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## CHAPTER 8

# Physiological mechanisms of salt stress tolerance in plants: An overview

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### 8.1 Introduction

Generally, environmental stresses reduce the quality and quantity of world agricultural production. In addition, abiotic stresses reduce crop yield by 71% (Ashraf *et al.*, 2008). It is estimated that potential yield losses are 17% by drought, 20% by salinity, 40% by high temperature, 15% by low temperature, and 8% by other factors (Ashraf & Harris, 2005). In fact, about 380 million ha (one-third of the area under cultivation) is affected by salt stress coupled with waterlogging and alkalinity (Ghassemi *et al.*, 1995).

Irrigation systems are particularly prone to salinization; about half the current irrigation systems in the world are influenced by salinization, alkalization or waterlogging (Munns, 2002). About 60 million ha are exposed to overirrigation, where a raised water table transports solute salts to the top layers of the soil. It has been estimated that, annually, the advance of agricultural salinization can degrade as much land as is newly irrigated each year. Unless it is controlled, this process of salinization may lead to a net loss of productive land area, which is already becoming exhausted (Emam *et al.*, 2013; Pirasteh-Anosheh *et al.*, 2011). Soil salinity is therefore a major environmental constraint on crop productivity worldwide.

The problem of salt in the soil could be increased by the use of poor-quality water for irrigation as well as poor drainage. In clay soils, improper management of salts may lead to soil sodicity whereby sodium binds to negatively charged clay, causing the dispersion of clay particles and making the soil unfavourable for crop production.

Salinity is a major factor limiting crop production in the world. It is reported that about 20% of agricultural land consists of salt soil (Munns & Tester, 2008). Salinity is a soil condition characterized by a high concentration of soluble salts. Classification of a soil as saline occurs when the  $EC_e$  is  $4 \text{ dS m}^{-1}$  or greater, equivalent to approximately 40 mM NaCl, and generates an osmotic pressure of approximately  $-0.2 \text{ MPa}$  (USDA, 2008). With this salinity, the value and yield of most crops is significantly reduced (Table 8.1). Glycophytes, i.e. most grain crops and vegetables, are highly susceptible to soil salinity even when the soil  $EC_e$  is  $4 \text{ dS m}^{-1}$ . Different threshold tolerance values as well as different reduction slopes in yield beyond threshold tolerance indicate variation in the mechanisms of salt tolerance among plants.

Stress refers to a condition that diverges from the normal range that a given plant encounters to such an extent as to prevent the plant from expressing fully its genetic potential for growth, development and reproduction (Hale & Orcutt, 1989). Salinity, an environmental stress, is the concentration of dissolved mineral salts present in waters and soil on a unit volume or weight basis (Lauchli & Epstein, 1990). Nieman & Shannon (1976) define salinity as the presence of excessive concentrations of soluble salts in the soil solution.

Soil is considered saline when the solute concentration in the water phase causes a reduction in crop production. Thus, soil salinity is a plant-dependent concept. In the agricultural context, a soil is defined as saline when the electrical conductivity of the saturation extract exceeds  $4 \text{ dS m}^{-1}$  at  $25^\circ\text{C}$  and the percentage of the cation exchange capacity of the soil occupied by sodium

**Table 8.1** Threshold tolerance of main agricultural plants to soil salinity, ordered based on sensitivity (Maas, 1990; Maas & Hoffman, 1977).

Plant	Threshold (dS m <sup>-1</sup> )	Yield reduction (slope % per dS m <sup>-1</sup> )
Carrot ( <i>Daucus carota</i> )	1.0	14.0
Bean ( <i>Phaseolus vulgaris</i> )	1.0	19.0
Eggplant ( <i>Solanum melongena</i> )	1.1	6.9
Onion ( <i>Allium cepa</i> )	1.2	16.0
Cowpea ( <i>Vigna sinensis</i> )	1.3	14.0
Clover berseem ( <i>T. alexandrinum</i> )	1.5	5.7
Sweet potato ( <i>Ipomoea batatas</i> )	1.5	11.0
Clover ( <i>Trifolium</i> spp.)	1.5	12.0
Pepper ( <i>Capsicum annuum</i> )	1.5	14.0
Broad bean ( <i>Vicia faba</i> )	1.6	9.6
Corn ( <i>Zea mays</i> ), grain	1.7	12.0
Corn ( <i>Zea mays</i> ), sweet	1.7	12.0
Sugarcane ( <i>Saccharum officinarum</i> )	1.7	5.9
Potato ( <i>Solanum tuberosum</i> )	1.7	12.0
Forage corn ( <i>Zea mays</i> )	1.8	7.4
Cabbage ( <i>Brassica oleracea</i> )	1.8	9.7
Alfalfa ( <i>Medicago sativa</i> )	2.0	7.3
Tomato ( <i>Lycopersicon esculentum</i> )	2.5	9.9
Sudangrass ( <i>Sorghum sudanense</i> )	2.8	4.3
Vetch ( <i>Vicia sativa</i> )	3.0	11.0
Rice, paddy ( <i>Oryza sativa</i> )	3.0	12.0
Peanut ( <i>Arachis hypogaea</i> )	3.2	29.0
Soybean ( <i>Glycine max</i> )	5.0	20.0
Wheat ( <i>Triticum aestivum</i> )	6.0	7.1
Sorghum ( <i>Sorghum bicolor</i> )	6.8	16.0
Sugar beet ( <i>Beta vulgaris</i> )	7.0	5.9
Cotton ( <i>Gossypium hirsutum</i> )	7.7	5.2
Barley ( <i>Hordeum vulgare</i> ) (forage)	6.0	7.1
Barley ( <i>Hordeum vulgare</i> ) (grain)	8.0	5.0

is less than 15 (Lauchli & Epstein, 1990). Because salinity stress is quantitatively expressed as a concentration, no sharp dividing line exists between salinity and lack of stress. Neither is there an absolute distinction between salt tolerance and salt sensitivity among plants as well as genotypes within a species (Hale & Orcutt, 1989).

## 8.2 Adverse impact of salinity on plants

Plants that grow on saline soils are confronted with soil solutions exhibiting diverse ionic compositions (ionic effects): varying proportions of Na<sup>+</sup>, Ca<sup>++</sup>, Mg<sup>2+</sup>,

K<sup>+</sup>, SO<sub>4</sub><sup>2-</sup>, CO<sub>3</sub><sup>2-</sup>, HCO<sub>3</sub><sup>-</sup> and Cl<sup>-</sup> and other ions and a wide range in the concentrations of dissolved salts (osmotic effect): concentrations fluctuate because of changes in water source, drainage, evapotranspiration, solute available, hydrostatic pressures, etc. (Lauchli & Epstein, 1990). When dissolved salt concentrations in soil solutions increase, water energy gradients decrease, making it more difficult for water and nutrients to move through root membranes and into the plant; therefore, the rate of water and solute uptake reduces. Internal excesses of particular ions may cause membrane damage, interfere with solute balances or cause shifts in nutrient concentrations. Some specific symptoms of plant damage may be recognized, especially in the leaves (i.e. colour change, tip burn, marginal necrosis, succulence, etc.) (Lauchli & Epstein, 1990).

### 8.2.1 How salinity affect plants

Soil salinity affects plants in two ways: a high percentage of salts in the soil, which makes it harder for roots to extract water (osmotic stress), and high concentrations of toxic salts within the plant (ion toxicity). Salts on the outside of roots have an adverse effect on cell growth and metabolism; however, toxic salts take time to accumulate inside plants before they influence plant functions (Munns & Tester, 2008).

Plants grown under saline conditions may encounter four types of stress.

- One of the most striking effects of high salt content is reduction in plant water uptake. Water is absorbed by the roots only along an osmotic gradient between soil and plant. Increasing salt content in soil solution lowers the osmotic potential (Munns & Tester, 2008). Thus, high salt levels in soils lead to water-deficit stress for plants as well as the other associated detrimental effects.
- Salts may cause severe ion toxicity, because Na<sup>+</sup> is not readily sequestered in vacuoles (Nawaz, 2007).
- The interactions of salts with mineral nutrients may result in nutrient imbalances and deficiencies (Nawaz, 2007).
- Salinity increases the production of activated oxygen radicals (AOR) such as H<sub>2</sub>O<sub>2</sub> (hydrogen peroxide), O<sub>2</sub><sup>-</sup> (superoxide), <sup>1</sup>O<sub>2</sub> (singlet oxygen) and ·OH (hydroxyl radical), in plant tissues, which may lead to cell membrane damage and hence cell death (Hernandez *et al.*, 2001).

