress: 1. Yield components and ion distribution. *Journal of Agronomy and Crop Science* 176:91-101.
- Ashraf M., Khanum A. (1997) Relationship between ion accumulation and growth in two spring wheat lines differing in salt tolerance at different growth stages. *Journal of Agronomy and Crop Science* 178:39-52.
- Ashraf M., Harris P.G.C. (2004) Biochemical indicators of salinity tolerance in plant. *Plant Science* 166:3-16.
- Aziz A., Martin-Tanguy J., Larher F. (1998) Stress-induced changes in polyamine and tyramine levels can regulate proline accumulation in tomato leaf discs treated with sodium chloride. *Physiologia Plantarum* 104:195-202.
- Bandeolu, E., Eyido an F., Yücel M., Avniktem H. (2004) Antioxidant responses of shoots and roots of lentil to NaCl-salinity stress. *Plant Growth Regulation* 42:69-77.
- Bayuelo-Jimenez, J., Craig R., Lynch J. (2002) Salinity tolerance of *Phaseolus* species during germination and early seedling growth. *Crop Science* 42:1584-1594.
- Bayuelo-Jiménez, J., Debouck D., Lynch J. (2003) Growth, gas exchange, water relations, and ion composition of *Phaseolus* species grown under saline conditions. *Field Crops Research* 80:207-222.
- Blumwald, E., Grover A., Good A. G. (2004) Breeding for abiotic stress resistance: challenges and opportunities New directions for a diverse planet, 4th International Crop Science Congress, Brisbane, Australia.
- Bohnert, H., Shen B. (1998) Transformation and compatible solutes. *Scientia Horticulturae* 78:237-260.
- Bohnert H., Nelson D., Jensen R. (1995) Adaptations to environmental stresses. *The Plant Cell* 7:1099-1111.

- Bolarian M., Fernandez F., Cruz, V., Cuartero J. (1991) Salinity tolerance in four wild tomato species using vegetative yield-salinity response curves. *Journal of the American Society for Horticultural Science (USA)* 116: 286–290.
- Bongi G., Loreto F. (1989) Gas-exchange properties of salt-stressed olive (*Olea europea L.*) leaves. *Plant Physiology* 90:1408-1415.
- Bouwer H. (2002) Integrated water management for the 21st century: problems and solutions. *J. Irrig. Drain. Eng* 28:193-202.
- Burg M., Kwon a., (1997) Regulation of gene expression by hypertonicity¹. *Annual Review of Physiology* 59:437-455.
- Carden D., Walker D., Flowers T., Miller A. (2003) Single-cell measurements of the contributions of cytosolic Na⁺ and K⁺ to salt tolerance. *Plant Physiology* 131:676-683.
- Carvajal M., Martinez V., Alcaraz C. (1999) Physiological function of water channels as affected by salinity in roots of *paprika pepper*. *Physiologia Plantarum* 105:95-101.
- Cheeseman J. (1988) Mechanisms of salinity tolerance in plants. *Plant Physiology* 87:547-550.
- Chen Z., Newman I., Zhou M., Mendham N., Zhang G., Shabala S. (2005) Screening plants for salt tolerance by measuring K⁺ flux: a case study for barley. *Plant Cell Environ* 28:1230-1246.
- Crowe J., Oliver A., Hoekstra F., Crowe L. (1997) Stabilization of dry membranes by mixtures of hydroxyethyl starch and glucose: the role of vitrification. *Cryobiology* 35:20-30.
- Cushman J., Meyer G., Michalowski C., Schmitt J., Bohnert H. (1989) Salt stress leads to differential expression of two isogenes of phosphoenolpyruvate carboxylase during Crassulacean acid metabolism induction in the common ice plant. *The Plant Cell Online* 1:715-725.
- Dajic Z. (2006) *Salt Stress//Physiology and Molecular Biology of Stress Tolerance in Plants/Eds Madhava Rao KV, Raghavendra AS, Janardhan Reddy K, Dordrecht: Springer-Verlag. pp: 41-99.*
- Dalton F., Maggio A., Piccinni G. (2000) Simulation of shoot chloride accumulation: separation of physical and biochemical processes governing plant salt tolerance. *Plant and Soil* 219:1-11.
- Davenport R., Tester M. (2000) A weakly voltage-dependent, nonselective cation channel mediates toxic sodium influx in wheat. *Plant Physiology* 122: 823-834.
- De-Pascale S., Maggio A., Ruggiero C., Barbieri G. (2003a) Growth, Water Relations, and Ion Content of Field-grown Celery *Apium graveolens L. var. dulce* under Saline Irrigation. *Journal of the American Society for Horticultural Science* 128:136-143.
- De-Pascale S., C Ruggiero, G Barbieri, A Maggio. (2003b) Physiological responses of pepper to salinity and drought. *Journal of the American Society for Horticultural Science* 128:48-54.
