

# Chapter 2

## Plant Response to Salt Stress and Role of Exogenous Protectants to Mitigate Salt-Induced Damages

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### 2.1 Introduction

World agriculture is facing a lot of challenges like producing 70% more food for an additional 2.3 billion people by 2050 while at the same time fighting with poverty and hunger, consuming scarce natural resources more efficiently and adapting to climate change (FAO 2009). However, the productivity of crops is not increasing in parallel with the food demand. The lower productivity in most of the cases is attributed to various abiotic stresses. Curtailing crop losses due to various environmental stressors is a major area of concern to cope with the increasing food requirements (Shanker and Venkateswarlu 2011).

As a sessile organism, plants often experience abiotic stress like salinity, drought, high or low temperature, flooding, metal toxicity, ozone, UV-radiations, herbicides, etc., which pose serious threat to the crop production (Bhatnagar-Mathur et al. 2008; Ahmad and Prasad 2012a, b). The complex nature of the environment along with its

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unpredictable conditions and global climate change are increasing gradually which is creating the situation more adverse (Mittler and Blumwald 2010). Abiotic stresses remain the greatest constraint to crop production worldwide. It has been projected that more than 50% of yield reduction is the direct result of abiotic stresses (Rodríguez et al. 2005; Acquaah 2007). The major abiotic stresses like drought, high salinity, cold, and heat negatively influence the survival, biomass production and yield of staple food crops up to 70% (Vorasoot et al. 2003; Kaur et al. 2008; Ahmad et al. 2010a; Thakur et al. 2010; Mantri et al. 2012; Ahmad et al. 2012); hence, threaten the food security worldwide.

Salinity is one of the most brutal environmental factors limiting the productivity of crop plants because most of the crop plants are sensitive to salinity caused by high concentrations of salts in the soil. A considerable amount of land in the world is affected by salinity which is increasing day by day. More than 45 million hectares (M ha) of irrigated land which account to 20% of total land have been damaged by salt worldwide and 1.5 Mha are taken out of production each year due to high salinity levels in the soil (Pitman and Läuchli 2002; Munns and Tester 2008). On the other hand, increased salinity of agricultural land is expected to have destructive global effects, resulting in up to 50% loss of cultivable lands by the middle of the twenty-first century (Mahajan and Tuteja 2005). In most of the cases, the negative effects of salinity have been attributed to increase in  $\text{Na}^+$  and  $\text{Cl}^-$  ions in different plants hence these ions produce the critical conditions for plant survival by intercepting different plant mechanisms. Although both  $\text{Na}^+$  and  $\text{Cl}^-$  are the major ions which produce many physiological disorders in plants,  $\text{Cl}^-$  is the most dangerous (Tavakkoli et al. 2010). Salinity at higher levels causes both hyperionic and hyperosmotic stress and can lead to plant demise. The outcome of these effects may cause membrane damage, nutrient imbalance, altered levels of growth regulators, enzymatic inhibition and metabolic dysfunction, including photosynthesis which ultimately leads to plant death (Mahajan and Tuteja 2005; Hasanuzzaman et al. 2012a). High salt concentration in the soil or in the irrigation water can also have a devastating effect on plant metabolism, disrupting cellular homeostasis and uncoupling major physiological and biochemical processes. Biochemical and molecular studies of salt stress responses in plants have revealed significant increases of reactive oxygen species (ROS), including singlet oxygen ( $^1\text{O}_2$ ), superoxide ( $\text{O}_2^-$ ), hydroxyl radical ( $\text{OH}^\bullet$ ) and hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) (Tanou et al. 2009; Ahmad et al. 2010a, 2012; Ahmad and Umar 2011). However, the effect of salt stress on plants depends on the concentration and time of exposure of salt, plant genotypes and environmental factors.

Mechanisms of salt tolerance, not yet completely clear, can be explained to some extent by stress adaptation effectors that mediate ion homeostasis, osmolyte biosynthesis, toxic radical scavenging, water transport and long distance response co-ordination (Hasegawa et al. 2000). However, attempts to improve yield under stress conditions by plant improvement have been largely unsuccessful, primarily due to the multi-genic origin of the adaptive responses. Therefore, a well-focused approach combining the molecular, physiological, biochemical and metabolic aspects of salt tolerance is essential to develop salt-tolerant crop varieties. Exploring suitable ameliorants

or stress alleviant is one of the tasks of plant biologists. In recent decades exogenous protectant such as osmoprotectants (proline, glycinebetaine, trehalose, etc.), plant hormone (gibberellic acids, jasmonic acids, brassinosteroids, salicylic acid, etc.), antioxidants (ascorbic acid, glutathione, tocopherol, etc.), signaling molecules (nitric oxide, hydrogen peroxide, etc.), polyamines (spermidine, spermine, putrescine), trace elements (selenium, silicon, etc.) have been found effective in mitigating the salt induced damage in plant (Hoque et al. 2007; Ahmad et al. 2010a, 2012; Azzedine et al. 2011; Hasanuzzaman et al. 2011a, b; Hayat and Ahmad 2011; Hossain et al. 2011; Poór et al. 2011; Ioannidis et al. 2012; Nounjan et al. 2012; Rawia et al. 2011; Iqbal et al. 2012; Tahir et al. 2012; Yusuf et al. 2012). These protectants showed the capacity to enhance the plant's growth, yield as well as stress tolerance under salinity.

This chapter provides a comprehensive review of the major responses of plants to saline environments and the mechanisms by which growth and development and physiology of plants are affected by salinity. We also discuss the nature and types of salinity and the possible mechanism of salt stress in plants. Finally, we focus the issue of using exogenous protectants to mitigate the salt-induced damages in plants.

## 2.2 Causes and Types of Salinity

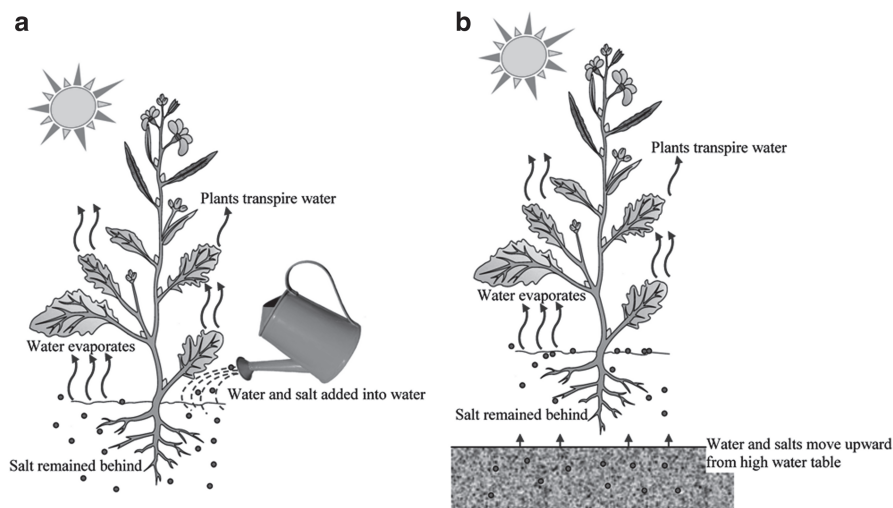
Among the abiotic stresses, salinity is the most destructive factor which limits the crop productivity considerably. A large area of land in the world is affected by salinity which is increasing day by day. Salinity is more prominent problem in irrigated crop lands. Worldwide, around 17% of the cultivated land is under irrigation and irrigated agriculture contributes more than 30% of the total agricultural production (Hillel 2000). It is estimated that at least 20% of total irrigated lands in the world is salt-affected (Pitman and Läuchli 2002). However, the statistics varies depending on sources. According to the FAO Land and Nutrition Management Service (2008), 6.5% of the total land in the world is affected by salt (either salinity or sodicity) which accounts for 831 Mha of land (Table 2.1).

There are different causes of the development of soil salinity. The major forms are viz. (i) natural or primary salinity and (ii) secondary or human-induced salinity. Primary salinity is occurred due to the long-term natural accumulation of salts in the soil or surface water. This is a natural process which is caused mainly by weathering of parent materials containing soluble salts through break down of rocks containing  $\text{Cl}^-$  of  $\text{Na}^+$ ,  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  and sometimes  $\text{SO}_4^{2-}$  and  $\text{CO}_3^{2-}$ . In addition, deposition of sea salt carried by wind and rain is also a reason, which varies with the types of soil. Secondary salinity occurs due to anthropogenic activities that disrupt the hydrologic balance of the soil between water applied (irrigation or rainfall) and water used by crops (transpiration) (Munns 2005; Garg and Manchanda 2008). In many irrigated areas, the water table has raised due to excessive amounts of applied water together with insufficient drainage. Most of the irrigation systems of the world have caused secondary salinity, sodicity or waterlogging (Garg and

**Table 2.1** Variation in salt-affected areas in the world, in million hectares (M ha)

Region	Total area (M ha)	Saline soils		Sodic soils	
		M ha	%	M ha	%
Africa	1,899	39	2.0	34	1.8
Asia, the Pacific and Australia	3,107	195	6.3	249	8.0
Europe	2,011	7	0.3	73	3.6
Latin America	2,039	61	3.0	51	2.5
Near East	1,802	92	5.1	14	0.8
North America	1,924	5	0.2	15	0.8
Total	12,781	397	3.1	434	3.4

Source: FAO land and plant nutrition service (2008)



**Fig. 2.1** Salinization in crop lands caused by salty irrigation water or rise of water table with saline water

Manchanda 2008). In irrigated lands, after irrigation, the water applied to the soil is consumed by the crop or evaporates directly from the moist soil. The excess salt is remained and accumulated in the soil which is called salinization (Fig. 2.1a). It is sometimes recognizable by a whitish layer of dry salt on the soil surface. In addition, salted groundwater may also contribute to salinization. Due to excessive irrigation and improper drainage the water table rises which allow the salty groundwater to reach in the upper soil layers and rhizosphere (Fig. 2.1b).

Based on the nature, characteristics and plant growth relationships in salt affected soils, two main types of soils have been coined by Szabolcs (1974). These are:

- A) Saline soils-The soluble salts are chiefly  $\text{NaCl}$  and  $\text{Na}_2\text{SO}_4$  and sometimes also contain appreciable quantities of  $\text{Cl}^-$  and  $\text{SO}_4^{2-}$  of  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$ . These soils contain sufficient neutral soluble salts to pose negative effect on growth of most crop plants.