Briefly, Ashraf & Harris (2004) categorized the deleterious effects of salt stress on crop growth into (1) water stress conditions, (2) ion imbalance, (3) specific ion effect (salt stress), or (4) a combination of these factors.

### 8.2.2 Sensitivity of growth stages

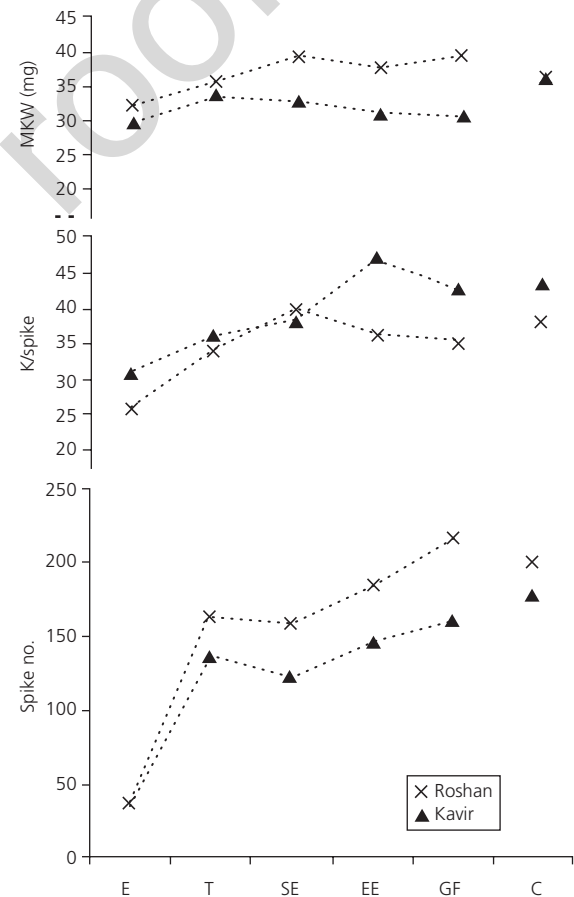
Tolerance of the plant to salt stress continually changes throughout the growing season. Most crops tolerate salinity at germination stage but the seedling emergence stage and early juvenile development are more susceptible to soil salinity. Most crops become increasingly tolerant during later stages of growth. In fact, salinity delays germination and seedling emergence. Delays in seedling emergence could be harmful if other stresses such as drought, high temperature fluctuations and soil crusting exist in the seed bed. Due to high evaporation at the soil surface, concentrating the salt in the seed bed, the percentage of seedling emergence would be decreased. In these conditions, the tiny roots of seedlings are exposed to a high degree of salinity which leads to loss of plants during this crucial phase, thus plant population density is reduced to suboptimal levels and yields are significantly reduced.

Maas *et al.* (1983) indicated that maize cultivars were relatively tolerant of salt stress at germination while emergence was quite sensitive to soil salinity. The salt tolerance threshold for ear and grain yields was much higher than for seedling growth. They concluded that maize is not salt tolerant during the vegetative growth stage. However, sorghum cultivars were most sensitive to salinity during the vegetative stage and least sensitive during maturation. Salinity during the reproductive stage also decreased biological yield of Double TX but the effect was smaller than that during the first stage. It is argued that since most of the vegetative growth occurs during the first stage, salinity has a lesser effect on biological yield when imposed during the second stage and no effect when imposed during the third stage (Maas *et al.*, 1986).

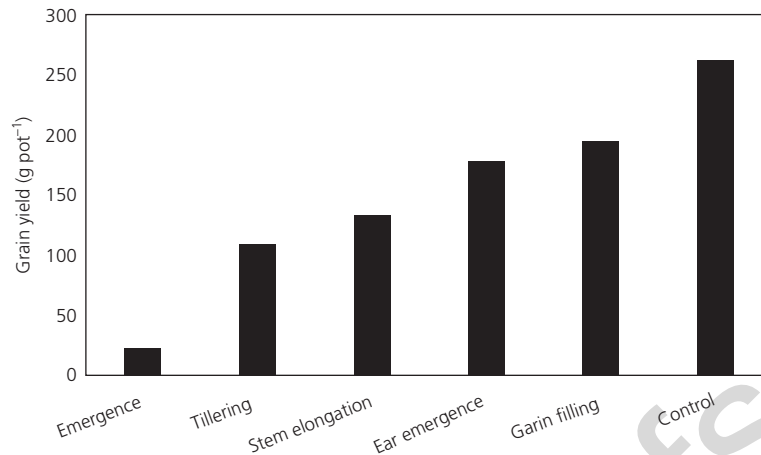
Maas & Poss (1989a) examined pod and seed yields from cowpea plants stressed during different growth stages and reported that cowpea was not tolerant to salinity during the vegetative stage and became tolerant when salinity was imposed after the vegetative stage. This was true for both vegetative shoot growth and seed yield. They also observed that vegetative growth was significantly reduced by salt stress during all three stages; however, the effect was much less when stress was imposed during the last two stages than during the first stage. A similar experiment

was carried out by these researchers (Maas & Poss, 1989b) in which it was shown that the sensitivity of wheat decreased at later plant growth stages. So, they emphasize the importance of keeping salinity lower during germination and emergence of seedlings than the other stages. These researchers finally recommended that irrigation of wheat and durum crops should use relatively saline water at the later stages of growth.

Root zone salinity also affects plant ontogeny. Grain yield is determined by components such as grain weight, kernel number, etc. Each yield component is determined significantly at a specific stage of growth. Salinity effects appear most pronounced on those components that are developing or growing at the time of imposing stress (Figure 8.1). When wheat was stressed prior to booting,



**Figure 8.1** Effect of salinity imposed at various growth stages on different yield components. (MKW, mean kernel weight; K/spike, kernel number per spike; Spike no., spike number per area of wheat). From Ranjbar (2010).



**Figure 8.2** Effect of salt stress imposed at various growth stages on grain yield of wheat. From Ranjbar (2010).

grain yield was markedly decreased in comparison with imposing the stress at later phases. Number of spikes was the yield component most affected by salt stress (Maas & Grieve, 1990). Most cereals are tolerant during seed germination but the initial growth of the young seedling is susceptible to salt stress (Maas, 1990) as is shown in Figure 8.2. Wheat seed can usually germinate in saline conditions, but at a delayed rate (Francois *et al.*, 1986; Maas, 1990; Ranjbar *et al.*, 2008).

Acceleration of maturation is a common response of cereals growing under saline conditions. Commonly, salt-stressed wheat was ready for harvest 1–2 weeks earlier than non-stressed plants. Maas & Grieve (1990) and Grieve *et al.* (1994) reported that salinity (140 mol m<sup>-3</sup> NaCl) promoted growth of the wheat shoot apex on the main stem by as much as 18 days and decreased the duration of the reproductive structures. The same results were reported by Romero & Maranon (1994) in sweet clover.

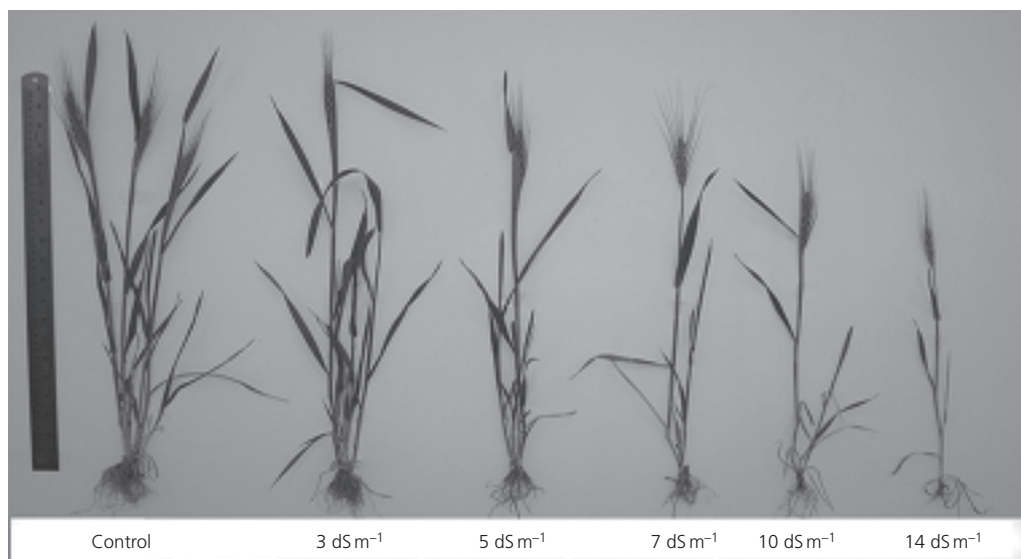
Salinity also prevented normal growth of leaf and tillering development (Munns & Tester, 2008). Grieve *et al.* (1993) found that salinity reduced the rate of leaf primordium initiation without affecting the duration of this growth phase, leading to fewer leaves (Figure 8.3). The lowest final leaf number was observed under high salinity levels. Compared with that of the control plants, the phyllochron intervals for a spring wheat and a durum cultivar salt stressed at  $-0.65$  MPa increased 12% and 9%, respectively (Maas & Grieve, 1990). Grieve *et al.* (1994) also reported that salt stress at both medium and high levels significantly reduced phyllochron

intervals. As already mentioned, the decrease in fertile tiller per plant was the main factor that reduced yield of salt-stressed wheat and durum (*Triticum turgidum* L.) (Maas & Grieve, 1990).