- De Bruxelles G., Peacock W., Dennis E., Dolferus R. (1996) Abscisic acid induces the alcohol dehydrogenase gene in Arabidopsis. *Plant Physiology* 111:381-391.
- De Lacerda C., Cambraia J., Oliva M., Ruiz H., Prisco J. (2003) Solute accumulation and distribution during shoot and leaf development in two sorghum genotypes under salt stress. *Environmental and Experimental Botany* 49:107-120.
- Delamor F., Martinez V., Cerda A. (2001) Salt tolerance of tomato plants as affected by stage of plant development. *Hort. Science*. 36:1260-1263.
- Delauney A., Hu C., Kishor P., Verma D. (1993) Cloning of ornithine delta-aminotransferase cDNA from *Vigna aconitifolia* by trans-complementation in *Escherichia coli* and regulation of proline biosynthesis. *Journal of Biological Chemistry* 268(25):18673-18678.

- Delfine S., Alvino A., Zacchini M., Loreto F. (1998) Consequences of salt stress on conductance to CO₂ diffusion, Rubisco characteristics and anatomy of spinach leaves. *Australian Journal of Plant Physiology* 25:395-402.
- Delfine S., Alvino A., Villani M., Loreto F. (1999) Restrictions to carbon dioxide conductance and photosynthesis in spinach leaves recovering from salt stress. *Plant Physiology* 119:1101-1106.
- Dietz K., Tavakoli N., Kluge C., Mimura T., Sharma S., Harris G., Chardonnens A., Golldack D. (2001) Significance of the V-type ATPase for the adaptation to stressful growth conditions and its regulation on the molecular and biochemical level. *Journal of Experimental Botany* 52:1969-1980.
- Dopp M., Larher F., Weigel P. (1985) Osmotic adaption in Australian mangroves. *Plant Ecology* 61:247-253.
- El-Baz F., Mohamed A., Aly A. (2003) Development of biochemical markers for salt stress tolerance in cucumber plants. *Pak. J. Biol. Science* 6:16-22.
- El-Hendawy S., Hu Y., Yakout G., Awad A., Hafiz S., Schmidhalter U. (2005) Evaluating salt tolerance of wheat genotypes using multiple parameters. *European Journal of Agronomy* 22:243-253.
- Everard J., Gucci R., Kann S., Flore J., Loescher W. (1994) Gas exchange and carbon partitioning in the leaves of celery (*Apium graveolens L.*) at various levels of root zone salinity. *Plant Physiology* 106:281-292.
- Fadzilla N., Finch R., Burdon R. (1997) Salinity, oxidative stress and antioxidant responses in shoot cultures of rice. *Journal of Experimental Botany* 48:325-331.
- FAO. (2008) Global network on integrated soil management for sustainable use of salt-affected soils. <http://www.fao.org/ag/agl/agll/spush>.
- Feigin A., Pressman E., Imas P., Miltau O. (1991) Combined effects of KNO₃ and salinity on yield and chemical composition of lettuce and Chinese cabbage. *Irrigation Science* 12:223-230.
- Fisarakis I., Chartzoulakis K., Stavarakas D. (2001) Response of Sultana vines (*V. vinifera L.*) on six rootstocks to NaCl salinity exposure and recovery. *Agricultural Water Management* 51:13-27.
- Flowers T., Troke P., Yeo A. (1977) The mechanism of salt tolerance in halophytes. *Annual Review of Plant Physiology* 28:89-121.
- Ford C. (1984) Accumulation of low molecular weight solutes in water-stressed tropical legumes. *Phytochemistry* 23:1007-1015.
- Fougère F., Le Rudulier D., Streeter J. (1991) Effects of salt stress on amino acid, organic acid, and carbohydrate composition of roots, bacteroids, and cytosol of alfalfa (*Medicago sativa L.*). *Plant Physiology* 96:1228-1236.
- Foyer C., Descourvieres P., Kunert K. (1994) Protection against oxygen radicals: an important defense mechanism studied in transgenic plants. *Plant Cell Environ* 17:507-523.
- Fridovich I. (1986) Biological effects of the superoxide radical. *Archives of Biochemistry and Biophysics* 247:1-11.
- Gadallah M. (1999) Effects of proline and glycinebetaine on *Vicia faba* responses to salt stress. *Biologia Plantarum* 42:249-257.
- Garg G. (2008) Salinity and its effects on the functional biology of legumes. *Acta Physiologiae Plantarum* 30: 595-618.

- Garratt L., Janagoudar B., Lowe K., Anthony P., Power J., Davey M. (2002) Salinity tolerance and antioxidant status in cotton cultures. *Free Radical Biology and Medicine* 33:502-511.
- Ghoulam C., Foursy A., Fares K. (2002) Effects of salt stress on growth, inorganic ions and proline accumulation in relation to osmotic adjustment in five sugar beet cultivars. *Environmental and Experimental Botany* 47:39-50.