**Table 2.2** Classification of water quality based on total salt concentration (Pitman and Läuchli 2002)

Water designation	Total dissolved salts (mg L <sup>-1</sup> )	EC (dS m <sup>-1</sup> )
Fresh water	<500	<0.6
Slightly brackish	500–1,000	0.6–1.5
Brackish	1,000–2,000	1.5–3.0
Moderately saline	2,000–5,000	3.0–8.0
Saline	5,000–10,000	8.0–15.0
Highly saline	10,000–35,000	15.0–45.0

**Table 2.3** Different measures of soil salinity

Measurement and units	Application
Conductivity (dS m <sup>-1</sup> )	Soils
Conductivity (μS cm <sup>-1</sup> )	Irrigation and river water
Total dissolved salts (mg L <sup>-1</sup> )	Irrigation and river water
Molarity of NaCl (mM)	Laboratory

- B) Sodic soils – These soils contain Na<sup>+</sup> salts capable of alkaline hydrolysis, mainly Na<sub>2</sub>CO<sub>3</sub>. Previously these soils have also been termed as ‘Alkali’.

Further categories of salt-affected soils which, though less extensive, are commonly found in different parts of the world are:

- C) Acid-sulfate soils: These soils have pH below 3.5 to 4.0 and found within a 50 cm depth that is directly or indirectly caused by H<sub>2</sub>SO<sub>4</sub> formed by the oxidation of pyrite (FeS<sub>2</sub>) or other reduced S compounds which is accelerated by brackish and saline mangrove swamps. Apart from high salinity, this soil also responsible for iron (Fe) and aluminium (Al) toxicities and deficiency of phosphorus (P) (Pons 1973; Abrol et al. 1988).
- D) Degraded sodic soils: These soils are an advanced stage of soil development coming from the washing out of salts. In this process there is a affinity for the dispersed clay and organic matter to move down the profile resulting in the formation of a dark, extremely compact layer having a sharply defined upper surface and merging gradually into the subsoil with increasing depth. These soils originally had enough exchangeable Na<sup>+</sup> but that most of this Na<sup>+</sup> has been lost through leaching (Abrol et al. 1988).

Based on the salt concentration, the saline water is classified into different types as presented in Table 2.2.

Soil salinity is measured by electrical conductivity (EC). The international system (SI) unit of EC is dS m<sup>-1</sup>. Salinity is also measured as mM which is vastly used in laboratory experiment (Table 2.3). In the field, the salinity of soil water or irrigation water is measured in terms of its electrical conductivity or in terms of osmotic potential. Pure water is a very poor conductor of electric current; the conductivity of a water sample is due to the ions dissolved in it. Generally, the higher the salt concentration in water, the greater it's electrical conductivity and the lower its osmotic potential/pressure (Taiz and Zeiger 2006).

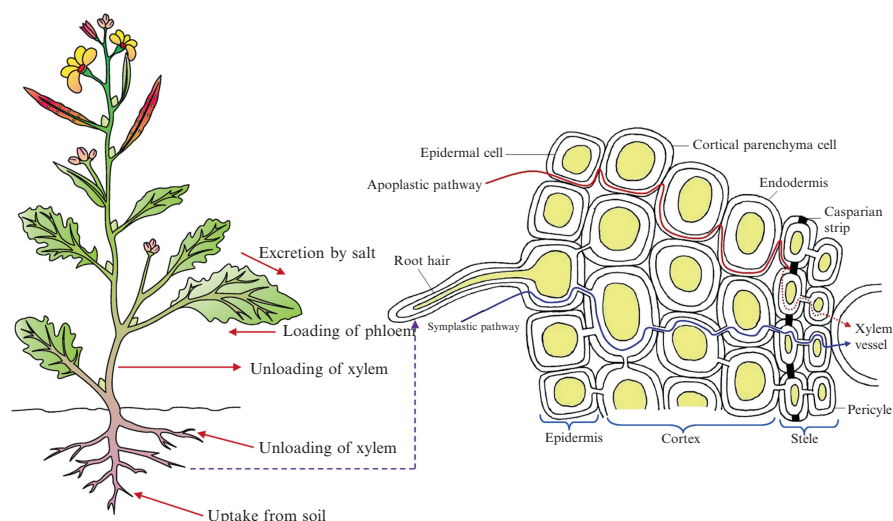
## 2.3 Nature and Mechanisms of Salt Stress

Most crops do not grow well on soils that contain salts. One reason is that salt causes a reduction in rate and amount of water that plant roots can take up from the soil. Also, some salts are toxic to plants when present in high concentration. The highly tolerant crops can withstand a salt concentration of the saturation extract up to 10 g L<sup>-1</sup>. The moderately tolerant crops can withstand salt concentration up to 5 g L<sup>-1</sup>. The limit of the sensitive group is about 2.5 g L<sup>-1</sup> (Brouwer et al. 1985). Some plants are more tolerant to a high salt concentration than others. Some examples are given in the Table 2.4.

Some of the negative effects of salinity have been caused mainly by Na<sup>+</sup> and Cl<sup>-</sup> ions in plants and these ions produce the decisive conditions for plant survival by intercepting different plant mechanisms. Plant roots are generally affected due to Na<sup>+</sup> and Cl<sup>-</sup> along with other cations present in the soils in different concentration (1–150 mM for glycophytes; more for halophytes). However, the uptake of these ions depends on the plant growth stage, genetic characters and environmental factors like temperature, relative humidity and light intensity. Excessive amount of salt in cultivated soils retards the growth, limits economic yield and even lead plants to death. There are some points at which salt transport is regulated. These are: (i) selective uptake from the soil solution, (ii) loading of xylem, (iii) removal of salt from the xylem in the upper part of the plant, (iv) loading of the phloem and (v) excretion through salt glands or bladders (Munns et al. 2002a, b; Fig. 2.2). For a salt tolerant plant growing for some time in a soil solution of 100 mM NaCl, the root concentrations of Na<sup>+</sup> and Cl<sup>-</sup> are typically about 50 mM, the xylem concentration

**Table 2.4** Major crops showing different salt-tolerance levels (Brouwer et al. 1985)

Highly tolerant	Moderately tolerant	Sensitive
<i>Hordeum vulgare</i> (Barley)	<i>Triticum aestivum</i> (Wheat)	<i>Pisum sativum</i> (Pea)
<i>Beta vulgaris</i> (Sugarbeet)	<i>Lycopersicon esculentum</i> (Tomato)	<i>Phaseolus</i> spp. (Beans)
<i>Gossypium</i> spp. (Cotton)	<i>Avena sativa</i> (Oat)	<i>Saccharum officinarum</i> (Sugarcane)
<i>Asparagus</i> spp.	<i>Medicago sativa</i> (Alfalfa)	<i>Trifolium pratense</i> (Red clover)
<i>Spinacia oleracea</i> (Spinach)	<i>Oryza sativa</i> (Rice)	<i>Pyrus communis</i> (Pear)
<i>Phoenix dactylifera</i> (Date palm)	<i>Zea mays</i> (Maize)	<i>Malus domestica</i> (Apple)
	<i>Linum usitatissimum</i> (Flax)	<i>Citrus aurantium</i> (Orange)
	<i>Solanum tuberosum</i> (Potato)	<i>Prunus</i> spp.
	<i>Daucus carota</i> (Carrot)	
	<i>Allium cepa</i> (Onion)	
	<i>Cucumis sativus</i> (Cucumber)	
	<i>Punica granatum</i> (Pomegranate)	
	<i>Ficus carica</i> (Fig)	
	<i>Olea europaea</i> (Olive)	
	<i>Vitis vinifera</i> (Grape)	



**Fig. 2.2** Transport and regulation of salt in soil-plant system

about 5 mM, and the concentration in the oldest leaf as high as 500 mM (Munns 2002a). The toxic ions move into the plant with the water flow. The ions move from soil to the vascular system of the root by symplastic and apoplastic pathways. In symplastic pathway, water enters into the roots through plasma membranes of epidermis and further cell-to-cell movement occurs through plasmodesmata until the xylem becomes saturated. In apoplastic pathway, water enters through intracellular spaces to unload the salt in xylem (Fig. 2.2). Differential osmotic potential is the dynamic force of energy driven pathways, i.e. symplastic, while apoplastic is a non-energy driven pathway. Hence, based on osmotic potential, plant can control the toxic ions like  $\text{Na}^+$  to enter into the cell through energy driven pathway (Garcia-deblas et al. 2003).

## 2.4 Plant Responses to Salt Stress

High salinity causes both hyperionic and hyperosmotic stresses and can lead to plant death (Hasegawa et al. 2000). It is reported that plants growing under saline conditions are affected in three ways: reduced water potential in root zone causing water deficit, phytotoxicity of ions such as  $\text{Na}^+$  and  $\text{Cl}^-$  and nutrient imbalance depressing uptake and transport of nutrients.  $\text{Na}^+$  competes with  $\text{K}^+$  for binding sites essential for cellular functions (Munns 2002a). Excess salt concentration also enhances the osmotic potential of soil matrix which restricts the water uptake by plants. Sodium is the primary toxic ion, because it interferes with  $\text{K}^+$  uptake as well as and disturbs stomatal regulation which ultimately causes water loss and necrosis.



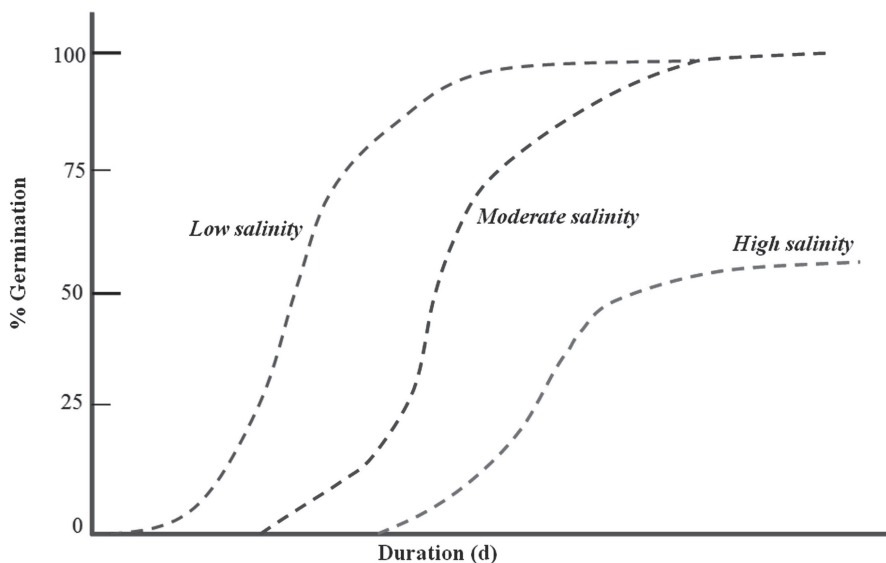
On the other hand,  $\text{Cl}^-$  induces chlorotic toxicity symptoms due to impaired production of chlorophyll (Chl). Although both  $\text{Na}^+$  and  $\text{Cl}^-$  are the major ions which produce many physiological disorders in plants, especially  $\text{Cl}^-$ , which is the most dangerous than  $\text{Na}^+$  (Tavakkoli et al. 2010). In plant cells,  $\text{Cl}^-$  is required for the regulation of some enzyme activities in the cytoplasm. It is also a co-factor in photosynthesis and is involved in turgor and pH regulation. However, it is toxic to plants at high concentrations, with critical levels for toxicity reported to be 4–7  $\text{mg g}^{-1}$  for  $\text{Cl}^-$ -sensitive species and 15–50  $\text{mg g}^{-1}$  for  $\text{Cl}^-$ -tolerant species (Xu et al. 2000; White and Broadley 2001). Higher accumulation of  $\text{Cl}^-$  led to a significant reduction in growth and water use efficiency in plants.