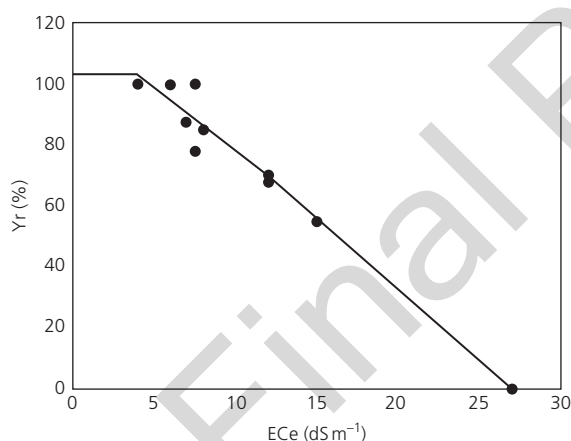
The magnitude of the reduction rate follows a declining function related to increasing salt stress (Maas *et al.*, 1994). The detrimental impact of tiller reduction on yield was also shown in the field (Francois *et al.*, 1994). Tiller duration is delayed up to 4 days by salinity (Maas & Grieve, 1990). Salinity reduced the time from planting to harvesting of wheat by decreasing the duration of specific growth stages, i.e. spike initiation, booting phase, ear emergence and flowering (Grieve *et al.*, 1994). Salinity affects the number of grains and the grain weight proportionally less than the tiller number (Grieve *et al.*, 1993). However, the effect of salt stress on grain weight was related to the duration of salinity treatments as well as the strength of the salt concentration (Francois *et al.*, 1994). Salt stress decreased seed yield by reducing grain number more than grain weight, indicating that salinity during tillering phase affected spikelet initiation (Maas & Poss, 1989; Munns & Tester, 2008). Grieve *et al.* (1993) indicated that salt stress had no significant effect on the rate of spikelet initiation although the duration of this stage was shortened.

### 8.2.3 Threshold tolerance

Farmers need to know how their crops will respond to saline conditions. Threshold salinity tolerance is a concept developed by Maas & Hoffman (1977) to address this concept. Based on the threshold concept, there is a



**Figure 8.3** Effect of different root zone salinity on leaf number, tillering and plant height as well as root growth of wheat plants.



**Figure 8.4** The piece-wise linear response function fitted to actual yield data obtained from wheat cv. Kavir. From Ranjbar & Banakar (2011).

biphasic response to salinity, whereby across lower salinity levels there is little reduction in crop growth and yield but above some threshold, crop yield is inversely related to salt concentration (Figure 8.4).

For salinity levels more than the threshold point for a given crop, relative yield ( $Y_r$ ) could be estimated with a linear response model (Maas & Hoffman):

$$Y_r = 100 - b(EC_e - a)$$

where  $a$  is the threshold point in  $dS\ m^{-1}$ ,  $b$  is the yield reduction slope, expressed in % per  $dS\ m^{-1}$ , and  $EC_e$  is the mean electrical conductivity of saturated soil extracts taken from the crop root zone. Based on the above function, various threshold values have been calculated for crops. There are some differences among crop cultivars related to salt tolerance (Table 8.2). Maas (1990) also showed that different climate and soil properties could result in different threshold values of a given crop cultivar.

Van Genuchten & Hoffman (1984) indicated that Maas and Hoffman's linear response model could be replaced by a sigmoid-shaped function. It seems that non-linear models more accurately describe the growth response of crops to salt stress. The van Genuchten (1983) model describes the inherent response in crop yield ( $Y_r$ ) relative to a maximum yield ( $Y_m$ ) where salt has no influence on yield:

$$Y_r = \frac{1}{1 + \left(\frac{C}{C_{50}}\right)^p}$$

$$Y_r = \frac{Y}{Y_m}$$

where  $Y$  is the absolute yield, equal to that produced by the test plant when subjected to a rooting solution whose salt concentration, or electrical conductivity,  $c$ ,



**Table 8.2** The differences among wheat cultivars in regard to threshold salinity tolerance.

Cultivar	Threshold (dS m <sup>-1</sup> )	Yield reduction per unit increase in salinity beyond threshold (%)	Salt tolerance rating	References
American (Old)	6.0	7.1	MT	Maas & Hoffman, 1977
American (New)	8.6	3.0	T	Francois <i>et al.</i> , 1986
Canadian	2.5	12.3–16.0	MS	Steppuhn & Wall, 1997
Iranian (Kavir)	5.0	4.5	MT	Ranjbar & Banakar, 2011
Iranian (Roshan)	4.6	4.1	MT	Ranjbar & Banakar, 2011

MS, moderate sensitivity; MT, moderate tolerance; T, tolerance.

remains constant over the growing period. The above equation describes a non-linear response where  $p$  is an empirical constant and  $C_{50}$  is the salt level at which the yield is reduced by 50%.

### 8.2.4 Responses of halophytic and glycophytic plants to salinity

Plants are generally grouped as halophytes and glycophytes by ecologists. Most crop plants, except for the coconut and date palm, are glycophytes or non-halophytes. Halophytes grow in saline soils, in high concentrations of salts, and are either facultative or obligate halophytes. Sometimes a finer classification is used by calling those that tolerate only moderate salinity oligohalophytes. Glycophytes cannot grow in the presence of high concentrations of salts; however, a few genotypes possess some mechanisms by which the protoplasm is not exposed to high salt concentrations (Hale & Orcutt, 1989).

In another comparison, leaves of crops cannot maintain high levels of salinity without injury; however, halophytes preferentially accumulate salt ions in their leaves to adjust the osmotic potential of the salts outside the plant (Volkmar *et al.*, 1998). Therefore, the adaptive

strategies of halophytes and glycophytes are different. It is interesting to know that some halophytes could not thrive in saline conditions without using the concentrated salt ions to balance the osmotic materials. Lacking this adaptive approach, glycophytes are unable to thrive in saline conditions in which halophytes survive. Whether glycophyte or halophyte, the biosynthetic processes such as photosynthesis and respiration are equally sensitive to salts (Volkmar *et al.*, 1998).

## 8.3 Plant performance under saline conditions

### 8.3.1 Germination, growth and production

Chartzoulakis and Klapaki (2000) reported that salinities up to 50 mM delayed seed germination of bell pepper hybrids (*Capsicum annuum* L.) but did not reduce the final germination percentage. It was reduced significantly at 100 and 150 mM NaCl in both hybrids. In this research, seedling growth was decreased markedly with salinity level more than 10 mM NaCl. Ranjbar *et al.* (2008) in a similar experiment found that the effect of salinity is more pronounced on delay in seed emergence rather than final germinated seeds of wheat.

Stunting of plant growth is the most common effect of salinity. The plants usually appear normal but they may have darker, thicker and more succulent leaves than the normal plants. Visual symptoms, such as leaf burn, necrosis and defoliation, occur in some species, particularly woody crops; however, these symptoms are rare in herbaceous crops unless plants are severely stressed. Consequently, it is difficult to diagnose a moderately salt-affected crop in the field without having a non-stressed crop nearby for comparison.

Chartzoulakis & Klapaki (2000) founded that height of the plant, leaf area index and dry matter were significantly decreased at salinities higher than 25 mM NaCl in both hybrids of bell pepper; however, by increasing soil salinity up to 10.2 dS m<sup>-1</sup>, the oil percentage in sunflower seed was relatively unaffected (Francois, 1996).

Since biological and grain yields of the plants are significantly suppressed, salt stress has adverse effects on the production of most crops worldwide (Shahbaz *et al.*, 2011). Determining the salt concentration in the soil is the common way to identify salinity problems. Crop salt threshold tolerance could be quantified by plotting relative growth as a continuous function of soil salinity

levels. Generally, yield reduction in higher salinity follows a sigmoidal relationship. In lower salt conditions, yield is independent from soil salinity and decreases slowly. At intermediate concentrations, yield decreases at a greater but relatively constant rate. Finally at high concentrations, yields asymptotically begin to decrease, approaching zero. Since some plants may die before their yields have reached zero, the lower part of the sigmoid curve might be eliminated. Because yields at higher salinity levels are too low and there is no commercial value, accuracy at the curve tail is not critical.