- Gomez-Cadenas A., Arbona V., Jacas J., Primo-Millo E., Talon M. (2003) Abscisic acid reduces leaf abscission and increases salt tolerance in citrus plants. *Journal of Plant Growth Regulation* 21:234-240.
- Gossett D., Millhollon E., Lucas M., Banks S., Marney M. (1994) The effects of NaCl on antioxidant enzyme activities in callus tissue of salt-tolerant and salt-sensitive cotton cultivars (*Gossypium hirsutum L.*). *Plant Cell Reports* 13:498-503.
- Grattan S., Grieve C. (1998) Salinity–mineral nutrient relations in horticultural crops. *Scientia Horticulture* 78:127-157.
- Greenway H., Munns R. (1980) Mechanisms of salt tolerance in nonhalophytes. *Annual Review of Plant Physiology* 31:149-190.
- Gulzar S., Khan M., Ungar I. (2003) Salt tolerance of a coastal salt marsh grass. *Communications in Soil Science and Plant Analysis* 34:2595-2605.
- Ha M., Martinez C. (2001) Contribution of proline and inorganic solutes to osmotic adjustment in cotton under salt stress. *Journal of Plant Nutrition* 24:599-612.
- Halperin S., Lynch J. (2003) Effects of salinity on cytosolic Na⁺ and K⁺ in root hairs of *Arabidopsis thaliana*: in vivo measurements using the fluorescent dyes SBFI and PBFI. *Journal of Experimental Botany* 54:2035-2043.
- Harir Y., Mittler R. (2009) The ROS Signaling Network of Cells. *Reactive Oxygen Species in Plant Signaling* pp: 165-174
- Hasegawa P., Bressan R., Zhu J., Bohnert H. (2000) Plant cellular and molecular responses to high salinity. *Annual Review of Plant Biology* 51:463-499.
- He Z., He C., Zhang Z., Zou Z., Wang H. (2007) Changes of antioxidative enzymes and cell membrane osmosis in tomato colonized by *arbuscular mycorrhizae* under NaCl stress. *Colloids and Surfaces B: Biointerfaces* 59:128-133.
- Hernandez J., Olmos E., Corpas F., Sevilla F., Del Rio L. (1995) Salt-induced oxidative stress in chloroplasts of pea plants. *Plant Sci* 105:151-67.
- Hester M., Mendelssohn I., McKee K. (1996) Intraspecific variation in salt tolerance and morphology in the coastal grass *Spartina patens* (*Poaceae*). *American Journal of Botany* 83:1521-1527.
- Hester M., Mendelssohn I., McKee K. (1998) Intraspecific variation in salt tolerance and morphology in *Panicum hemitomon* and *Spartina alterniflora* (*Poaceae*). *International Journal of Plant Sciences* 159:127-138.
- Hester M., Mendelssohn I., McKee K. (2001) Species and population variation to salinity stress in *Panicum hemitomon*, *Spartina patens*, and *Spartina alterniflora*: morphological and physiological constraints. *Environmental and Experimental Botany* 46:277-297.
- Hoffman G., Maas E., Prichard T., Meyer J. (1983) Salt tolerance of corn in the Sacramento-San Joaquin Delta of California. *Irrigation Science* 4:31-44.
- Hong Z., Lakkineni K., Zhang Z., Verma D. (2000) Removal of feedback inhibition of delta 1-pyrroline-5-carboxylate synthetase results in increased proline accumulation and protection of plants from osmotic stress. *Plant Physiology* 122:1129-1135.

- Hurkman W., Tao H., Tanaka C. (1991) Germin-like polypeptides increase in barley roots during salt stress. *Plant Physiology* 97:366-371.
- Imlay J. (2003) Pathways of oxidative damage. *Annual Reviews in Microbiology* 57:395-418.
- Ingram J., Bartels D. (1996) The molecular basis of dehydration tolerance in plants. *Annual Review of Plant Biology* 47:377-403.
- Iyengar E., Reddy M. (1996) Photosynthesis in highly salt tolerant plants. *Handbook of photosynthesis*. Marshal Dekar, Baten Rose, USA pp: 897-909.
- James R., Rivelli A., Munns R., von Caemmerer S. (2002) Factors affecting CO₂ assimilation, leaf injury and growth in salt-stressed durum wheat. *Functional Plant Biology* 29:1393-1403.
- Jiménez-Casas M. (2009) Effects of NaCl on growth and physiology of *Pinus leiophylla* seedlings, PhD thesis Department of Renewable Resources, University of Alberta, Edmonton, Alberta. pp: 218.
- Jimenez M., Gonzalez-Rodriguez A., Morales D., Cid M., Socorro A., Caballero M. (1997) Evaluation of chlorophyll fluorescence as a tool for salt stress detection in roses. *Photosynthetica* 33:291-301.