### 2.4.1 Germination

Seed germination is one of the most fundamental and vital phases in the growth cycle of plants that determine plant establishment and the yield of the crops. The available literature revealed the effects of salinity on the seed germination of various crops like *Oryza sativa* (Xu et al. 2011), *Triticum aestivum* (Akbarimoghaddam et al. 2011), *Zea mays* (Carpıcı et al. 2009; Khodarahmpour et al. 2012), *Brassica* spp. (Ibrar et al. 2003; Ulfat et al. 2007), *Glycine max* (Essa 2002), *Vigna* spp., (Jabeen et al. 2003) and *Helianthus annuus* (Mutlu and Buzcuk 2007). It is well established that salt stress has negative correlation with seed germination and vigor (Rehman et al. 2000). Higher level of salt stress inhibits the germination of seeds while lower level of salinity induces a state of dormancy (Khan and Weber 2008). Salinity have many-fold effects on the germination process: it alters the imbibition of water by seeds due to lower osmotic potential of germination media (Khan and Weber 2008), causes toxicity which changes the activity of enzymes of nucleic acid metabolism (Gomes-Filho et al. 2008), alters protein metabolism (Yupsanis et al. 1994; Dantas et al. 2007), disturbs hormonal balance (Khan and Rizvi 1994), and reduces the utilization of seed reserves (Promila and Kumar 2000; Othman et al. 2006). It may also negatively affect the ultrastructure of cell, tissue and organs (Koyro 2002; Rasheed 2009). However, there are various internal (plant) and external (environmental) factors that affect seed germination under saline conditions which includes nature of seed coat, seed dormancy, seed age, seed polymorphism, seedling vigor, temperature, light, water and gasses (Wahid et al. 2011). The germination rates and percentage of germinated seeds at a particular time varies considerably among species and cultivars. Läuchli and Grattan (2007) proposed a generalized relationship between percent germination and time after adding water at different salt levels (Fig. 2.3).

In *Solanum lycopersicum*, high concentrations of salt (150 mM NaCl) in the germination media significantly delays onset and reduced the rate of germination (Foolad and Lin 1997, 1998). Further investigation in *S. lycopersicum*, Kaveh et al. (2011) found a significantly negative correlation between salinity and the rate and





**Fig. 2.3** Relationship between rate of germination and time after sowing at different salinity levels

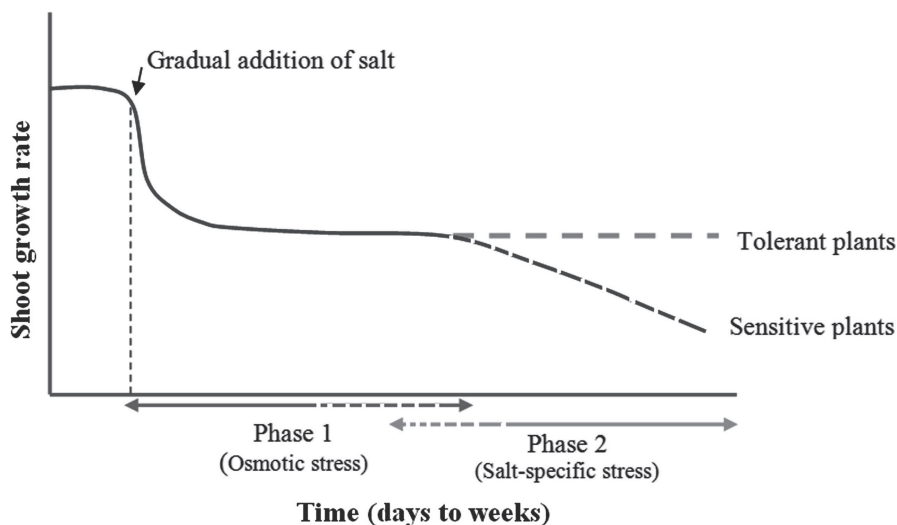
percentage of germination which resulted in delayed germination and reduced germination percentage. Cuartero and Fernandez-Munoz (1999) reported that seeds need 50% more days to germinate at 80 mM NaCl and about 100% more days at 190 mM NaCl than control. Neamatollahi et al. (2009) reported that increasing of NaCl concentration in priming treatments reduced germination percentage due to higher osmotic pressures. Lombardi and Lupi (2006) reported that an increase in NaCl concentration progressively retarded and decreased germination of *Hordeum secalinum*, where 10-day treatment with 400 and 500 mM NaCl caused 40% and 38% reductions in germination rate, respectively. Bordi (2010) reported that the germination percentage in *B. napus* significantly reduced at 150 and 200 mM NaCl. Germination rate also decreased on increasing concentration of salinity levels. Compared with control, germination percentage and germination speed were decreased by 38% and 33%, respectively at 200 mM NaCl. This was caused due to ionic imbalance, osmotic regulation disorders and finally decreased water absorption by seeds. While studying with four rice cultivars, we observed a significant reduction in germination rate when exposed to various concentration of salt (30–150 mM). However, the sensitive cultivars were more prone to germination reduction under salt stress (Hasanuzzaman et al. 2009). In *Vigna radiata*, germination percentage decreased up to 55% when irrigated with 250 mM NaCl (Nahar and Hasanuzzaman 2009). In a recent study, Khodarahmpour et al. (2012) observed drastic reduction in germination rate (32%), length of radicle (80%) and plumule (78%), seedling length (78%) and seed vigor (95%) in *Zea mays* seeds exposed to 240 mM NaCl.

**Table 2.5** Time-dependent effect of salinity on plant growth

Time scale	Causes	Effects
Second to minutes	Water stress	<i>Morphological:</i> Immediate reduction in root and leaf elongation rate which is sometimes partially recoverable. <i>Cellular:</i> Shrinkage of cell volume followed by restoration due to regaining turgor
Hours	Water stress, $\text{Ca}^{2+}$ deficiency	<i>Morphological:</i> Permanent reduction in root and leaf elongation <i>Cellular:</i> Changes rheological behavior of cell wall
Days	Water stress, $\text{Ca}^{2+}$ deficiency	<i>Morphological:</i> Reduction in leaf emergence, increase in root: shoot ratio <i>Cellular:</i> Inhibition of cell development
Weeks	Water stress, ion toxicity	<i>Morphological:</i> Reduced branches/tiller formation, death of older leaves <i>Cellular:</i> Alteration of apical development, excessive accumulation of $\text{Na}^+$ and $\text{Cl}^-$
Months	Water stress, ion toxicity	<i>Morphological:</i> Alteration in flowering time and reduced seed production. Immature death of plants <i>Cellular:</i> Alteration in the development of reproductive organs, Reduction of assimilate production

## 2.4.2 Growth

One of the initial effects of salt stress on plant is the reduction of growth rate. Salinity can affect growth of plant in various ways. First, the presence of salt in the soil reduces the water uptake capacity of the plant, and this causes quick reduction in the growth rate. This first phase of the growth response is due to the osmotic effect of the soil solution containing salt, and produces a package of effects similar to water stress (Munns 2002b). The mechanisms by which salinity affects growth of a plant depend on the time scale over which the plant is exposed to salt (Table 2.5). Munns (2002b) summarized the sequential events in a plant grown in saline environment. He stated that “In the first few seconds or minutes, water is lost from cells and shrunk. Over hours, cells recover their original volume but the elongation rates are still reduced which led to lower growth rates of leaf and root. Over days, cell division rates are also affected, and contribute to lower rates of leaf and root growth. Over weeks, changes in vegetative development and over months changes in reproductive development can be seen”. Later on, Munns (2005) developed the ‘two-phase growth response to salinity’ for better understanding the temporal differences in the responses of plants to salinity (Fig. 2.4). The first phase of growth reduction is a quicker process which is due to osmotic effect. The second phase, on the other hand, is much slower process which is due to the salt accumulation in leaves, leading to salt toxicity in the plants. The later one may results in death of



**Fig. 2.4** Overview of the two-phase growth response to salinity for plant differing in salt sensitivity

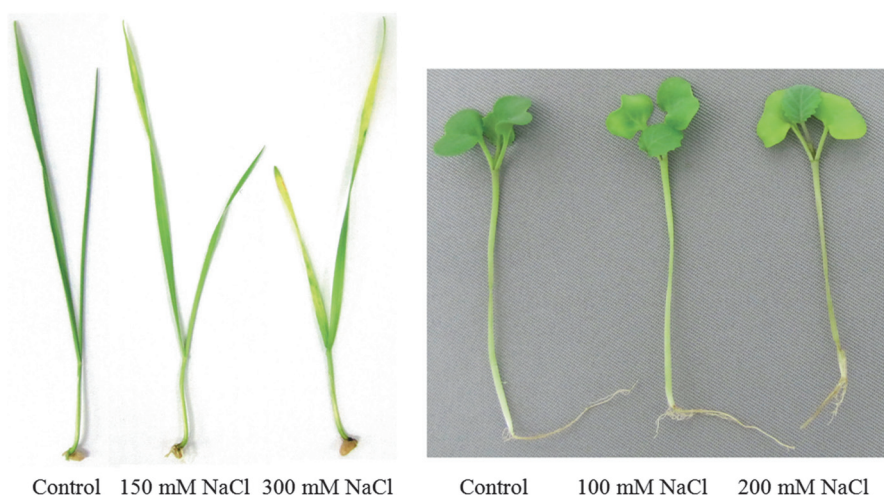
leaves and reduce the total photosynthetic leaf area which reduce the supply of photosynthate in plants and ultimately affect the yield. With annual species, the timescale is day or week, depending on species and salinity level. With perennial species, the timescale is months or year. During phase 1, growth of both genotypes is reduced due to the osmotic effect of the saline solution adjacent to roots. During phase 2, leaves of more sensitive genotype are died and the photosynthetic capacity of the plant is greatly reduced which imposes an additional effect on growth. Upon addition of salt at one step, the growth rate plummets to zero or below and takes 1–24 h to regain the new steady rate, depending on the extent of the osmotic shock (Munns 2002a).