Francois (1996) indicated that relative yield of sunflower crop was not affected by soil salinity up to 4.8 dS m<sup>-1</sup>. Each unit increase in salinity above this point reduced yield by 5.0%. Based on the Maas & Hoffman (1977) data, sunflower is classified as moderately salt tolerant. Total fruit yield of pepper was significantly reduced by 95% at 150 mM NaCl (Chartzoulakis & Klapaki, 2000).

### 8.3.2 Biochemical traits

Oxidative damage due to salt stress is well known. This is caused by reactive oxygen species (ROS) that are harmful to many cellular components, including membrane lipids. Production of ROS is increased under saline conditions and ROS-mediated membrane damage has been shown to be a main cause of the cellular toxicity in salt conditions (Kim *et al.*, 2005). Plants that show activity of antioxidants tolerate the oxidative damage of the ROS.

It seems that under saline conditions, ROS enhance the activity and expression levels of the genes encoding detoxifying enzymes. Transgenic plants with the ability of expressing ROS scavenging enzymes, i.e. ascorbate peroxidase, superoxide dismutase and glutathione S-transferase/ glutathione peroxidase, showed increasing oxidative stress tolerance. Commonly, activation of antioxidant enzymes is increased in the root and shoot due to salt stress; however, the increase was more significant and consistent in the root (Kim *et al.*, 2005) while antioxidant enzymes such as CAT activity were drastically increased. Ashraf & Harris (2004) found that in saline conditions, there are remarkable differences in the tolerance mechanisms of antioxidant enzymes against ROS, so use of antioxidant as a definite criterion for salt stress tolerance is ambiguous. They indicated that further studies are needed to prove the validity of this mechanism.

Generally, plants use ions rather than biosynthesis of organic osmolytes (proline, betaine, polyols, sugar alcohols, soluble sugars) for osmotic adjustment under salinity. Glycine betaine and trehalose act as osmoprotectants by fixing quaternary structures of proteins and highly ordered states of membranes. Mannitol acts as a free radical scavenger; however, proline is a storage sink for carbon and nitrogen and scavenged free radicals (Chinnusamy *et al.*, 2005).

### 8.3.3 Photosynthesis and pigments

Photosynthesis, as the most fundamental and intricate physiological process, is severely influenced in all its phases by salt stress. The mechanisms of photosynthesis involve various components such as photosynthetic pigments and photosystems, the electron transport system and CO<sub>2</sub> reduction pathways; therefore, any damage of salt stress at any level reduces the photosynthetic capacity of plants (Ashraf & Harris, 2013). In numerous studies it has been demonstrated that salt-induced inhibition in photosynthesis is accompanied by stomata closure under short-term salt exposure and non-stomatal limitations under long-term salt exposure (Shahbaz *et al.*, 2011).

Shahbaz *et al.* (2011) reported that salt stress markedly reduced different gas exchange characteristics such as photosynthetic rate, water use efficiency (photosynthetic rate to transpiration rate ratio), transpiration rate, internal CO<sub>2</sub> concentration and stomatal conductance in all examined sunflower cultivars. The effect of 150 mM NaCl stress was non-significant on chlorophyll *a* and *b* contents and chlorophyll *a/b* ratio; however, salt stress markedly enhanced C<sub>i</sub>/C<sub>a</sub> ratio. These authors concluded that salt tolerance in tolerant cultivars was associated with improved gas exchange characteristics. Usually, salt stress increased the chlorophyll *a/b* ratio because, during the process of chlorophyll degradation, chlorophyll *b* may be converted into chlorophyll *a*, consequently resulting in enhanced chlorophyll *a* content (Eckardt, 2009; Fang *et al.*, 1998).

In barley plants, photosynthesis rate (P<sub>n</sub>) was increased under no and light salinity throughout the experiment while it was unchanged under moderate salt stress and decreased under higher salinity levels (9 and 12 dS m<sup>-1</sup>). Lu *et al.* (2002) showed that chlorophyll content index (CCI) and carotenoid were not unchanged in plants under stress; however, in such cases CCI was increased under stress conditions (Bredemeier, 2005; Majidian



**Table 8.3** Effect of salinity treatments on chlorophyll content index (CCI) in barley plants (Pirasteh-Anosheh *et al.*, 2014).

Salinity (dS m <sup>-1</sup> )	Days after sowing		
	14	42	70
0.62	9.3 <sup>a</sup>	10.2 <sup>de</sup>	11.1 <sup>e</sup>
3.0	9.3 <sup>a</sup>	10.8 <sup>d</sup>	11.9 <sup>d</sup>
6.0	9.2 <sup>a</sup>	11.6 <sup>c</sup>	13.0 <sup>c</sup>
9.0	9.4 <sup>a</sup>	14.0 <sup>ab</sup>	16.2 <sup>b</sup>
12.0	9.1 <sup>a</sup>	14.5 <sup>a</sup>	19.4 <sup>a</sup>

The means with similar letters in each column had non-significant differences based on LSD (5% probability level).

*et al.*, 2008, Pirasteh-Anosheh & Emam, 2012a). Since salinity affected biological yield more than plant N uptake, in such cases the percentage of nitrogen in leaves increased and leaves become darker than in the non-saline conditions; therefore, CCI might be higher than in normal conditions. Pirasteh-Anosheh *et al.* (2014b) observed that there was no significant difference among the salinity treatments in terms of CCI until 14 days after sowing (DAS). From 14 to 42 DAS, CCI was increased in all salinity treatments. Nevertheless, this increase was greatest at the highest salinity regime. The highest (14.5) and lowest (10.2) CCIs were found in 12 and 0.67 dS m<sup>-1</sup>, respectively (Table 8.3).

On the other hand, the effect of salinity on CCI changes in plants might be different. Jaleel *et al.* (2008) observed variations in responses of chlorophyll to different salinity levels. They observed that at lower salt stress levels, chlorophyll *a* and *b* and total chlorophyll content would be decreased slightly and under higher salt stress media a significant reduction in the content of these pigments could be observed. Salinity also affected the ratio of chlorophyll *a* to chlorophyll *b*.

It is concluded that destruction of chlorophyll pigments and instability of the pigment protein complex is the main result of reduction of chlorophyll content in salinity media. It also could be due to the interference of salts with the *de novo* synthesis of proteins, the structural component of chlorophyll, rather than the breakdown of chlorophyll (Jaleel *et al.*, 2007, 2008). On the other hand, it has been reported that in salt-tolerant species, chlorophyll content is increased while salinity decreases it in salt-sensitive species (Hamada & El-Enany, 1994; Khan *et al.*, 2009). Therefore, chlorophyll content could

not be considered as an overall index for salt stress tolerance and must be integrated with other indices.

Ashraf & Harris (2013) recommended use of carotenoids as a reliable criterion for salt tolerance. They also indicated that growth improvement in plants under salinity has been widely reported to be due to the significant role of zeaxanthin in alleviating oxidative damage of membranes.

Photosynthetic rate (*A*), water use efficiency (WUE) calculated as *A/E*, transpiration rate (*E*), internal CO<sub>2</sub> concentration (*C<sub>i</sub>*) and stomatal conductance (*g<sub>s</sub>*) of sunflower cultivars were significantly reduced in saline conditions (Shahbaz *et al.*, 2011). Chlorophyll *a*, *b* content and their ratio were not affected by 150 mM NaCl; however, *C<sub>i</sub>/C<sub>a</sub>* ratio increased significantly. Shahbaz *et al.* concluded that there is a correlation between salt tolerance traits in tolerant cultivars with improved gas exchange characteristics.

### 8.3.4 Cell and leaf growth

Leaf cell growth and development are not tolerant to salt ions even when the normal conditions of export and compartmentalization processes are functioning optimally. This results from the consumption of energy for maintaining popular gradients in ion compartmentation, and synthesis of organic solutes to adjust the osmotic potential of salt ions in the vacuole (Volkmar *et al.*, 1998). Loading of ions in the vacuole is another energy-consuming process that could be used to power biosynthetic processes in normal conditions.

Based on the cell elongation model, the rate of cell elongation (*r*) is adjusted by changes in cell wall extensibility (*φ*), turgor pressure (*P*), and cell wall threshold (*Y*) (Lockhart, 1965): *φ* and *Y* are the physical characteristics of the cell wall, but its threshold correlated to the value of turgor pressure below which no irreversible cell wall extension occurs. This concept could be expressed as:

$$r = \phi(P - Y)$$

Therefore, cell growth could be decreased by reduction in *φ*, *P*, increase in *Y*, or a combination of these factors. Since salt concentration reduced osmotic potential of the soil around the roots, therefore salt stress affects cell growth by decreasing cell turgor (Volkmar *et al.*, 1998). However, this type of reduction in cell turgor is not the main reason for the large reduction in leaf elongation rate of plants that thrive for long periods in saline solutions.