- Katerji N., Van Hoorn J., Hamdy A., Mastrorilli M., Karzel E. (1997) Osmotic adjustment of sugar beets in response to soil salinity and its influence on stomatal conductance, growth and yield. *Agricultural Water Management* 34:57-69.
- Kaya C., Kirnak H., Higgs D. (2001) Enhancement of growth and normal growth parameters by foliar application of potassium and phosphorus in tomato cultivars grown at high(NaCl) salinity. *Journal of Plant Nutrition* 24:357-367.
- Kaymakanova M., Stoeva N. (2008) Physiological reaction of bean plant (*Phaseoluse Vulg L.*) to salt stress. *Gen. Appl. Plant Physiology* 34:177-188.
- Kennedy B., De Filippis L. (1999) Physiological and oxidative response to NaCl of the salt tolerant *Grevillea ilicifolia* and the salt sensitive *Grevillea arenaria*. *Journal of plant physiology* 155:746-754.
- Kerepesi I., Galiba G. (2000) Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings. *Crop Science* 40:482-490.
- Ketchum R., Warren R., Klima L., Lopez-Gutierrez F., Nabors M. (1991) The mechanism and regulation of proline accumulation in suspension cell cultures of the halophytic grass *Distichlis spicata*. *Journal of plant physiology* 137:368-374.
- Khan M., Ungar I., Showalter A. (2000) Effects of salinity on growth, water relations and ion accumulation of the subtropical perennial halophyte, *Atriplex griffithii* var. *stocksii*. *Annals of Botany* 85:225-231.
- Khan M.A., Ungar I.A., Showalter A. (2000) Effects of sodium chloride treatments on growth and ion accumulation of the halophyte *Haloxylon recurvum*. *Communications in Soil Science and Plant Analysis* 31:2763-2774
- Khan M., Ungar I., Showalter A., Dewald H. (1998) NaCl-induced accumulation of glycinebetaine in four subtropical halophytes from Pakistan. *Physiologia Plantarum* 102:487-492.
- Khatkar D., Kuhad M. (2000) Short-term salinity induced changes in two wheat cultivars at different growth stages. *Biologia Plantarum* 43:629-632.
- Khavari-Nejad R., Chaparzadeh N. (1998) The effects of NaCl and CaCl₂ on photosynthesis and growth of alfalfa plants. *Photosynthetica* 35:461-466.

- Khavari-Nejad R., Mostofi Y. (1998) Effects of NaCl on photosynthetic pigments saccharides, and chloroplast ultra structure in leaves of tomato cultivars. *Photosynthetica* 35:151-154.
- Khedr A., Abbas M., Wahid A., Quick W., Abogadallah G. (2003) Proline induces the expression of salt-stress-responsive proteins and may improve the adaptation of *Pancreaticum maritimum L.* to salt-stress. *Journal of Experimental Botany* 54:2553-2561.
- Kingsbury R., Epstein E. (1984) Selection for salt-resistant spring wheat. *Crop Science* 24:310.
- Knight H., Trewavas A., Knight M. (1997) Calcium signalling in *Arabidopsis thaliana* responding to drought and salinity. *Plant Journal* 12:1067-1078.
- Koyro H. (2006) Effect of salinity on growth, photosynthesis, water relations and solute composition of the potential cash crop halophyte *Plantago coronopus (L.)*. *Environmental and Experimental Botany* 56:136-146.
- Kurban H., Saneoka H., Nehira K., Adilla R., Premachandra G.S. (1999) Effect of salinity on growth, photosynthesis and mineral composition in leguminous plant *Alhagi pseudoalhagi*. *Soil Sci. Plant Nutr* 45:851-862.
- Lauchli A., Schubert S. (1989) The role of calcium in the regulation of membrane and cellular growth processes under salt stress. NATO ASI series. Series G: Ecological Sciences 19:131-138.
- Lee D., Kim Y., Lee C. (2001) The inductive responses of the antioxidant enzymes by salt stress in the rice (*Oryza sativa L.*). *Journal of plant physiology* 158:737-745.
- Levitt J. (1980) Responses of plants to environmental stresses, Volume 1, chilling freezing, and high temperature stresses. Academic Press: New York.
- Liu J., Zhu J. (1997) An Arabidopsis mutant that requires increased calcium for potassium nutrition and salt tolerance. *Proceedings of the National Academy of Sciences of the United States of America* 94:14960.
- Longstreth D., Nobel P. (1979) Salinity effects on leaf anatomy: consequences for photosynthesis. *Plant Physiology* 63:700-705.
- Loreto F., Centritto M., Chartzoulakis K. (2003) Photosynthetic limitations in olive cultivars with different sensitivity to salt stress. *Plant Cell and Environment* 26:595-602.