In plants, where  $\text{Na}^+$  and  $\text{Cl}^-$  build up in the transpiring leaves over a long period of time, resulting in high salt concentration and leaf death. Leaf injury and death are attributed to the high salt load in the leaf that exceeds the capacity of salt compartmentation in the vacuoles, causing salt to build up in the cytoplasm to toxic levels (Munns 2002a, 2005; Munns et al. 2006). There are abundant literature indicating that plants are particularly susceptible to salinity during the seedling and early vegetative growth stage. In our study, we observed a remarkable reduction in plant height and tiller number and leaf area index in *O. sativa* plants grown in saline soil (Hasanuzzaman et al. 2009). Under saline condition, some crops are most sensitive during vegetative and early reproductive stages, less sensitive during flowering and least sensitive during the seed filling stage. In all these studies, seed weight is the yield component of interest but similar conclusions regarding growth stage sensitivity were obtained with both determinate crops (the grain crops) and indeterminate (cowpea) crops (Läuchli and Grattan 2007). Khatun and Flowers (1995) studied the

effect of salinity on sterility and seed set in *O. sativa*. Salinity increased the number of sterile florets and viability of pollen, becoming more pronounced with increased salinity. Seed set was reduced by 38% when female plants were grown in as low as 10 mM NaCl. In *Suaeda salsa*, plant height, number of branches, length of branches and diameter of shoot were significantly affected by salt stress which was due to the increased content of Na<sup>+</sup> and Cl<sup>-</sup> (Guan et al. 2011). While studying with *G. max*, Dolatabadian et al. (2011) observed that salinity stress significantly decreased shoot and root weight, total biomass, plant height and leaf number. However, leaf area was not affected by salinity stress.

### 2.4.3 Photosynthesis

The reduction in photosynthetic rates in plants under salt stress is mainly due to the reduction in water potential. Photosynthesis is also inhibited when high concentrations of Na<sup>+</sup> and/or Cl<sup>-</sup> are accumulated in chloroplasts. As photosynthetic electron transport is relatively insensitive to salts, either carbon metabolism or photophosphorylation may be affected due to salt stress (Sudhir and Murthy 2004). A positive correlation between salt stress induced photosynthetic rate and yield has been obtained in different crops (Pettigrew and Meredith 1994; Sudhir and Murthy 2004). Fisarakis et al. (2001) reported a positive growth inhibition caused by salinity associated with a marked inhibition of photosynthesis. However, there are many reports showing no or little relationship between growth and photosynthetic capacity (Rogers and Noble 1992; Hawkins and Lewis 1993). In fact, the effect of salinity on photosynthetic rate depends on salt concentration as well as plant species or genotypes. There is evidence that at low salt concentration salinity sometimes stimulate photosynthesis. For instance, in *Bruguiera parviflora*, Parida et al. (2004) observed that rate of photosynthesis increased at low salinity while decreased at high salinity, whereas stomatal conductance remained unchanged at low salinity and decreased at high salinity. There are some other factors that reduced photosynthetic rates under salt stress are: enhanced senescence, changes in enzyme activity, induced by alterations in cytoplasmic structure and negative feedback by reduced sink activity (Iyengar and Reddy 1996). The reduction in stomatal conductance which results in restricting the availability of CO<sub>2</sub> for carboxylation reactions is also a factor that reduces photosynthesis under stress (Brugnoli and Björkman 1992). It was reported that stomatal closure minimizes loss of water through transpiration and this affects light-harvesting and energy-conversion systems thus leading to alteration in chloroplast activity (Iyengar and Reddy 1996). Higher stomatal conductance in plants is known to increase CO<sub>2</sub> diffusion into the leaves and thereby favor higher photosynthetic rates. One of the most notable effects of salt stress is the alteration of photosynthetic pigment biosynthesis (Maxwell and Johnson 2000). The decrease in Chl content under salt stress is a commonly reported phenomenon and in various studies and the Chl concentration were used as a sensitive indicator of the cellular metabolic state (Chutipaijit et al. 2011). In *Oryza sativa* leaves, the reduction of



**Fig. 2.5** Salt-induced chlorosis in wheat and rapeseed leaves. Hydropinically grown wheat (6-day-old) and rapeseed (12-day-old) seedlings were exposed to salt stress for 4 days and 2 days, respectively

Chl *a* and *b* contents of leaves was observed after NaCl treatment (200 mM NaCl, 14 days) where reduction of the Chl *b* content of leaves (41%) was affected more than the Chl *a* content (33%) (Amirjani 2011). In another study, *Oryza sativa* exposed to 100 mM NaCl showed 30%, 45% and 36% reduction in Chl *a*, Chl *b* and carotenoids (Car) contents as compared to control (Chutipaijit et al. 2011). Saha et al. (2010) observed a linear decrease in the levels of total Chl, Chl *a*, Chl *b*, Car and xanthophylls as well as the intensity of Chl fluorescence in *Vigna radiata* under increasing concentrations of NaCl treatments. Compared to control, the pigment contents decreased on an average, by 31% for total Chl, 22% for Chl *a*, 45% for Chl *b*, 14% for carotene and 19% for xanthophylls (Saha et al. 2010). Associated with the decline in pigment levels, there was an average 16% loss of the intensity of Chl fluorescence as well. In our recent study, we observed a higher chlorosis in wheat and rapeseed leaves when subjected to salt stress (Fig. 2.5).

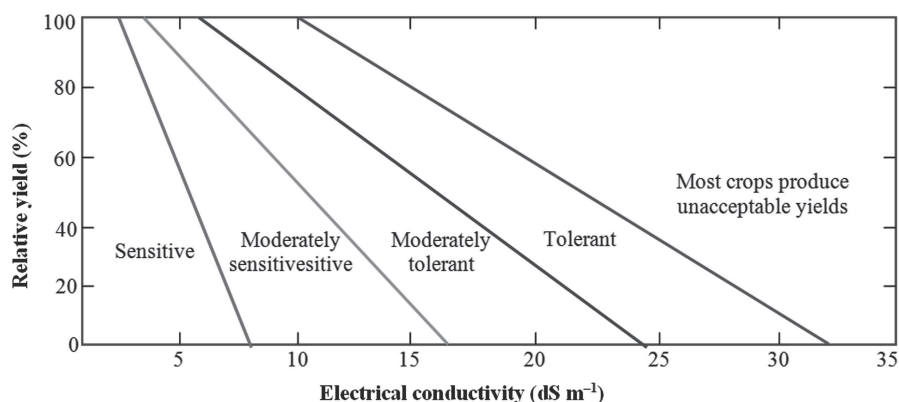
#### 2.4.4 Water Relation

According to Romero-Aranda et al. (2001) increase of salt in the root medium can lead to a decrease in leaf water potential and, hence, may affect many plant processes. Osmotic effects of salt on plants are the result of lowering of the soil water potential due to increase in solute concentration in the root zone. At very low soil water potentials, this condition interferes with plant's ability to extract water from the soil and maintain turgor. However, at low or moderate salt concentration (higher

soil water potential), plants adjust osmotically (accumulate solutes) and maintain a potential gradient for the influx of water. Salt treatment caused a significant decrease in relative water content (RWC) in sugar beet varieties (Ghoulam et al. 2002). According to Katerji et al. (1997), a decrease in RWC indicates a loss of turgor that results in limited water availability for cell extension processes. Steudle (2000) reported that in transpiring plants, water is thought to come from the soil to the root xylem through apoplastic pathway due to hydrostatic pressure gradient. However, under salt stressed condition, this situation changes because of the restricted transpiration. Under these situations, more of water follows cell-to-cell path, flowing across membranes of living cells (Vysotskaya et al. 2010).

### 2.4.5 Nutrient Imbalance

It is well-established that crop performance may be adversely affected by salinity-induced nutritional disorders. However, the relations between salinity and mineral nutrition of crops are very complex (Grattan and Grieve 1999). The nutritional disorders may result from the effect of salinity on nutrient availability, competitive uptake, transport or distribution within the plant. Numerous reports indicated that salinity reduces nutrient uptake and accumulation of nutrients into the plants (Rogers et al. 2003; Hu and Schmidhalter 2005). However, very few evidences exist that addition of nutrients at levels above those considered optimal in non-saline environments, improves crop yield (Grattan and Grieve 1999). In fact, these processes may occur simultaneously and whether they affect the crop yield or quality depends on the toxic level, composition of salts, the crop species and surrounding environment (Grattan and Grieve 1999). Numerous plant studies have demonstrated that salinity could reduce N accumulation in plants. Decreased N uptake under saline conditions occurs due to interaction between  $\text{Na}^+$  and  $\text{NH}_4^+$  and/or between  $\text{Cl}^-$  and  $\text{NO}_3^-$  that ultimately reduce the growth and yield of the crop (Rozeff 1995). This reduction in  $\text{NO}_3^-$  uptake is associated with  $\text{Cl}^-$  antagonism (Bar et al. 1997) or reduced water uptake under saline conditions (Lea-Cox and Syvertsen 1993). The availability of P was reduced in saline soils due to (a) ionic strength effects that reduced the activity of  $\text{PO}_4^{3-}$ , (b) phosphate concentrations in soil solution was tightly controlled by sorption processes and (c) low solubility of Ca-P minerals. Hence, it is noteworthy that phosphate concentration in field grown agronomic crops decreased as salinity increased (Qadir and Schubert 2002). Different plant studies indicated that high level of external  $\text{Na}^+$  caused a decrease in both  $\text{K}^+$  and  $\text{Ca}^{2+}$  concentrations in plant tissues of many plant species (Hu and Schmidhalter 1997, 2005; Asch et al. 2000). This reduction in  $\text{K}^+$  concentration in plant tissue might be due to the antagonism of  $\text{Na}^+$  and  $\text{K}^+$  at uptake sites in the roots, the influence of  $\text{Na}^+$  on the  $\text{K}^+$  transport into xylem or the inhibition of uptake processes (Suhayda et al. 1990). In another study, Hu and Schmidhalter (1997) also stated that  $\text{Mg}^{2+}$  concentration decreased due to salinity in *T. aestivum* leaves.



**Fig. 2.6** Relative yield in response to different salinity levels and varying degree of salt tolerance (Mass 1986)

The availability of micronutrients in saline soils is dependent on the solubility of micronutrients, the pH of soil solution, redox potential of the soil solution and the nature of binding sites on the organic and inorganic particle surfaces. In addition, salinity can differently affect the micronutrient concentrations in plants depending upon crop species and salinity levels (Oertli 1991). Micronutrient deficiencies are very common under salt stress because of high pH (Zhu et al. 2004).