It is indicated that reduction of leaf growth can occur without any alteration in cell turgor pressure, suggesting that the lower growth of plants in saline conditions over longer times may be attributable to factors other than decreased cell turgor (Volkmar *et al.*, 1998). For example, leaf growth rate of salinized plants was not increased when leaf turgor was artificially raised by pressurizing the root system.

It seems that under salt stress, plant roots send a growth regulator-like chemical signal to the shoot and inhibit shoot growth (Munns & Tester, 2008); however, the possibility that salt stress reduces cell growth by increasing the  $Y$  value or reducing the  $\phi$  value has been proposed. A reduction in  $\phi$  has been observed for both maize roots (Neumann *et al.*, 1994) and leaves (Cramer & Bowman, 1991; Neumann, 1994) in saline conditions.

Salt stress could increase the  $Y$  value of root and leaf tissues (Cramer & Bowman, 1991; Pritchard *et al.*, 1991). Similar results have been reported by Neumann *et al.* (1994) on the growth prevention of maize root cells in response to  $100 \text{ mol m}^{-3} \text{ NaCl}$ . The ability of leaf cells to accumulate the export of salt from root cells is closely correlated to growth rate. New plant leaf cells provide a continually replenishing storage reservoir for the vacuolar compartmentalization of salt from the root cells. Therefore, throughout the growing period, plant leaf cells can adjust the concentration of ions in the cytoplasm. On the other hand, when growth is directly inhibited by the salt in the root zone, its capacity to allocate the delivery of salt to the shoot is injured.

It has been observed that in salt stress conditions, the tentative equilibrium established between plant root cell export of salt ions and leaf cell allocation is disturbed, as more pressure is imposed on the salt sequestration capacity of the vacuole. In this sense, salt ions will move either toward the cytoplasm or into the intercellular spaces. Accumulation of salt ions in new places is dangerous for cell function. By accumulating salt in the cytoplasm, cell function will be directly inhibited due to ion toxicity. When salt accumulates in the intercellular spaces, due to the driving force for cell expansion, cell growth will cease entirely and turgor pressure will have dropped below that of the  $Y$  value of the cell wall. In such cases, limitation of the water in leaf cells concentrates cell solutes to a level at which cell metabolism is irreversibly affected (Volkmar *et al.*, 1998).

In addition, differences in saline sensitivity among the plants are associated with the difference in the time it takes for salt ions to reach maximum concentration in the leaf vacuoles. Thus, salt-tolerant plants are able to compartmentalize salts in their leaves effectively even when the rate of salt ion delivery to leaf cells is exacerbated (Pessaraki, 2014). Salt ions could alter patterns of plant cell growth and development. Long-term plant exposure to high root zone salinity progressively decreases leaf size (Munns *et al.*, 1988). In this sense, rate of cell division, and expansion and duration of cell expansion would be reduced. Overall, the final size of leaf cells would be decreased if cell division was affected by salt stress (Volkmar *et al.*, 1998).

#### 8.4 Mechanism of salinity tolerance

Salt tolerance is the ability of a plant to grow and develop its life cycle in a medium that contains high percentage of soluble salts. Salt tolerance is usually measured as the relative yield production in saline compared to non-saline conditions during the growing season (Munns, 2002). Salt tolerance could be evaluated as plant survival, but for annual species, the amount of biological yield is more useful, as this is usually related to grain yield.

Plant salt tolerance will be different in different growth stages. Among cereals, barley is more tolerant than rice. Some legumes are very sensitive, even more sensitive than rice. Bread wheat is moderately tolerant and durum wheat is less so. Alfalfa and lucerne are moderately tolerant, and halophytes such as saltbush (*Atriplex* spp.) grow well at salinities greater than that of seawater. The variation in salinity tolerance in dicotyledonous species is even greater than in monocotyledonous species (Lauchli, 1984; Munns & Tester, 2008). Results have shown that at a given salinity level, a salt-tolerant species such as sugar beet might have a reduction of only 20% in dry weight, a moderately tolerant species such as cotton might have a 60% reduction, and a sensitive species such as soybean might be dead (Greenway & Munns 1980).

Plants use extra biochemical and molecular mechanisms to overcome salinity. Mechanisms of salt tolerance would be either low- or high-complexity processes. The former appear to involve alteration in many biochemical pathways while the latter involve changes that protect

major mechanisms such as photosynthesis and respiration (Botella *et al.*, 1994; Parida & Das, 2005; Walbot & Cullis, 1985).

Some plants have adapted to cope with salt stress; however, the majority of crops are salt sensitive and will not survive under conditions of high salt ions in the root zone or will survive but with decreased biomass production (Hale & Orcutt, 1989).

#### 8.4.1 Role of vacuole

There are two mechanisms used by the plant to exclude salt reaching the leaf from the cytoplasm. Salt ions can accumulate in the apoplast or move to the vacuole. Build-up of salt ions in the apoplast leads to an increase in the osmotic gradient between the inside and outside of the cell. To adjust a thermodynamic equilibrium, water inside the cell diffuses to the intercellular spaces, leading to progressive cellular dehydration and, eventually, cell death. Therefore, salt-tolerant traits are more associated with the amount of salt ions that accumulate in the cell vacuole (Volkmar *et al.*, 1998).

Salt ions pass across the cell membrane and the cytoplasm to enter the vacuole. The quantity of salt ions that pass across the cell membrane must not be more than the amount deposited into the vacuole to minimize the risk of salt hazard (Volkmar *et al.*, 1998). The amount of salt flow is controlled by the storage capacity of the root and the salt concentration in the soil solution. Therefore, salt-tolerant plants require an active vacuolar compartmentation capacity to store the high amount of salt ions delivered from the xylem to the leaf (Lauchli & Epstein, 1990).

#### 8.4.2 Osmotic adjustment

The compartmentalization of salt ions between the cytoplasm and vacuole creates a strong osmotic gradient across the vacuolar membrane. This flow is balanced by an increase in the synthesis of chemical and biochemical molecules in the cytoplasm, a process known as osmotic adjustment. Osmotic adjustment is used by plants as an important mechanism to overcome salt stress (Pessaraki, 2014).

Compatible solutes such as proline, glycine-betaine, proline betaine, B-alaninebetaine, D-sorbitol, D-mannitol, sucrose, glucose, fructose, D-pinitol, L-quebrachitol, Myo-inositol, b-dimethylsulphone and propionate are used by plants in osmotic adjustment mechanisms (Lauchli & Epstein, 1990). Generally, 'compatible solutes' is often

used to describe these organic osmolytes because of their presumed compatibility with cytoplasmic entities and processes (Munns & Tester, 2008). For example, proline synthesis in tobacco plants increased up to 80 times under saline conditions. Genetic evidence of the importance of glycine-betaine in improving salt tolerance has been shown in barley and maize (Volkmar *et al.*, 1998). Similar evidence has been demonstrated for mannitol, an important osmoprotectant in celery (Tarcynski *et al.*, 1993).

Plants consume significant quantities of carbon to produce sufficient osmotic substances and this process potentially limits normal growth and development of the plant (Munns & Tester, 2008). Plants also use high concentrations of inorganic ions for osmotic adjustment (Greenway & Munns, 1980). The energetic cost of this approach is much lower than the synthesis of organic components in the cell (Munns & Tester, 2008; Yeo, 1983).

In leaf cells, to accumulate one mole of NaCl as an osmoticum, about seven moles of ATP are needed. In comparison, the amount of ATP required to synthesize one mole of an organic compatible solute is markedly higher. The ATP requirement for the synthesis or accumulation of solutes has been estimated as 3.5 for Na<sup>+</sup>, 34 for mannitol, 41 for proline, 50 for glycine-betaine, and approximately 52 for sucrose (Munns & Tester, 2008). Overall, production of osmoticum might be an adaptation for plants surviving in saline conditions but this mechanism affected growth of the plant due to ion toxicity and deficiency (Munns & Tester, 2008; Volkmar *et al.*, 1998).

#### 8.4.3 Salt inclusion versus exclusion

Since cell membranes have selection processes for ion absorption, the entrance of sodium becomes limited. Therefore, salt ion levels in the roots and stems of plants are sometimes higher than in the leaves. Due to variations in the selectivity of the membranes among plant species, they may be divided into salt excluders and salt non-excluders (Hale & Orcutt, 1989).