- Lovato M., Martins P., Lemos Filho J. (1994) Germination in *Stylosanthes humilis* populations in the presence of NaCl. *Australian Journal of Botany* 42:717-724.
- Lu C., Zhang J. (1998) Thermostability of photosystem II is increased in salt-stressed sorghum. *Australian Journal of Plant Physiology* 25:317-324.
- Lu C., Vonshak A. (1999a) Characterization of PSII photochemistry in salt-adapted cells of cyanobacterium *Spirulina platensis*. *New Phytologist* 141:231-239.
- Lu C., Vonshak A. (1999b) Photoinhibition in outdoor *Spirulina platensis* cultures assessed by polyphasic chlorophyll fluorescence transients. *Journal of Applied Phycology* 11:355-359.
- Lu C., Qiu N., Wang B., Zhang J. (2003) Salinity treatment shows no effects on photosystem II photochemistry, but increases the resistance of photosystem II to heat stress in halophyte *Suaeda salsa*. *Journal of Experimental Botany* 54:851-858.
- Lu C., Qiu N., Lu Q., Wang B., Kuang T. (2002) Does salt stress lead to increased susceptibility of photosystem II to photo inhibition and changes in photosynthetic pigment composition in halophyte *Suaeda salsa* grown outdoors. *Plant Science* 163:1063-1068.
- Luhua S., Ciftci-Yilmaz S., Harper J., Cushman J., Mittler R. (2008) Enhanced tolerance to oxidative stress in transgenic Arabidopsis plants expressing proteins of unknown function. *Plant Physiology* 148:280-285.

- Lutts S., Majerus V., Kinet J. (1999) NaCl effects on proline metabolism in rice (*Oryza sativa*) seedlings. *Physiologia Plantarum* 105:450-458.
- Maas E., Poss J. (1989) Salt sensitivity of wheat at various growth stages. *Irrigation Science* 10:29-40.
- Maggio A., Miyazaki S., Veronese P., Fujita T., Ibeas J., Damsz B., Narasimhan M., Hasegawa P., Joly R., Bressan R. (2002) Does proline accumulation play an active role in stress-induced growth reduction? *The Plant Journal* 31:699-712.
- Mansour M. (1998) Protection of plasma membrane of onion epidermal cells by glycinebetaine and proline against NaCl stress. *Plant Physiology Biochemistry* 36:767-772.
- Mansour M. (2000) Nitrogen containing compounds and adaptation of plants to salinity stress. *Biologia Plantarum* 43:491-500.
- Marcum K., Pessaraki M. (2006) Salinity tolerance and salt gland excretion efficiency of Bermuda grass turf cultivars. *Crop Science* 46:2571-2575.
- Maricle B., Lee R., Hellquist C., Kiirats O., Edwards G. (2007) Effects of salinity on chlorophyll fluorescence and CO₂ fixation in C₄ estuarine grasses. *Photosynthetica* 45:433-440.
- Marler T., Zozor Y. (1996) Salinity influences photosynthetic characteristics, water relations, and foliar mineral composition of *Annona squamosa* L. American Society for Horticultural Science (USA).
- Maxwell K., Johnson G. (2000) Chlorophyll fluorescence--a practical guide. *Journal of Experimental Botany* 51:659-664.
- Meloni D., Gulotta M., Mart nez C., Oliva M. (2004) The effects of salt stress on growth, nitrate reduction and proline and glycinebetaine accumulation in *Prosopis alba*. *Brazilian Journal of Plant Physiology* 16:39-46.
- Meneguzzo S., Navari-Izzo F., Izzo R. (1999) Antioxidative responses of shoots and roots of wheat to increasing NaCl concentrations. *Journal of plant physiology* 155:274-280.
- Mer R.K., Prajith P., Pandya D.H., Pandya N.A. (2000) Effect of salts on germination of seeds and growth of young plants of *Hordeum vulgare*, *Triticum aestivum*, *Cicer arietinum* and *Brassica juncea* J. Agron. *Crop Science* 185:209-217.
- Mitsuya S., Takeoka Y., Miyake H. (2000) Effects of sodium chloride on foliar ultra structure of sweet potato (*Ipomoea batatas* Lam.) plantlets grown under light and dark conditions in vitro. *Journal of plant physiology* 157:661-667.
- Mittova V., Tal M., Volokita M., Guy M. (2002) Salt stress induces up-regulation of an efficient chloroplast antioxidant system in the salt-tolerant wild tomato species *Lycopersicon pennellii* but not in the cultivated species. *Physiologia Plantarum* 115:393-400.
- Mittova V., Tal M., Volokita M., Guy M. (2003) Up-regulation of the leaf mitochondrial and peroxisomal antioxidant systems in response to salt-induced oxidative stress in the wild salt-tolerant tomato species *Lycopersicon pennellii*. *Plant Cell and Environment* 26:845-856.