### 2.4.6 Yield

The above mentioned effects of salt stress on plants ultimately lead to reduction of yield of crop which is most countable effect of salt stress in agriculture. Except some halophytes, yield of most of the crops reduced greatly due to salt stress. Tolerance and yield stability are multigenic traits that are complicated to establish in crops since salt stress may be imposed continuously or intermittently, or become gradually more severe and at any stage during development (Yokoi et al. 2002). Crop species have exhibited substantial differences in salt tolerance based on their relative yields. Relative yield often exhibits a linear decrease after a threshold salinity has been reached (Fig. 2.6), and salt tolerance has been defined in terms of two parameters: the threshold electrical conductivity and the percent decrease in relative yield per unit of electrical conductivity in  $\text{dS m}^{-1}$  above the threshold. It was observed that relative yield varied greatly depending on the salinity levels and the degree of tolerance (Mass 1986). Different yield components of *V. radiata* were significantly affected by salinity stress as reported by Nahar and Hasanuzzaman (2009). Number of pods per plant, seeds per pod and seed weight were negatively correlated with salinity levels. The reproductive growth of *V. radiata* was also affected by salinity as the number of pods per plant substantially decreased with increasing salinity levels. An application



of 250 mM NaCl reduced 77%, 73% and 66% yield in *V. radiata* cv. BARI mung-2, BARI mung-5 and BARI mung-6, respectively over control (Nahar and Hasanuzzaman 2009). This reduction of yield and its component rated under salt stress condition may also be attributed to low production, expansion, senescence and physiologically less active green foliage (Wahid et al. 1997), thus reduced photosynthetic rate might be a supplementary effect (Seemann and Critchley 1985). In *O. sativa* varieties, grain yield, which is the ultimate product of yield components is greatly influenced by salinity levels. The loss of grain yield due to 150 mM salinity are 50%, 38%, 44% and 36% over control for the cultivars BR11, BRRI dhan41, BRRI dhan44 and BRRI dhan46, respectively (Hasanuzzaman et al. 2009). The severe inhibitory effects of salts on fertility may be due to differential competition in carbohydrate supply between vegetative growth and constrained supply of these to the developing panicles (Murty and Murty 1982). Also reduced viability of pollen under stress condition could result in failure of seed set (Abdullah et al. 2001). Grain yield reduction of rice varieties due to salt stress is also reported earlier by Linghe and Shannon (2000) and Gain et al. (2004). As reported by Greenway and Munns (1980), after some time in 200 mM NaCl, 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. On the other hand, a halophyte such as *Suaeda maritima* might be growing at its optimum rate (Flowers et al. 1986).

### 2.4.7 Salinity Induced Oxidative Stress

Salt stress can lead to stomatal closure, which reduces CO<sub>2</sub> availability in the leaves and inhibits carbon fixation, exposing chloroplasts to excessive excitation energy which in turn increase the generation of reactive oxygen species (ROS) such as superoxide (O<sub>2</sub><sup>•-</sup>), hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), hydroxyl radical (OH•) and singlet oxygen (<sup>1</sup>O<sub>2</sub>) (Parida and Das 2005; Ahmad and Sharma 2008; Ahmad et al. 2010a, 2011). On the other hand, as salt stress is complex and imposes a water deficit because of osmotic effects on a wide variety of metabolic activities (Greenway and Munns 1980; Cheeseman 1988). This water deficit leads to the formation of ROS (Halliwell and Gutteridge 1985; Elstner 1987). ROS are highly reactive and may cause cellular damage through oxidation of lipids, proteins and nucleic acids (Pastori and Foyer 2002; Apel and Hirt 2004; Ahmad et al. 2010a, b). In many plant studies, it was observed that production of ROS is increased under saline conditions (Hasegawa et al. 2000) and ROS-mediated membrane damage has been demonstrated to be a major cause of the cellular toxicity by salinity in different crop plants such as rice, tomato, citrus, pea and mustard (Gueta-Dahan et al. 1997; Dionisio-Sese and Tobita 1998; Mittova et al. 2004; Ahmad et al. 2009, 2010b). Long-term salinity treatments (EC 5.4 and 10.6 dS m<sup>-1</sup>, 60 days) caused significant increase in H<sub>2</sub>O<sub>2</sub> and lipid peroxidation in wheat seedlings, which were higher in salt-sensitive cultivar than salt-

tolerant cultivar (Sairam et al. 2002). In recent study, increased lipid peroxidation and levels of  $H_2O_2$  was observed with increased salinity in *B. napus* (Hasanuzzaman et al. 2011a) and *T. aestivum* (Hasanuzzaman et al. (2011b).

## 2.5 Role of Exogenous Protectants to Mitigate Salt-Induced Damages

Numerous research results have indicated that exogenous application of osmoprotectants, plant hormones, antioxidants, signaling molecules, polyamines and trace elements provided significant protection against salt-induced damages in plants (Table 2.6). These protectants enhanced salt stress tolerance by enhancing their germination, growth, development, photosynthesis, antioxidative capacities and yield.

### 2.5.1 Osmoprotectants

#### 2.5.1.1 Proline

The accumulation of osmolytes such as proline (Pro) is a well-known adaptive mechanism in plants against salt stress conditions. It has also been suggested that Pro accumulation can serve as a selection criterion for the tolerance of most species to stressed conditions (Parida and Das 2005; Ashraf and Foolad 2007; Ahmad et al. 2009). Since the first report on Pro accumulation in wilting perennial rye grass (Kemble and MacPherson 1954), a number of research works has been carried out concerning the role of Pro as a compatible osmolyte and osmoprotectant and its roles in salt stress tolerance. Several studies have attributed an antioxidant feature to Pro, suggesting ROS scavenging activity and Pro acting as a  $^1O_2$  quencher (Smirnoff and Cumbes 1989; Matysik et al. 2002). Working with *Arabidopsis* mutants, Werner and Finkelstein (1995) found that a Pro-deficient mutant, selected for its ability to germinate on saline media, was unable to continue growth on that media because it could not accumulate Pro to the equivalent level of the wild type. Proline also induces the expression of salt-stress-responsive proteins and may improve the plant adaptation to salt-stress (Khedr et al. 2003). They reported that severe salt stress inhibited the activities of antioxidant enzymes catalase (CAT) and peroxidase (POD) in *Pancreaticum maritimum* plants, but the activities of these enzymes were significantly higher in the presence of Pro than in its absence. It was expected that up-regulation of antioxidant system offered by Pro protect plants against NaCl-induced oxidative damage. Hoque et al. (2008) showed that Pro improves salt tolerance in *Nicotiana tabacum* plants by increasing the activity of enzymes involved in the antioxidant defense system. Earlier, it has been reported that Pro protects higher plants against osmotic stresses not only by adjusting osmotic pressure but also by stabilizing many

**Table 2.6** Summary of the protective effects of different exogenous protectants under salt stress

Name of the crop	Salinity dose and duration	Dose of protectant	Protective effects	References
<i>Olea europaea</i> L. cv. Chemlali	100 and 200 mM NaCl, 6 months	25 and 50 mM Pro	Modulated antioxidative enzyme activities Increased photosynthetic activity and plant growth Maintained suitable plant water status	Ahmed et al. (2010)
<i>Nicotiana tabacum</i> BY-2 cells	200 mM, NaCl, 7 days	20 mM Pro	Increased fresh weight Enhanced the activities of POD and CAT	Hoque et al. (2007)
<i>Oryza sativa</i> L. sub sp. indica	150 mM NaCl, 14 days	50 mM GB, 14 days	Increased Chl and Car content Increased WUE	Cha-Um and Kirdmanee (2010)
<i>Nicotiana tabacum</i> BY-2 cells	200 mM, NaCl, 7 days	20 mM GB	Increased seed weight and yield Increased fresh weight	Hoque et al. (2007)
<i>Oryza sativa</i> L. cv. Nipponbare	25 mM NaCl, 12 h	1 and 5 mM Pro and GB	Increased the activity of POD Suppressed Na <sup>+</sup> -enhanced apoplastic flow to reduce Na <sup>+</sup> uptake in rice plants	Sobahan et al. (2009)
<i>Cucumis melo</i> L. cv. Yuhuang and cv. Xuemei	100 mM NaCl, 5 days	0.2 mM Pro	Increased K <sup>+</sup> /Na <sup>+</sup> ratio Increased fresh and dry weights Increased <i>Pn</i> , <i>Fv/Fm</i> , $\Phi$ PSII and Chl content Reduced the O <sub>2</sub> <sup>-</sup> level and the H <sub>2</sub> O <sub>2</sub> content	Yan et al. (2011)
<i>Oryza sativa</i> L. cv. KDML105	100 mM NaCl, 6 days	10 mM Pro	Enhanced activities of SOD, POD, APX, CAT and DHAR Increased fresh and dry weight Reduced the Na <sup>+</sup> /K <sup>+</sup> ratio Increased endogenous Pro and transcript levels of P5CS and P5CR Decreased the activity of the antioxidant enzymes and upregulated the transcription of genes encoding several antioxidant enzymes	Nounjan et al. (2012)
<i>Oryza sativa</i> L. cv. Nipponbare	150 mM NaCl, 5 days	5 mM GB	Prevented the salt-induced swelling of thylakoids, disintegration of grana staking and intergranal lamellae and disruption of mitochondria	Rahman et al. (2012)
<i>Oryza sativa</i> L. cv. KDML105	100 mM NaCl, 6 days	10 mM Tre	Increased fresh and dry weight Reduced the Na <sup>+</sup> /K <sup>+</sup> ratio and strongly decreased endogenous Pro	Nounjan et al. (2012)