Sodium exclusion by roots occurs to prevent toxic concentrations of Na<sup>+</sup> in leaves. Accumulation of Na<sup>+</sup> manifests its toxic effects after days or weeks, depending on the species, and causes premature death of older leaves (Munns & Tester, 2008).

Salt-tolerant plants showed some evidence of exclusion of Na<sup>+</sup> from the leaf. This is especially true for many glycophytic species, including crop plants such as

wheat and barley, corn, chickpea and beans, as well as some halophytes (Volkmar *et al.*, 1998).

Since in most species,  $\text{Na}^+$  appears to reach a toxic concentration before  $\text{Cl}^-$  does, many studies have focused on  $\text{Na}^+$  exclusion mechanisms within the plant. However, for some species such as soybean,  $\text{Cl}^-$  is considered to be the more toxic ion. Generally, plants tolerated high amounts of  $\text{Na}^+$  and  $\text{Cl}^-$  arriving in their leaves by use of some anatomical alterations and intracellular partitioning mechanisms (Munns & Tester, 2008). There are some differences between amounts of  $\text{Na}^+$  and  $\text{Cl}^-$  in root and leaf cells. Roots had the lowest  $\text{Cl}^-$  concentration compared to leaves, which increased with increasing salinity, while  $\text{Na}^+$  in leaves was much lower than  $\text{Cl}^-$  (Chartzoulakis & Klapaki, 2000).

In some dicotyledonous halophytes, there is a salt-induced increase in cell size due to increases in vacuole volume (succulence), and in others the excretion of  $\text{Na}^+$  and  $\text{Cl}^-$  creates salt glands or bladders at the leaf or stem surfaces. Some evidence has shown that salt glands are the only anatomical adaptations that occur in some monocotyledonous halophytes (Munns & Tester, 2008). Barley crops that thrive in saline conditions showed, contrary to  $\text{K}^+$ , a greater accumulation of  $\text{Cl}^-$  in epidermal compared with mesophyll cells (Munns & Tester, 2008).

Most halophytes use salt ions as an osmoticum to control the concentration of external ions. In many glycophytes, there is no obvious relationship between salt exclusion and salt tolerance. While  $\text{Na}^+$  exclusion is a general characteristic reported in some salt-tolerant wheat lines, a salt-sensitive line had much lower shoot  $\text{Na}^+$  levels than the more tolerant lines. In a similar experiment, tolerant maize cultivars transported more  $\text{Na}^+$  to the shoot than intolerant cultivars. Therefore it seems that, at least in some glycophytes, salt exclusion is not necessarily associated with salt-tolerant characteristics (Volkmar *et al.*, 1998).

#### 8.4.4 $\text{Na}^+/\text{K}^+$ discrimination

It is indicated that selection of ions by plants is a clear way to tolerate salt conditions. For example, in the  $\text{Na}^+/\text{K}^+$  discrimination concept,  $\text{Na}^+$  uptake can be substituted by  $\text{K}^+$  to allow the plant to tolerate salt conditions. Therefore  $\text{Na}^+/\text{K}^+$  discrimination could be considered as an important criterion in selecting commercial crops (Volkmar *et al.*, 1998). However, the  $\text{Na}^+/\text{K}^+$  discrimination trait is not necessarily a salt tolerance criterion in glycophytes.

For example, some salt-tolerant cultivated barley strains and their wild relatives do not show the enhanced  $\text{Na}^+/\text{K}^+$  discrimination trait. Similarly, while some wild relatives of wheat tend to be better at discriminating against  $\text{Na}^+$  than cultivated wheat, it is believed that this is not due to enhanced discrimination but rather, to greater control of salt accumulation (Munns & Tester, 2008). Halophytes prefer to include  $\text{Na}^+$  rather than  $\text{K}^+$ , as a tolerance tool for osmotic adjustment. There is a positive relationship between  $\text{Na}^+$  inclusion and salt tolerance in these plants (Volkmar *et al.*, 1998).

## 8.5 Salt and water stress

Salinity as well as water stress reduces the ability of plants to take up water, and plant growth rates decrease due to changes in plant metabolism (Munns, 2002). Generally, under saline conditions the osmotic potential of the soil solution is similar to drought stress. There are some differences between the symptoms of salt-stressed and water-stressed plants. Commonly, plants under saline conditions are stunted and not wilted, which means that the cells must have water potentials that enable them to compete for water from the xylem (Hale & Orcutt, 1989).

Salinity also prevents the development of lateral shoots and affects reproductive development, such as early flowering or a reduction in number of florets. All these changes in plant growth are responses to the osmotic effect of the salt, and are similar to drought responses. Therefore, under drought stress, similar to salt stress, plants accumulate compatible solutes, such as proline and mannitol, for osmotic adjustment (Munns & Tester, 2008).

Hormonal responses are similar; for example, ABA content would be increased as a result of water and salt stresses (He & Cramer 1996). In long-term exposure, photosynthesis is also decreased in water and salt stress (Munns, 2002).

## 8.6 Seed priming for higher salinity tolerance

Salinity affects plant growth and development at any time during the cycle. On the other hand, plants experience salt stress at different growth stages, such as

germination, vegetative and reproductive growth. Under stressful environments, rapid and uniform germination of crops, particularly of annuals, is necessary to achieve enhanced quality and yield potential (Pirasteh-Anosheh *et al.*, 2014a). An important approach to increase crop yield under salt stress is seed invigoration. Seed invigoration strategies include hydro-priming, osmo-priming, halo-priming, thermo-priming and hormo-priming.

Plant establishment is improved by seed priming in many crop species. Priming is defined as seed presowing in solutions that allow them to imbibe water to improve the first stage of seed germination; however, this prevents radical protrusion through the seed coat (Heydecker *et al.*, 1973). As Taylor *et al.* (1998) suggest, seed priming includes presoaking hydration, coating technologies and seed conditioning. Therefore, seed priming can be classified as hydro-priming (soaking in water) or osmo-priming (soaking in osmotic solutions such as polyethylene glycol).

### 8.6.1 Hydro-priming

In hydro-priming, seeds are soaked in water before sowing and this may or may not be followed by air-drying of the seeds (Pill & Necker, 2001). Improvement in salt tolerance of plants following hydro-priming has been observed in many studies. Hamidi *et al.* (2013) reported that the effect of hydro-priming on the germination percentage of wheat was more than for other priming types. However, its effect on shoot height was equal to and on leaf area was less than other priming treatments. The mechanisms that improve plant growth and seed yield in saline or non-saline conditions by application of this simple technique are not yet clear (Ashraf *et al.*, 2008).

### 8.6.2 Osmo-priming

In osmo-priming (osmo-conditioning or osmotic conditioning), seeds are soaked for a certain time period in solutions of sugars, polyethylene glycol (PEG), glycerol, sorbitol or mannitol followed by air-drying before sowing. The low water potential of these solutions causes partial seed imbibition, then initial metabolic processes are activated; however, germination does not proceed (Pill & Necker, 2001). Pirasteh-Anosheh & Hamidi (2013) reported that the percentage of germination, radicle and seedling length in rapeseed (*Brassica napus*) was significantly affected by application of PEG in seed

priming. Seed priming with PEG had a higher effect on radicle length. However, in some experiments it was shown that PEG significantly reduced germination percentage, but increased seedling growth of sunflower (Hamidi & Pirasteh-Anosheh, 2013).

Osmo-priming not only improves seed germination but also enhances general crop performance under normal or salt stress environments. Application of 20% PEG-8000 for 2 days at 10°C enhanced germination rate, percentage germination, seedling growth and dry matter production under water-stressed, waterlogged, cold stress or saline conditions in Italian ryegrass (*Lolium multiflorum*) and sorghum (*Sorghum bicolor*) (Hur, 1991).

### 8.6.3 Halo-priming

Halo-priming (soaking seed in solutions of inorganic salts) has been shown to have a significant and positive effect on seed germination and emergence, seedling establishment and crop production in saline conditions (Ashraf *et al.*, 2008). Hamidi *et al.* (2013) compared the effect of halo-priming with hydro-priming on wheat (*Triticum aestivum*) germination and growth. Halo-priming treatments consisted of different combinations of KNO<sub>3</sub>, KH<sub>2</sub>PO<sub>4</sub> and nitrogen + phosphorus. They observed that both seed priming types had significant effects on all measured traits and increased germination percentage, seedling and radicle length, plant height and leaf area. Increasing KNO<sub>3</sub> and KH<sub>2</sub>PO<sub>4</sub> and decreasing N+P were associated with a more positive effect so the best combinations for KNO<sub>3</sub>, KH<sub>2</sub>PO<sub>4</sub> and N+P were 100 mM, 500 mM, 50 mM +10 mM, respectively.