- Mittova V., Guy M., Tal M., Volokita M. (2004) Salinity up-regulates the antioxidative system in root mitochondria and peroxisomes of the wild salt-tolerant tomato species *Lycopersicon pennellii*. *Journal of Experimental Botany* 55:1105-1113.
- Munns R. (1993) Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. *Plant Cell and Environment* 16:15-15.
- Munns R. (2002) Comparative physiology of salt and water stress. *Plant Cell and Environment* 25:239-250.
- Munns R., Tester M. (2008) Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol* 59:651-681.

- Murakezy P., Nagy Z., Duhazé C., Bouchereau A., Tuba Z. (2003) Seasonal changes in the levels of compatible osmolytes in three halophytic species of inland saline vegetation in Hungary. *Journal of Plant Physiology* 160:395-401.
- Muranaka S., Shimizu K., Kato M. (2002) Ionic and osmotic effects of salinity on single-leaf photosynthesis in two wheat cultivars with different drought tolerance. *Photosynthetica* 40:201-207.
- Murphy L., Kinsey S., Durako M. (2003) Physiological effects of short-term salinity changes on *Ruppia maritima*. *Aquatic Botany* 75:293-309.
- Muthukumarasamy M., Gupta S., Panneerselvam R. (2000) Enhancement of Peroxidase, Polyphenol Oxidase and Superoxide Dismutase Activities by Triadimefon in NaCl Stressed *Raphanus Sativus* L. *Biologia Plantarum* 43:317-320.
- Nikoleudi A. (2003) salinity tolerance in strawberry (*Fragaria spp*) as influenced by genotypes, Department of Horticulture, Michigan State University, Michigan. pp. 164-172
- Nobel P. (1999) *Physicochemical & environmental plant physiology* Academic Press.
- Noble C., Rogers M. (1992) Arguments for the use of physiological criteria for improving the salt tolerance in crops. *Plant and Soil* 146:99-107.
- Omami N.E. (2005) Response of amaranth to salinity stress. 235p, Thesis (Ph. D.). University of Pretoria etd. Pretoria. South Africa.
- Oster J.D. (1994) Irrigation with poor quality water. *Agric. Water Manage* 25:271-297.
- Pardossi A., Bagnoli G., Malorgio F., Campiotti C., Tognoni F. (1999) NaCl effects on celery (*Apium graveolens* L.) grown in NFT. *Scientia Horticulturae* 81:229-242.
- Parida A., Das A. (2005) Salt tolerance and salinity effects on plants: a review. *Ecotoxicology and Environmental Safety* 60:324-349.
- Parida A., Das A., Das P. (2002) NaCl stress causes changes in photosynthetic pigments, proteins, and other metabolic components in the leaves of a true mangrove, *Bruguiera parviflora*, in hydroponic cultures. *Journal of Plant Biology* 45:28-36.
- Parida A., Das A., Mitra B. (2004) Effects of salt on growth, ion accumulation, photosynthesis and leaf anatomy of the mangrove, (*Bruguiera parviflora*). *Trees-Structure and Function* 18:167-174.
- Parvaiz A., Satyawati S. (2008) Salt stress and phyto-biochemical responses of plants-a review. *Plant Soil and Environment* 54:89-96.
- Pedranzani H., Racagni G., Alemano S., Miersch O., Ram rez I., Pe a-Cortés H., Taleisnik E., Machado-Domenech E., Abdala G. (2003) Salt tolerant tomato plants show increased levels of jasmonic acid. *Plant Growth Regulation* 41:149-158.
- Percival G., Fraser G. (2001) Measurement of the salinity and freezing tolerance of *Crataegus* genotypes using chlorophyll fluorescence. *Journal of Arboriculture* 27:233-245.
- Perez-Alfocea F., Balibrea M., Cruz A., Estan M. (1996) Agronomical and physiological characterization of salinity tolerance in a commercial tomato hybrid. *Plant and Soil* 180:251-257.
- Pessarakli M., Tucker T. (1985) Uptake of nitrogen-15 by cotton under salt stress. *Soil Science Society of America Journal* 49:149-152.
- Pessarakli M., Tucker T. (1988a) Nitrogen-15 uptake by eggplant under sodium chloride stress. *Soil Science Society of America Journal* 52:1673-1676.
- Pessarakli M., Tucker T. (1988b) Dry matter yield and nitrogen-15 uptake by tomatoes under sodium chloride stress. *Soil Science Society of America Journal* 52:698-700.

- Pessaraki M., Huber J. (1991) Biomass production and protein synthesis by alfalfa under salt stress. *Journal of Plant Nutrition* 14:283-293.
- Pessaraki M., Tucker T., Nakabayashi K. (1991) Growth response of barley and wheat to salt stress. *Journal of Plant Nutrition* 14:331-340.
- Petrusa L., Winicov I. (1997) Proline status in salt-tolerant and salt-sensitive alfalfa cell lines and plants in response to NaCl. *Plant Physiology and Biochemistry* 35:303-310.