<i>Zea mays</i> , cv. Giza 2	-0.2 MPa, 14 days	10 mM Tre, presoaking for 8 h	Increased plant height, root and shoot dry weight and leaf relative water content Increased photosynthetic pigments and nucleic acids content Increased soluble sugars and soluble protein content Increased germination percentage, seed vigor index and growth parameters	Zeid (2009)
<i>Medicago sativa</i>	NaCl 15 dS m <sup>-1</sup> , 7 days	0.5 mM SA, 6 h (Pretreatment)	Decreased electrolyte leakage Improved plant growth Decreased electrolyte leakage Improved photosynthesis and transpiration rate Enhanced activities of CAT, POX and SOD Increased plant height, root length and biomass Decreased Na <sup>+</sup> and Cl <sup>-</sup> content Reduced plant growth Imbalanced antioxidant metabolism	Torabian (2010)
<i>Brassica juncea</i>	NaCl 150 mM, 3 days	10 µM SA spray	Increased plant height, root length and biomass Decreased Na <sup>+</sup> and Cl <sup>-</sup> content Reduced plant growth Imbalanced antioxidant metabolism	Yusuf et al. (2012)
<i>Viola odorata</i> L.	NaCl 50 mM, 120 days	SA at 30 mg L <sup>-1</sup> , 120 days	Increased plant height, root length and biomass Decreased Na <sup>+</sup> and Cl <sup>-</sup> content Reduced plant growth Imbalanced antioxidant metabolism	Hussain et al. (2011a)
<i>Pisum sativum</i> cv. Lincoln	70 mM NaCl, 25 days	SA 25–100 µM, 7 days × 2 spray	Increased plant height, root length and biomass Decreased Na <sup>+</sup> and Cl <sup>-</sup> content Reduced plant growth Imbalanced antioxidant metabolism	Barba-Espín et al. (2011)
<i>Capsicum annuum</i> cv. Beldi	4 g L <sup>-1</sup> NaCl, 28 days	0.5 mg L <sup>-1</sup> EBR, 28 days	Increased plant height, root length and biomass Decreased electrolyte leakage Improved seed germination	Houimli et al. (2010)
<i>Cucumis sativus</i> L. cv. Zhongnong 8	250 mM NaCl, 48 h	5 µM EBR, 48 h	Increased plant height, root length and biomass Decreased electrolyte leakage Improved seed germination	Wang et al. (2011a)
<i>Zea mays</i> L. cv. Partap-1	25, 50 and 75 mM NaCl, 30 days	10 <sup>-8</sup> , 10 <sup>-6</sup> and 10 <sup>-4</sup> mM HBR, 12 h seed soaking	Enhanced antioxidant enzymes' activities and increased protein content Decreased lipid peroxidation	Arora et al. (2008)
<i>Vigna sinensis</i>	25, 50, 100, and 150 mM, 45 days	0.05 ppm brassinolide (2 sprays)	Increased fresh weight, dry weight and length of root and shoot Increased antioxidant enzymes; activities Decreased lipid peroxidation	El-Mashad and Mohamed (2012)
<i>Capsicum annuum</i> L. cv. Beldi	70 mM NaCl, 21 days	10 µM EBR, 21 days	Increased relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) Increased photosynthesis, stomatal conductance Increased WUE	Samira et al. (2012)
				(continued)

(continued)



<i>Glycine max</i>	60 mM NaCl, 2 weeks	20 and 30 $\mu$ M MeJA, 24 h	Increased plant growth Increased Chl content, leaf photosynthetic rate, leaf transpiration rate and Pro content Increased ABA levels Increased survival rate of seedlings Decreased lipid peroxidation	Yoon et al. (2009)
<i>Lycopersicon esculentum</i> Mill. cv. MS2	300 mM NaCl, 9 h	0.5 mM AsA, 24 h		Shalata and Neumann (2001)
<i>Cicer arietinum</i> L.	20 and 40 mM NaCl, 6 weeks	4 mM AsA	Increased the contents of Chl <i>a</i> and Chl stability index (CSI %)	Beltagi (2008)
<i>Triticum durum</i> Desf. var. Waha	150 mM NaCl, 2 weeks	0.7 mM AsA	Increased leaf area Improved Chl and Car contents and enhanced Pro accumulation Decreased H <sub>2</sub> O <sub>2</sub> content Protected the photosynthetic machinery	Azzedine et al. (2011)
<i>Triticum aestivum</i> L. cv. S-24 and MH-97	100 mM NaCl, 4 weeks	50, 100 mg L <sup>-1</sup> AsA (spray)		Khan and Weber (2008)
<i>Glycine max</i> L. cv. SHAR and DPX	12.5 and 50 mM NaCl, 10 days	400 mg L <sup>-1</sup> , 4 h	Increased growth Enhanced antioxidant activities	Dehghan et al. (2011)
<i>Saccharum</i> sp. cv. HSF 240	100, 120 and 140 mM NaCl, 30 days	0.5 mM AsA, 24 h	Increased root growth Increased activities of antioxidant enzymes Increased soluble protein contents Increased growth Increased photosynthetic pigments Enhanced antioxidant enzymes' activities	Munir and Aftab (2011)
<i>Brassica napus</i> L. cv. Serw and cv. Pactol	100 mM and 200 mM NaCl, 3 weeks	100 mg L <sup>-1</sup> GSH, 24 h		Kattab (2007)
<i>Tagetes erecta</i> L.	1,500 ppm NaCl	100 and 200 ppm GSH	Increased plant height, no. of branches, fresh and dry weight of herb and flowers, no. of flowers Increased total carbohydrates(%), total phenols and zathaphylls pigment content Increased mineral ions percentage	Rawia et al. (2011)

(continued)

Table 2.6 (continued)

Name of the crop	Salinity dose and duration	Dose of protectant	Protective effects	References
<i>Allium cepa</i> L., Giza 6	150 mM NaCl, 3 h	0.5 mM GSH, 2 h	Ameliorated NaCl-induced plasma membrane changes and maintained its permeability and cell viability	Salama and Al-Mutawa (2009)
<i>Triticum aestivum</i>	6 and 9 dS m <sup>-1</sup> , 30, 60 and 90 days	100 mg L <sup>-1</sup> GSH, 6 h	Increased growth and yield Improved endogenous antioxidant content	Sakr and El-Metwally (2009)
<i>Helianthus annuus</i> L. cv. Hysun 336 and Euroflor	1.56, 4.68 and 7.83 dS m <sup>-1</sup>	25 and 50 mg L <sup>-1</sup> $\alpha$ -Tocopherol, 12 h	Enhanced antioxidant enzymes' activities Improved mineral nutrient uptake	Rady et al. (2011)
<i>Triticum aestivum</i> L. cv. Giza 168	0.12, 0.35 and 0.70% NaCl, 65 days	$\alpha$ -Tocopherol 100 mg L <sup>-1</sup> (spray)	Decreased the Na <sup>+</sup> and Cl <sup>-</sup> content Increased the K, Ca and Mg content. Increased antioxidant enzymes' activities Decreased the levels of H <sub>2</sub> O <sub>2</sub> and lipid peroxidation Increased seed germination Enhanced seed respiration rate and ATP synthesis	Farouk (2011)
<i>Triticum aestivum</i> L. cv. Huaimai 17	300 mM NaCl, 1–5 days	100 $\mu$ M SNP, 20 h		Zheng et al. (2009)
<i>Cucumis sativus</i> L. cv. Jinchun 2	50 mM NaCl, 8 days	100 $\mu$ M SNP, 8 days	Increased seedling growth, photosynthetic pigment content, Pro accumulation, net photosynthetic rate, <i>gs</i> and Tr	Fan et al. (2007)
<i>Cucumis sativus</i> L. cv. Jinchun 2	50 mM NaCl, 8 days	100 $\mu$ M SNP, 8 days	Increased growth and dry matter partitioning Increased PAs biosynthesis	Fan et al. (2010)
<i>Cicer arietinum</i> L. cv HC-3	25 mM NaCl, 2, 4 and 6 days	0.2 and 1 mM SNP, 2, 4 and 6 days	Increased RWC Decreased relative membrane injury	Sheokand et al. (2010)
<i>Lycopersicon esculentum</i> Mill. cv. Hufan1480 and Hufan2496	100 mM, 8 days	100 $\mu$ M SNP, 8 days	Increased plant growth and biomass accumulation	Wu et al. (2011)



<i>Oryza sativa</i> L.	80 mM NaCl, 5 days	100 and 200 $\mu$ M SNP, 16 h	Increased seed germination	Habib et al. (2010)
<i>Triticum aestivum</i> L. cv. Pradip	150, and 300 mM NaCl, 4 days	1 mM SNP, 1 days	Increased the content of non-enzymatic antioxidant Enhanced the activities of antioxidant enzymes	Hasanuzzaman et al. (2011b)
<i>Triticum aestivum</i> L. cv. MH-97	150 mM NaCl, variable time	1, 40, 80 and 120 mM $H_2O_2$ , 8 h	Decreased lipid peroxidation Improved photosynthetic capacity	Wahid et al. (2007)
<i>Hordeum vulgare</i> L. cv. Alfa	150 mM NaCl, 4 and 7 days	1 and 5 $\mu$ M $H_2O_2$ , 2 days	Increased antioxidant defense Greater tissue $K^+$ , $Ca^{2+}$ , $NO_3^-$ - $PO_4^{3-}$ levels and improved $K^+ : Na^+$ ratio	Fedina et al. (2009)
<i>Capsicum annuum</i> L. cv. California Wonder	NaCl, 200 mM, 10 days	1.5 mM $H_2O_2$ , 24 h	Improved $CO_2$ fixation Enhanced antioxidant defense Increased seed germination Accelerated flowering and increased fruit yield	Yadav et al. (2011)
<i>Oryza sativa</i> L. cv. IKP and Pokkali	50 and 100 mM, 5 days	1 mM Put, 5 days	Reduces $Na^+$ accumulation Increased PA content	Quinet et al. (2010)
<i>Punica granatum</i> L. cv. Rabbab	40, 80 and 120 mM NaCl, 72 h	1 and 2 mM Put and Spd	Decreased Na and Cl content Increased Pro content	Amri et al. (2011)
<i>Citrus karna</i> Raf.	3.0 dS $m^{-1}$ , 90 days	50 mg $L^{-1}$ Put	Reduced the membrane injury index Increased RWC, photosynthetic rate, and pigments content Improved the activities of SOD and POD Increased Pro content	Sharma et al. (2011)
<i>Oryza sativa</i> L. cv. Pokkali and KDM105	150 mM NaCl, 7 days	1 mM Spd, 24 h	Improved growth Increased membrane stabilization Efficient scavenging of free radicals and decreased MDA	Saleethong et al. (2011)
<i>Cucumis sativus</i> L. cv. Changchun mici and Jinchun No. 2	50 mM NaCl, 7 days	0.1 mM Spd, 7 days	Maintained $K^+ / Na^+$ status Reduced induced membrane damage Increased growth and photosynthesis Increase in PA and Pro contents Up-regulated antioxidant enzyme activities	Duan et al. (2008)

(continued)