Halo-priming improves seedling emergence as well as subsequent plant growth, thereby enhancing final plant yield. Ashraf *et al.* (2008) found that pre-soaking seed in solutions of inorganic salts improved growth and yield in many plants such as broad bean (*Vicia faba*), wheat, soybean (*Glycine max*), *Pennisetum americanum* and *Sorghum bicolor* under saline conditions. Pirasteh-Anosheh *et al.* (2011) evaluated the effect of some halo-priming methods on seed viability and some physiological attributes of maize under saline conditions. Urea priming led to more germination percentage, germination rate and shoot length compared to other priming types while KNO<sub>3</sub> priming significantly increased root length in comparison with the other primers. The effect of halo-priming on S/R and proline content was not significant. These authors concluded



that seedling establishment and root development were improved by using  $\text{KNO}_3$  and urea in saline conditions.

#### 8.6.4 Thermo-priming

Thermo-priming is defined as exposing seeds to low or high temperatures to improve seed germination and seedling establishment in stressful conditions. It is indicated that seed germination of some species is positively improved by low-temperature treatment (Ashraf & Foolad, 2005). It is also interesting to know that seed presowing treatment with some specific temperatures improves later plant growth and development as well as seed germination and seedling emergence (Ashraf *et al.*, 2008). It has been reported that chilling treatment of *Brassica juncea* (Sharma & Kumar, 1999) and pearl millet (*Pennisetum glaucum*) (Ashraf *et al.*, 2003) seeds resulted in enhanced germination under salt stress. The role of temperature treatment in seed germination, seedling establishment, plant growth and grain yield of different crops in salt stress remains unclear.

#### 8.6.5 Hormo-priming

In plants lacking the inherent ability to maintain optimum levels of plant growth regulators (PGRs) under saline conditions, exogenous application of PGRs may overcome this deficiency (Ashraf & Foolad, 2005). PGRs can be applied as foliar spray, through root growing media or as presowing seed treatment. The latter is generally called seed priming. However, seed priming with different PGRs (hormo-priming) such as chlormequat chloride (CCC), salicylic acid (SA), auxins (IAA, IBA, NAA), gibberellins (GA), kinetin, abscisic acid, polyamines (PAs), ethylene, brassinolide (BR), triacontanol and ascorbic acid has been used as a practical approach to improving seed germination and seedling establishment in osmotic stress conditions in several plant species (Pirasteh-Anosheh *et al.*, 2014a). Pretreatment of seeds with optimal concentrations of hormones can effectively promote seed establishment, plant growth and development and crop production in saline and non-saline conditions. Hormo-priming beneficial to plant development and crop production of some crop species in stressful conditions was found to be associated with improved nutrient availability as well as increased plant physiological process and root proliferation (Ashraf & Foolad, 2005; Singh, 1995).

Afria *et al.* (1998) reported that CCC-primed guar (*Cyamopsis tetragonoloba* L.) plants (1.5 g l<sup>-1</sup>) had higher

leaf area, straw and seed yield as well as reduced transpiration and harvest index under salt stress conditions. Triticale and barley plants primed with CCC had seedlings with significantly more leaf and tiller, high leaf area index and a higher shoot dry matter. These altered processes were found to be beneficial for increased crop yield (Naylor *et al.*, 1989). Furthermore, Kanp *et al.* (2009) showed that seed pretreatment with CCC markedly improved the capacity of seed storage and crop performance of pea (*Pisum sativum* L.) and horse gram (*Dolichos biflorus* L.). Pirasteh-Anosheh *et al.* (2014a) examined the effect of CCC priming on final germination and plant development in wheat, barley, maize, sunflower, safflower and rapeseed under stressful conditions and reported that priming with optimum CCC reduced adverse effects of the stress on seedling emergence and vegetative growth and improved the level of leaf free proline and chlorophyll content index. The positive effect of CCC priming on wheat, maize and rapeseed was more pronounced at moderate osmotic levels; however, barley and safflower were affected by priming treatments at all levels of osmotic stress. In some cases, due to a thick achene coat, sunflower did not respond to CCC priming. CCC priming, by diverting a major proportion of assimilates to the root, increased root to shoot dry weight ratio under all osmotic stress levels. Treating seed of sudan grass (*Sorghum sudanense*) with CCC reduced adverse effects of salinity on the rate and percentage of germination (Ismaeil *et al.*, 1993).

Salicylic acid (SA) or its analogues was found to affect seed germination (Hayat *et al.*, 2010). However, there are different reports on the role of SA in the promotion or inhibition of germination. Presowing seed treatment with SA has been shown to be an effective means of counteracting harmful effects of salt stress in many plant species (Ashraf *et al.*, 2010). Enhanced germination and seedling growth were recorded in wheat, when the grains were subjected to presowing treatment in SA (Shakirova, 2007). In another study, Hayat *et al.* (2005) reported that leaf number as well as fresh and dry mass per plant were increased in wheat seedlings when the seed was soaked in lower concentrations (10<sup>-5</sup> M) of SA. Afzal *et al.* (2005) demonstrated that SA-treated wheat seeds exhibited enhanced germination rates and produced more vigorous seedlings under saline conditions. Dolatabadian *et al.* (2008) indicated that if wheat seeds are treated with SA prior to planting, seed germination is improved in both saline and non-saline conditions.



In this study, cell division in roots and shoots was accelerated in treated seeds which resulted in improving plant growth and development. In such cases, it is indicated that applications of SA may also promote subsequent plant growth and crop yield (Ashraf *et al.*, 2010). For example, seed germination of *Arabidopsis* spp. was enhanced by the addition of SA in saline conditions (Rajjou *et al.*, 2006). Aldesuquy *et al.* (1998) showed that SA priming of wheat seed could reduce the effects of salinity on initial plant growth by decreasing stomata number and size and reducing transpiration flow. Kaydan *et al.* (2007) also indicated that priming of wheat seeds by SA improved seedling emergence and increased leaf solute potential, shoot and root dry mass,  $K^+/Na^+$  ratio, chlorophyll *a*, *b*, and carotenoid content in salt stress. Deef (2007) showed that SA pretreatment of wheat and barley seeds was associated with improved levels of glutathione, a potential non-enzymatic antioxidant, as well as salt tolerance of the pretreated seedlings. These researchers also noted that betaine production in the seedlings of both species under salt stress was demonstrated in pretreated seeds. In another study, tomato seedlings pretreated with SA for 3 weeks showed a remarkable improvement in the activities of certain antioxidant enzymes, including superoxide dismutase, catalase and peroxidase, under salt stress (Szepesi *et al.*, 2008). Szepesi (2006) indicated that pretreatment of tomato seedlings with SA resulted in a marked accumulation of  $Na^+$  and compatible osmolytes consisting of glucose, fructose, sorbitol and proline in the leaves of plants subjected to salt media. In fact, reduction in leaf water potential led to improved accumulation of ABA in the roots, enabling the plants to induce the ABA signal transduction pathways and gene expression under salt stress. In saline media, the SA-pretreated plants also produced higher amounts of compatible osmolytes such as glucose, fructose, sorbitol and proline that improved plant growth and enhanced photosynthetic efficiency. Gemes *et al.* (2008) showed that tomato plants treated with SA had higher photosynthetic capacity, photosynthetic pigments, and accumulation of soluble sugars under salt stress.

Brassinolide seed priming led to significant increases in germination parameters in *Eucalyptus camaldulensis* (Sasse *et al.*, 1995) as well as barley and common bean (Abd El-Fattah, 2007) under saline conditions. In the latter case, it was shown that BR seed priming caused accumulation in betaine (a potential osmoprotectant)

and glutathione (a non-enzymatic antioxidant). IAA, NAA or GA seed priming (Balki & Padole, 1982) as well as IAA, IBA or GA seed soaking (Gulnaz *et al.*, 1999), enhanced seed germination of wheat under salt stress. GA seed priming at different concentrations improved seed germination under saline conditions in wheat (Parashar & Varma, 1988), tomato (*Lycopersicon esculentum*) (Kang *et al.*, 1996) and okra (*Abelmoschus esculentus*) (Vijayaraghavan, 1999). Other plant hormones also have considerable effects on seed germination, growth and yield, for example seed priming of kinetin and ascorbic acid in pigeon pea (Jyotsna & Srivastava, 1998), kinetin in wheat (Iqbal & Ashraf, 2005a) and PAs in wheat (Iqbal & Ashraf, 2005b).