- Pilon-Smits E., Ebskamp M., Paul M., Jeuken M., Weisbeek P., Smeekens S. (1995) Improved performance of transgenic fructan-accumulating tobacco under drought stress. *Plant Physiology* 107, Issue 1:125-130.
- Popova L., Stoinova Z., Maslenkova L. (1995) Involvement of abscisic acid in photosynthetic process in *Hordeum vulgare* L. during salinity stress. *Journal of Plant Growth Regulation* 14:211-218.
- Pospil P., Dau H. (2000) Chlorophyll fluorescence transients of Photosystem II membrane particles as a tool for studying photosynthetic oxygen evolution. *Photosynthesis Research* 65:41-52.
- Quintero F., Garcíadeblas B., Rodríguez-Navarro A. (1996) The SAL1 gene of Arabidopsis, encoding an enzyme with 3'(2'), 5'-bisphosphate nucleotidase and inositol polyphosphate 1-phosphatase activities, increases salt tolerance in yeast. *The Plant Cell* 8:529-537.
- Reddy M., Sanish S., Iyengar E. (1992) Photosynthetic studies and compartmentation of ions in different tissues of *Salicornia brachiata* under saline conditions. *Photosynthetica (Praha)* 26:173-179.
- Rhodes D., Hanson A. (1993) Quaternary ammonium and tertiary sulfonium compounds in higher plants. *Annual Review of Plant Biology* 44:357-384.
- Rogers M., Noble C., Halloran G., Nicolas M. (1997) Selecting for salt tolerance in white clover (*Trifolium repens*): chloride ion exclusion and its heritability. *New Phytologist* 135:645-654.
- Romero-Aranda M., Jurado O., Cuartero J. (2006) Silicon alleviates the deleterious salt effect on tomato plant growth by improving plant water status. *Journal of plant physiology* 163:847-855.
- Romero-Aranda R., Soria T., Cuartero J. (2001) Tomato plant-water uptake and plant-water relationships under saline growth conditions. *Plant Science* 160:265-272.
- Saadallah K., Drevon J., Hajji M., Abdely C. (2001) Genotypic variability for tolerance to salinity of N₂-fixing common bean (*Phaseolus vulgaris*). *Agronomie* 21:675-682.
- Sabir P., Ashraf M. (2007) Screening of local accessions of *Panicum maliaceum* L., for salt tolerance at the seedling stage using biomass production and ion accumulation as selection criteria. *Pak. J. Bot* 39:1655-1661.
- Sacher R., Staples R. (1985) Inositol and sugars in adaptation of tomato to salt. *Plant Physiology* 77:206-210.
- Saneoka H., Shiota K., Kurban H., Chaudhary M., Premachandra G., Fujita K. (1999) Effect of salinity on growth and solute accumulation in two wheat lines differing in salt tolerance. *Soil Science and Plant Nutrition* 45:873-880.
- Savvas D., Lenz F. (2000) Effects of NaCl or nutrient-induced salinity on growth, yield, and composition of eggplants grown in rock wool. *Scientia Horticulturae* 84:37-47.
- Shannon M. (1985) Principles and strategies in breeding for higher salt tolerance. *Plant and Soil* 89:227-241.
- Shannon M. (1997) Adaptation of plants to salinity. *Advances in agronomy* 60: 75-120

- Shannon M., Grieve C. (1998) Tolerance of vegetable crops to salinity. *Scientia Horticulturae* 78:5-38.
- Shannon M.C., Grieve C.M., Francois L.E. (1994) Whole-plant response to salinity. *Plant-environmental interactions*. New York, Marcel-Decker: 199-244.
- Sifola M.I., Postiglione L. (2002) The effect of increasing NaCl in irrigation water on growth, gas exchange and yield of tobacco Burley type *Field Crops Research* 74:81-91.
- Silvera J.A.G., Melo A.R.B., Viegas R.A., Oliveira J.T. (2001) Salinity-induced effects on nitrogen assimilation related to growth in cowpea plants. *Environ. Exp. Bot.* 46:171-179.
- Singer M., Lindquist S. (1998) Multiple effects of trehalose on protein folding in vitro and in vivo. *Molecular Cell* 1:639-648.
- Singh S., Sharma H., Goswami A., Datta S., Singh S. (2000) In vitro growth and leaf composition of grapevine cultivars as affected by sodium chloride. *Biologia Plantarum* 43:283-286.
- Smethurst C., Gill W., Shabala S. (2009) Using excised leaves to screen lucerne for salt tolerance: Physiological and cytological evidence. *Plant Signaling & Behavior* 4:39-41.
- Smirnov N. (1998) Plant resistance to environmental stress. *Current Opinion in Biotechnology* 9:214-219.