**Table 2.6** (continued)

Name of the crop	Salinity dose and duration	Dose of protectant	Protective effects	References
<i>Sorghum bicolor</i> (L.) Moench	180 mM NaCl, 7 days	0.25 mM Spm	Increased growth	Chai et al. (2010)
<i>Oryza sativa</i> L. cvs. M-1-48, Nonabokra and Gobindobhog	200 mM NaCl, 15 days	1 mM Spd or 1 mM Spm, 15 days	Increased antioxidant capacity Increased Chl content Decreased Na <sup>+</sup> content Decreased MDA and H <sub>2</sub> O <sub>2</sub> levels Increased antioxidant metabolism	Roychoudhury et al. (2011)
<i>Cucumis sativus</i> L. cv. Polan	50 mM NaCl, 14 days	5, 10, or 20 $\mu$ M Na <sub>2</sub> SeO <sub>4</sub> , 14 days	Improved the growth rate, photosynthetic pigments and Pro contents Decreased Cl <sup>-</sup> ions Enhanced antioxidative capacity	Hawrylak-Nowak (2009)
<i>Cucumis sativus</i>	2,000 ppm NaCl, 7 days	1 ppm Se, 14 days	Increased activities of POD, CAT, SOD, APX and PAL Reduction in electrolyte leakage and MDA content	Walaa et al. (2010)
<i>Brassica napus</i> L. cv. BINA Sharisha 3	100 and 200 mM NaCl	25 $\mu$ M Na <sub>2</sub> SeO <sub>4</sub> , 48 h	Improved antioxidative capacity Decreased MDA and H <sub>2</sub> O <sub>2</sub> levels Decreased chlorosis	Hasanuzzaman et al. (2011a)
<i>Brassica napus</i> L. cv. BINA Sharisha 3	100 and 200 mM NaCl, 48 h	1 mM SiO <sub>2</sub> , 48 h	Enhanced antioxidative defense Decreased MDA and H <sub>2</sub> O <sub>2</sub> levels	Hasanuzzaman and Fujita (2011b)
<i>Brassica napus</i> L. cv. Hayola	150 mM NaCl, 25 days	2 mM Na <sub>2</sub> SiO <sub>3</sub> , 25 days	Increased the ROS scavenging capacity Decreased tissue Na <sup>+</sup> contents Maintained the membrane integrity of root cells	Hashemi et al. (2010)

<i>Zea mays</i>	120 mM NaCl, 28 days	0.4 -3.2 mM Si(OH) <sub>4</sub> , 28 days	Increased growth Increased CO <sub>2</sub> assimilation rate (A), gs, Tr, and leaf sub-stomatal CO <sub>2</sub> concentration Increased activities of antioxidant enzymes	Parveen and Ashraf (2010) Wang et al. (2011b)
<i>Medicago sativa</i> L. cv. Zhongmu No. 1 and Defor	120 mM NaCl, 15 days	1 mM K <sub>2</sub> SiO <sub>3</sub> , 15 days		
<i>Glycine max</i> L. cv. Taekwangkong	80 mM NaCl, 14 days	2.5 mM Na <sub>2</sub> SiO <sub>3</sub> , 14 days	Increased plant growth Improved Chl content Improved growth Decreased Na <sup>+</sup> and Na <sup>+</sup> :K <sup>+</sup> ratio	Lee et al. (2010) Tahir et al. (2012)
<i>Triticum aestivum</i> cv. SARC-3) and Auqab 2000	150 mM NaCl, 10 days	2 mM Si, 12 days		

functional units such as complex II electron transport, membranes, and proteins and enzymes such as RuBisCo (Hamilton and Heckathorn 2001). Proline perform these functions by protecting the photosynthetic apparatus (Ashraf et al. 2008), by functioning as an oxygen radical scavenger (Heuer 2003), and by displaying an antioxidant activity (Okuma et al. 2004). While studying with olive trees, Ahmed et al. (2010) observed that Pro supplements seemed to improve salt tolerance in olive tree by modulating some antioxidative enzyme activities, photosynthetic activity, and thus maintained better plant growth and water status. Moreover, the decrease of soluble sugar content in Pro treated-plants revealed the important osmoprotective effect played by added Pro. The Pro application mitigated the reduction of growth and photosynthetic activity under salt stress in olive trees. The increment rate of leaf RWC in the presence of 25 and 50 mM Pro was 4.45% and 6.67%, respectively, in comparison to values recorded in 100 mM NaCl-treated plants. In 200 mM NaCl plus Pro-treated plants, this increase was 1.14 times for 25 mM Pro and 1.19 times for 50 mM Pro higher than those recorded in severe salt stress treatment (200 mM NaCl). Deivanai et al. (2011) demonstrated that rice seeds pretreated with Pro (1, 5 and 10 mM) and grown at different NaCl concentrations counteracted the adverse effect of salt. Pretreatment of Pro with a concentration of 1 mM was found to be effective and stimulated cellular activities, whereas 10 mM Pro was ineffective in improving plant growth under high level of salt (300 and 400 mM NaCl).

Hoque et al. (2007) examined the growth and activities of antioxidant enzymes in tobacco Bright Yellow-2 (BY-2) culture cells in suspension under salt stress and found that both Pro and betaine mitigated the inhibition of growth of BY-2 cells under salt stress. Salt stress significantly decreased the activities of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) in BY-2 cells. However, exogenous application of Pro or betaine alleviated the reduction in CAT and POD activities but not SOD activity under salt stress. Neither Pro nor betaine directly scavenged  $O_2^{\cdot-}$  or  $H_2O_2$ . They also concluded that the mitigating effect of Pro was more than that of betaine because of its superior ability to increase the activities of antioxidant enzymes. Sobahan et al. (2009) further reported that exogenous Pro and betaine suppressed  $Na^+$ -enhanced apoplastic flow to reduce  $Na^+$  uptake in rice plants. In their study, addition of Pro or betaine to the saline medium suppressed Na-induced trisodium-8-hydroxy-1,3,6-pyrenetrisulphonic acid (an apoplastic tracer) uptake and  $Na^+$  accumulation, while the  $K^+$  content was slightly increased, which led to a high  $K^+/Na^+$  ratio under saline conditions. Lima-Costa et al. (2008) cultured a salt-sensitive *Citrus sinensis* 'Valencia late' cell line which had a lower growth rate and accumulates Pro when exposed to salt (>200 mM NaCl). However, the addition of exogenous Pro to this cell line was evaluated in terms of cell metabolism. Thus, a positive influence on the relieve of salt stress symptoms due to the presence of exogenous Pro 5 mM and 100 mM NaCl was obtained, with increased growth of this salt sensitive citrus cell line. Yan et al. (2011) found that application of exogenous 0.2 mM Pro to salinized nutrient solution alleviated the decrease in fresh and dry weights of *Cucumis melo* seedlings. Exogenous Pro significantly alleviated the decrease of  $Pn$ ,  $Fv/Fm$ ,  $\Phi PSII$  and Chl content under saline conditions. Compared with NaCl alone, exogenous Pro also reduced the  $O_2^{\cdot-}$  level and the  $H_2O_2$

content which was accompanied by the enhanced activities of SOD, POD, APX, CAT and DHAR. In a recent study, Nounjan et al. (2012) observed that salt stress resulted in growth reduction, increase in the  $\text{Na}^+/\text{K}^+$  ratio, increase in Pro level and up-regulation of Pro synthesis genes (pyrroline-5-carboxylatesynthetase, P5CS; pyrroline-5-carboxylate reductase, P5CR) as well as accumulation of  $\text{H}_2\text{O}_2$ , increased activity of antioxidative enzymes (SOD, POX, APX, CAT) and transcript up-regulation of genes encoding antioxidant enzymes (Cu/ZnSOD, MnSOD, CytAPX, CatC) of *O. sativa* seedlings. On the other hand, exogenous Pro supplementation under salt stress condition reduced the  $\text{Na}^+/\text{K}^+$  ratio, further increased the endogenous Pro and transcript levels of P5CS and P5CR, but decreased the activity of the antioxidant enzymes. In addition, the transcription of genes encoding several antioxidant enzymes was upregulated.

### 2.5.1.2 Glycinebetaine

Glycinebetaine (GB) is a small organic metabolite soluble in water and non-toxic at high concentrations which can potentially play a protective role against salt stress (Ashraf and Foolad 2007; Chen and Murata 2008). The major role of GB in plants exposed to salt is probably protecting cells by osmotic adjustment (Gadallah 1999), protein stabilization (RuBisCo) (Mäkelä et al. 2000), photosynthetic apparatus protection (Allakhverdiev et al. 2003; Cha-Um and Kirdmanee 2010), and reduction of ROS (Ashraf and Foolad 2007).

Lutts (2000) suggested that GB may have a positive impact on both absorption and translocation of monovalent cations in salt-stressed rice plants and that its synthesis by transferring gene coding for choline monooxygenase (CMO) may constitute an interesting goal for genetic engineering in this species. From their study, it was observed that the presence of GB in nutrient solution had no deleterious effect on unstressed plants, but it clearly improved surviving percentages and growing abilities of salt-treated plants. The positive effect of exogenous GB was associated with reduced  $\text{Na}^+$  accumulation and with the maintenance of  $\text{K}^+$  concentration in all parts of salinized plants. Rahman et al. (2002) reported the beneficial effect of GB on the ultrastructure of salt-stressed *O. sativa* seedlings. While exposed to 150 mM NaCl, the seedlings ultrastructural damages such as swelling of thylakoids, disintegration of grana staking and intergranal lamellae and disruption of mitochondria have been reported. However, these damages were largely prevented by pretreatment of plants with GB. These effects might be due to the production of many vacuoles in the root cells which acted as store of  $\text{Na}^+$  and prevented its accumulation in the shoots. In their experiment, Cha-Um and Kirdmanee (2010) applied GB as foliar spray in salt-sensitive *O. sativa* plants exposed to 150 mM of NaCl stress. The results showed that GB treated plants maintained water use efficiency (WUE) and pigment stabilization, leading to high photosynthetic performance in Chl *a* fluorescence and  $\text{CO}_2$  assimilation, and increasing plant height under salt stress condition which provided a notion that exogenous application of GB in optimum doses should be used as a short-term technique for the improvement of salt tolerance in *O. sativa*.

### 2.5.1.3 Trehalose

Trehalose (Tre) functions as compatible solute and is upregulated in plants under abiotic stress (Zeid 2009; López-Gómez and Lluch 2012). It plays an osmoprotective role in physiological responses, enhancing the plant's tolerance to abiotic stress. Nounjan et al. (2012) reported that exogenous Tre treatment under salt stress condition reduced the  $\text{Na}^+/\text{K}^+$  ratio and strongly decreased endogenous Pro in *O. sativa* seedlings. Transcription of P5CS and P5CR was enhanced while the activities of SOD and POX were decreased and the activity of APX increased and the transcription of all antioxidant enzyme genes upregulated. However, exogenous Tre did not alleviate growth inhibition during salt stress. Pre-soaking maize seeds with Tre (10 mM) showed better performance under salinity stress condition as reported by Zeid (2009). Trehalose pretreatment alleviated the adverse effects of salinity stress in maize seedlings. Hill-reaction activity, photosynthetic pigments and nucleic acids content increased in response to Tre application. Trehalose treatment also ameliorated salinity stress through stabilization of plasma membranes by decreasing the rate of ion leakage, and increasing the ratio of  $\text{K}^+/\text{Na}^+$  in the leaves of *Z. mays* seedlings.

However, some results indicated that Tre genetically engineered plants exhibit altered morphology, possibly caused by toxicity of high trehalose concentrations, indicating that Tre is a noncompatible solute (Schluepmann et al. 2003; Cortina and Culiánez-Maciá 2005). Thus the role of Tre as compatible solute in plants under abiotic stress is still under discussion. Although transgenic plants with microbial Tre biosynthesis often lead to developmental aberrations, diverse studies have shown that Tre accumulation is involved in protecting plants from stress like salinity (López-Gómez and Lluch 2012). These results are promising for the generation of crops resistant to stress. Further studies are required for better understanding the role of Tre in plant protection.