## 8.7 Foliar application of salicylic acid (SA)

The use of plant growth regulators (PGRs) in agriculture to promote plant growth, production and quality is becoming increasingly more common (Ashraf *et al.*, 2008). Both beneficial and adverse effects of PGRs on growth and development as well as plant metabolism have been addressed extensively. Endogenous concentrations and ratios of different PGRs are influenced by numerous internal and external stimuli (Ashraf *et al.*, 2010). For example, environmental stresses, which often cause a plethora of complex physiological, molecular and biochemical changes in plants, may alter the levels and ratios of different endogenous PGRs (Wang *et al.*, 2005), thereby modifying their signal transduction pathways. Such modifications often cause serious metabolic disorders, leading to a general inhibition in plant growth processes under salt stress (Lerner & Amzallag, 1994). Salinity commonly reduced production, and also degradation of PGRs in plants (Kuiper *et al.*, 1988). However, in stressful conditions, it is reported that seed priming by PGRs before sowing or application of PGRs to the growing plant may reduce deficiency of PGRs in plants and decrease the prevention effects of stress (Ashraf & Foolad, 2007; Ashraf *et al.*, 2008). Exogenous application of natural and synthetic PGRs would reduce harmful effects of salt stress and enhance plant salt tolerance. However, the mechanisms underlying such effects remain unclear, and have not been directly related to the physiological roles of these compounds (Pirasteh-Anosheh & Emam, 2012a, b). It is also not

clear how exogenous PGRs adjust the imbalance of regulatory substances caused by the stress (Debez *et al.*, 2001; Khan *et al.*, 2000). Nevertheless, from a practical point of view, use of PGRs offers a potential approach to mitigating the inhibitory effects of salinity on plant growth and grain yield (Hayat *et al.*, 2010).

Salicylic acid is naturally synthesized in plants and has important roles in metabolic processes such as photosynthesis-related processes, stomatal regulation and ion uptake and transport. Salicylic acid also causes changes in leaf anatomy and chloroplast ultrastructure (Ashraf *et al.*, 2010; Kaydan *et al.*, 2007). In addition, it has been shown that SA is involved in leaf senescence as well as salt tolerance, by scavenging ROS such as  $^1O_2$ ,  $O_2^-$ ,  $\cdot OH$  and  $H_2O_2$  (Chen *et al.*, 1993; Morris *et al.*, 2000). Khodary (2004) indicated that SA induced a significant increase in growth parameters, pigment contents and photosynthetic rate of maize. Hussein *et al.* (2007) demonstrated that foliar application of SA in wheat shoots irrigated with Mediterranean sea water showed an enhancement in plant height, leaf number and area, stem diameter and dry matter of stem and leaves. Moreover, proline content was significantly increased in the plants exposed to SA.

In a field and greenhouse study, Pirasteh-Anosheh & Emam (2012a) reported that SA foliar application had positive effects on free proline (increasing 51%), soluble proteins (increasing 57%), CT (decreasing 14%) and SPAD unit (decreasing about 13%). Furthermore, the sensitivity of two wheat cultivars to SA differed significantly. It is clear that the metabolic activity of plants in stress conditions is markedly reduced, leading to inhibited overall growth. Therefore SA could alleviate some of the harmful effects of salt stress (Hayat *et al.*, 2010). Eraslan *et al.* (2007) also revealed that SA significantly improved plant growth as well as root dry weight. In a field study, Pirasteh-Anosheh *et al.* (2012) showed that although drought stress increased canopy temperature and decreased leaf area index and plant height in two wheat cultivars, exogenous applications of SA alleviated these harmful effects considerably. Pirasteh-Anosheh & Emam (2012b) also examined the effect of SA on grain yield and its components in two wheat cultivars under different water regimes. In their study, it was shown that SA could increase ear length, grain number per spikelet, grain and spikelet number per ear, thousand grain weight as well as the grain and biological yield.

They concluded that although stress decreased most yield components, SA could compensate for some of these losses.

A large body of literature has demonstrated that exogenous application of SA can potentially alleviate the toxic effects generated by salinity (Hayat *et al.*, 2010). Observations were also made in tomato plants treated with SA which were presumed to be due to the improved activation of some enzymes, such as aldose reductase and ascorbate peroxidase, and to the accumulation of certain osmolytes such as proline (Szepesi *et al.*, 2005; Tari *et al.*, 2004). Exogenous application of SA also has been reported to modulate activities of the intracellular antioxidant enzymes superoxide dismutase (SOD) and peroxidase (POD) and increase plant tolerance to environmental stresses (Parida & Das, 2005; Yeo, 1983). Exogenous SA application also improved the amount of carbohydrate in corn (Khodary, 2004). Pirasteh-Anosheh *et al.* (2012) reported that application of SA increased total soluble proteins, chlorophylls *a* and *b* and peroxidase activity. They assumed that the benefits of SA in decreasing the adverse effects of water stress may be due to improving stomatal regulation, maintaining leaf chlorophyll content, increasing water use efficiency and stimulation of root growth. Wheat seedlings accumulated high amounts of proline under salt stress; however, it was further increased when SA was used exogenously, thereby alleviating the harmful effects of salt stress (Shakirova *et al.*, 2003). The SA foliar application prevented lowering of IAA and cytokinin levels in salt-stressed wheat plants, which resulted in improved cell division in root apical meristem, thereby increasing plant growth and development (Shakirova, 2007). These authors also indicated that application of SA resulted in the accumulation of ABA which might have contributed to the preadaptation of wheat seedlings to salt stress, since ABA promote the synthesis of a wide range of anti-stress proteins, providing a protection system in the plants. Application of SA also lowered the level of ROS species and decreased the activities of SOD and POD in the roots of young wheat seedlings (Shakirova *et al.*, 2003).

In some cases, the influence of SA on antioxidant enzymes was related to concentrations of PGR; for example, lower concentrations of SA improved activities of SOD and POD in *Vanilla planifolia*, while at higher amounts it decreased the activity of these enzymes (Chuan-Jai *et al.*, 2003). In tomato plants grown in saline

areas, application of moderate concentrations of SA reduced lipid peroxidation and increased activities of the antioxidant enzymes SOD, CAT, GPX and DHAR as well as the content of ascorbate and glutathione (He & Zhu, 2008). In Indian mustard, application of very low concentrations of SA to seedlings grown under salt stress improved photosynthetic capacity and increased activity of carbonic anhydrase and nitrate reductase (Yusuf *et al.*, 2008). In addition, the activities of SOD, CAT and POD were improved. It is also indicated that SA may induce plant defence mechanisms by stimulating different antioxidant enzymes. By modifying the activity of these enzymes, SA plays an important role in plant protection against abiotic and biotic stresses (Catinot *et al.*, 2008; Yusuf *et al.*, 2008).

Exogenous application of SA in barley plants enhanced the photosynthetic rate and also maintained the stability of membranes, thereby improved plant growth (El Tayeb, 2005). Exogenous use of SA has also been shown to modify the uptake and transport of inorganic ions in some plants. Corn plants under salt stress treated with SA accumulated more N, Mg<sup>2+</sup>, Fe<sup>2+</sup>, Cu<sup>2+</sup> and Mn<sup>2+</sup> than Na<sup>+</sup> and Cl<sup>-</sup> (Gunes *et al.*, 2005). Use of SA in tomato significantly reduced NaCl toxicity. In fact, in these conditions, the plants take up more K<sup>+</sup> and Mg<sup>2+</sup> in the roots and shoots than Na<sup>+</sup> (He & Zhu, 2008).

## 8.8 Conclusions and future prospects

Salinity can be considered as the most important abiotic stress, more important than drought, since salt stress can occur anywhere, even though the water resources are not limited. Effect of salt stress on plants happens in two phases: osmotic stress inhibiting growth of young leaves in a rapid phase, and ionic stress accelerating senescence of mature leaves in a slower phase. Plants have developed some mechanisms to overcome salinity. It seems that the main physiological mechanisms of salinity tolerance include:

- selective accumulation and/or exclusion of ions
- ion uptake control 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 some plant hormones.

Generally, the best way to assess plant salt tolerance is by measuring reduction percentage in yield or biomass in saline conditions, especially over a prolonged period during germination, while seedlings are susceptible to salt stress. Also, plants generally become more tolerant during later phases of development. The tolerance threshold of plants differs and considerably depends on species and even cultivar in a species.

There are numerous indices for salt tolerance of plants such as ion accumulation and distribution, biochemical traits, photosynthesis pigments, photosynthesis gas exchange, etc. However, given the variation in literature, none of them could be a definitive index for determining salinity tolerance. Indeed, all of them are necessary but not sufficient. Further research to determine the best criteria for each plant under each condition is necessary. Use of PGRs has been proven but needs large-scale assessment. Osmotic separation from ionic phases might be a novel approach in understanding the physiological mechanisms of salinity tolerance.

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