- Sohan D., Jasoni R., Zajicek J. (1999) Plant-water relations of NaCl and calcium-treated sunflower plants. *Environmental and Experimental Botany* 42:105-111.
- Song J., Feng G., Tian C., Zhang F. (2005) Strategies for adaptation of *Suaeda physophora*, *Haloxylon ammodendron* and *Haloxylon persicum* to a saline environment during seed-germination stage. *Annals of Botany* 96:399-405.
- Sonneveld C., De Kreij C. (1999) Response of cucumber (*Cucumis sativus L.*) to an unequal distribution of salts in the root environment. *Plant and Soil* 209:47-56.
- Spychalla J., Desborough S. (1990) Superoxide dismutase, catalase, and alpha-tocopherol content of stored potato tubers. *Plant Physiology* 94:1214-1218.
- Strasser R., Srivastava A., Tsimilli-Michael M. (2000) The fluorescence transient as a tool to characterize and screen photosynthetic samples. *Probing photosynthesis: Mechanisms, Regulation and Adaptation*: 445-483.
- Tester M., Davenport R. (2003) Na⁺ tolerance and Na⁺ transport in higher plants. *Annals of Botany* 91:503-527
- Thomas J., McElwain E., Bohnert H. (1992) Convergent induction of osmotic stress-responses: abscisic acid, cytokinin, and the effects of NaCl. *Plant Physiology* 100:416-423.
- Torabi M., Halim R. A. (2010) Variation of root and shoot growth and free proline accumulation in Iranian alfalfa ecotypes under salt stress. *Journal of Food, Agriculture & Environment* 8 (3&4): 323-327.
- Torabi M., Halim R. A., Sinniah U. R., Choukan R. (2011) Influence of salinity on the germination of Iranian alfalfa ecotypes. *African Journal of Agricultural Research* 6(19): 4624-4630.
- Vaidyanathan R., Kuruvilla S., Thomas G. (1999) Characterization and expression pattern of an abscisic acid and osmotic stress responsive gene from rice. *Plant science (Limerick)* 140:21-30.
- Vaughan L., MacAdam J., Smith S., Dudley L. (2002) Root growth and yield of differing alfalfa rooting populations under increasing salinity and zero leaching. *Crop Science* 42:2064-2071.

- Vicente O., Boscaiu M., Naranjo M.A., Estrelles E., Belles J.M., Soriano P. (2004) Responses to salt stress in the halophyte *Plantago crassifolia* (*Plantaginaceae*) J. Arid Environ 58: 463-481.
- Wahome P., Jesch H., Grittner I. (2001) Mechanisms of salt stress tolerance in two rose rootstocks: *Rosa chinensis* 'Major' and *R. rubiginosa*. Scientia Horticulturae 87:207-216.
- Waisel Y., Breckle S. (1987) Differences in responses of various radish roots to salinity. Plant and Soil 104:191-194.
- Wang Y., Nil N. (2000) Changes in chlorophyll, ribulosebiphosphate carboxylase oxygenase, glycine betaine content, photosynthesis and transpiration in *Amaranthus tricolor* leaves during salt stress J. Hort. Science Biotechnol 75:623-627.
- White P., Broadley M. (2001) Chloride in soils and its uptake and movement within the plant: a review. Annals of Botany 88:967-988.
- Wise R., Naylor A. (1987) Chilling-enhanced photooxidation: evidence for the role of singlet oxygen and superoxide in the breakdown of pigments and endogenous antioxidants. Plant Physiology 83:278-282.
- Yamada T., Takatsu Y., Manabe T., Kasumi M., Marubashi W. (2003) Suppressive effect of trehalose on apoptotic cell death leading to petal senescence in ethylene-insensitive flowers of gladiolus. Plant science (Limerick) 164:213-221.
- Yamaguchi T., Blumwald E. (2005) Developing salt-tolerant crop plants: challenges and opportunities. Trends in plant science 10:615-620.
- Zhao G., Ma B., Ren C. (2007) Growth, gas exchange, chlorophyll fluorescence, and ion content of naked oat in response to salinity. Crop Science 47:123-131
- Zhifang G., Loescher W. (2003) Expression of a celery mannose 6-phosphate reductase in *Arabidopsis thaliana* enhances salt tolerance and induces biosynthesis of both mannitol and a glucosyl-mannitol dimer. Plant Cell and Environment 26:275-283.
- Zhu J. (2001) Plant salt tolerance. Trends in plant science 6:66-71.
- Zhu J. (2003) Regulation of ion homeostasis under salt stress. Current Opinion in Plant Biology 6:441-445.
- Zhu J., Shi J., Singh U., Wyatt S., Bressan R., Hasegawa P., Carpita N. (1993) Enrichment of vitronectin-and fibronectin-like proteins in NaCl-adapted plant cells and evidence for their involvement in plasma membrane-cell wall adhesion. The Plant Journal 3:637-646.