## 2.5.2 Plant Hormones

### 2.5.2.1 Absciscic Acid

Absciscic acid (ABA) is an important phytohormone that plays an important role in response to various abiotic stresses and stress signaling. ABA also play important roles in many physiological processes like seed dormancy and delays in germination, development of seeds, acceleration of stomatal closure, synthesis of storage proteins and lipids, leaf senescence, etc. (Tuteja 2007). One of the major functions of ABA seems to be the regulation of plant water balance and osmotic stress tolerance. Although the direct relation between stress tolerance and increased levels of ABA does not always exist during the last two decades, it has been well established that ABA is a vital cellular signal that mediates the expression of a number of salt and water deficit-responsive genes. Koornneef et al. (1998) reported several ABA deficient mutants viz. *aba1*, *aba2* and *aba3* in *Arabidopsis*. ABA deficient mutants

for *N. tabacum*, *L. esculentum* and *Z. mays* have also been reported (Swamy and Smith 1999). It was observed that without any stress treatment the growth of these mutants is comparable to wild type plants. However, under salt stress ABA deficient mutants showed poor growth (Xiong et al. 2001).

Upon exposure to salinity, plant shows a proportional increase in ABA concentration which is mostly correlated with water potential of leaf or soil. This suggests that salt-induced endogenous ABA is due to water deficit rather than ionic toxicity (Zhang et al. 2006a). This may not be similar to the prolonged increasing of endogenous ABA levels that can occur in association with slowly increasing salinity stresses in nature or field situations (Etehadnia et al. 2008). Increase of endogenous ABA concentration in leaf tissue for salt stressed crop were reported in many plant studies (Cramer and Quarrie 2002; Kang et al. 2005; Cabot et al. 2009; Atkinson and Urwin 2012; Babu et al. 2012). Jeschke et al. (1997) reported that the increase of ABA concentration in the xylem is correlated with reduced leaf conductance and general inhibition of leaf growth. Salt stress stimulated ABA synthesis in roots and its xylem transport are well correlated to the stomatal reactions. This may be explained by the fact, when roots are directly exposed to salt, ABA in roots stimulates ion accumulation in vacuoles which may be necessary for adaptation to saline conditions (Jeschke et al. 1997). Later, Fricke et al. (2004) observed that ABA induced the increase of xylem water potential as well as water uptake to the plant under saline condition.

While studying with salt sensitive (IR29) and tolerant (IR651) varieties of indica rice (*O. sativa*) to a range of salinity (0 and 100 mM NaCl), Saeedipour (2011) observed that tolerance of IR29 to saline stress was generally improved by ABA treatment and leaf  $\text{Na}^+$  content reduced to their respective control treatment. This ABA effect was evident in IR29 (sensitive) the ability to recover from stress increased up to 7-fold. Independent of the saline treatment, the absolute endogenous leaf ABA content in sensitive variety was significantly more than tolerant one. However, upon stress, the increase in endogenous ABA synthesis was higher in tolerant than in sensitive varieties. On the other hand, using inhibitor of ABA synthesis, the opposite effect was observed in most of the cases. In another experiment, Gurmani et al. (2011) found that the addition of ABA to *O. sativa* cv. IR-6 has a significant role in reducing salinity stress. ABA was found to be effective in reducing  $\text{Na}^+$  and  $\text{Cl}^-$  concentrations and  $\text{Na}^+/\text{K}^+$  ratio, increasing  $\text{K}^+$  and  $\text{Ca}^{2+}$  concentrations, Pro accumulation, soluble sugar content. Compared to NaCl alone, ABA treatment increased grain yield by 21%. Keskin et al. (2010) reported that the *MAPK4*-like, *TIP1* and *GLP1* genes were induced more rapidly in response to ABA treatment in *T. aestivum*.

### 2.5.2.2 Indole Acetic Acid

Although there are very few reports regarding the relationship between auxin level and salt stress in plants as well as the role of auxin in alleviating salt-induced damages. Some research reports indicated that indole acetic acid (IAA) responded



to salinity in crop plants. The differences in IAA content under stress conditions appeared to be similar to those of ABA (Ribaut and Pilet 1991).

A significant decline in the level of IAA in the root system of *T. aestivum* plants under salinity was reported by Sakhabutdinova et al. (2003). Similar reduction of IAA level after NaCl treatment was reported in *O. sativa* (Nilsen and Orcutt 1996) and *L. esculentum* (Dunlap and Binzel 1996). Pre-soaking *T. aestivum* seeds with IAA alleviated the growth inhibiting effect of salt stress (Sastry and Shekhawa 2001; Afzal et al. 2005). There is a report that an increase in IAA contents promotes the formation of an attraction signal in the leaf growth zone in response to salt stress (Akhiyarova et al. 2005). It was reported that germination of wheat seed declined with higher salinity level, while this adverse effect was reversed by treatment of seeds with IAA (Gulnaz et al. 1999). Later, Akbari et al. (2007) showed that application of auxin increased hypocotyls length, seedling fresh and dry weight and hypocotyls dry weight of wheat plants under salinity. In *Z. mays* plants, foliar application of IAA, especially at 2 mM, counteracted some of the salt induced adverse effects by enhancing essential inorganic nutrients as well as by maintaining membrane permeability (Kaya et al. 2009). Exogenous IAA significantly reduced  $\text{Na}^+$  concentration and increased those of  $\text{Ca}^{2+}$  and  $\text{K}^+$ . Application of IAA also increased Chl content, RWC and grain yield while electrolyte leakage and Pro content decreased (Kaya et al. 2009). In contrary, it was observed that when IAA was added with NaCl, the root growth was inhibited (Jemâa et al. 2011).

### 2.5.2.3 Gibberellic Acid

Gibberellic acids (also called Gibberellin  $\text{A}_3$ , GA, and  $\text{GA}_3$ ) are generally involved in growth and development; they control seed germination, leaf expansion, stem elongation and flowering (Magome et al. 2004; Kim and Park 2008). Additionally, GAs interact with other hormones to regulate various metabolic processes in the plants. However, many conflicting theories have been put forward concerning their interactions (Yang et al. 1996; Van Huizen et al. 1997). In order to alleviate deleterious effects of salinity, different types of phytohormones have been used. Among them,  $\text{GA}_3$  have been the main focus of some plant scientists. Innumerable works have confirmed the potential of  $\text{GA}_3$  to synergistically improve crop performance under normal conditions. In recent decades, light has been thrown on the influence of  $\text{GA}_3$  during salt stress (Kaya et al. 2009). Maggio et al. (2010) reported that  $\text{GA}_3$  treatment in *L. esculentum* reduced stomatal resistance and enhanced plant water use at low salinity.  $\text{GA}_3$ -priming-induced increase in *T. aestivum* grain yield was attributed to the  $\text{GA}_3$ -priming-induced modulation of ions uptake and partitioning (within shoots and roots) and hormones homeostasis under saline conditions (Iqbal and Ashraf 2010). Under saline conditions, seed germination has been improved by application of  $\text{GA}_3$  and in this experiment, growth and grain yield of wheat were decreased with increasing salinity levels, but increased relatively by seed treatment with  $\text{GA}_3$  (Kumar and Singh 1996). In addition, GAs interacts with other hormones to regulate various metabolic processes in the plants. In *B. juncea*, the application of

10  $\mu\text{M}$   $\text{GA}_3$  appeared to mitigate the adverse effects of salinity stress on the overall performance and productivity. Application of  $\text{GA}_3$  significantly increased leaf area, dry mass, leaf Chl content, stomatal conductance and photosynthesis rate compared to salt alone (Shah 2007). In another study, application of  $\text{GA}_3$  counteracted the adverse effects of NaCl salinity on relative water content, electrolyte leakage and Chl content (Ahmad et al. 2009).  $\text{GA}_3$  was sufficient to attenuate partially the stimulatory effect of NaCl supply on Pro and GB biosynthesis in *B. juncea* (Ahmad 2010). Application of  $\text{GA}_3$  also reduced lipid peroxidation in the leaves, which was increased during salt stress and thus indicated that application of  $\text{GA}_3$  reduced the harmful effects of salinity and increased resistance to salinity (Ahmad et al. 2009). In sugarcane plantlets, foliar application of  $\text{GA}_3$  (100 ppm) play an important role on imparting salt tolerance in terms of enhancing nutrient uptake, as well as the morphological and physiological aspects. The inhibition of the growth of sugarcane plantlets by salt stress was removed by  $\text{GA}_3$ . Exogenous GA also increased sugar and soluble protein content, while Chl content remained unchanged (Shomeili et al. 2011). The application of  $\text{GA}_3$  reduced the inhibitory effect of NaCl on growth attributes and photosynthetic pigments in *Hibiscus sabdariffa* by inducing the enzyme activity and enhancing RWC and thus  $\text{GA}_3$  helped in the tolerance of plants to salt stress (Ali et al. 2011). Priming of *Beta vulgaris* seeds with  $\text{GA}_3$  increased the final germination percentage and germination rate under saline condition. Priming is also responsible for the alleviation of adverse effect of salt stress on sugar beet in terms of root and shoot length and root and shoot fresh weights of plants. (Jamil and Rha 2007). Hamayun et al. (2010) reported that exogenous  $\text{GA}_3$  also mitigated the adverse effects of salt stress in *Glycine max* by regulating the level of phytohormones, thus aids the plant in resuming its normal growth and development. Phytohormonal analysis of soybean showed that the level of bioactive gibberellins ( $\text{GA}_1$  and  $\text{GA}_4$ ) and jasmonic acid increased in  $\text{GA}_3$  treated plants, while the endogenous ABA and salicylic acid (SA) contents declined under the same treatment (Hamayun et al. 2010). Recently, Iqbal and Ashraf (2010) reported that increased grain yield in *Triticum aestivum* was attributed to the  $\text{GA}_3$ -priming-induced modulation of ions uptake and partitioning (within shoots and roots) and hormones homeostasis under saline conditions. However, the mechanisms by which  $\text{GA}_3$ -priming induce salt tolerance in plants are not yet clear. Salinity perturbs the hormonal balance in plants. The hormonal homeostasis under salt stress therefore might be the possible mechanism of  $\text{GA}_3$ -induced plant salt tolerance. Iqbal and Ashraf (2010) hypothesized that pre-sowing treatment with  $\text{GA}_3$  could modulate growth by interacting with other endogenous plant hormones.

#### 2.5.2.4 Jasmonic Acid

Jasmonic acid (JA) and its methyl esters are ubiquitous in plants and have hormone properties. These are important cellular regulators involved in diverse developmental processes, such as seed germination, root growth, fertility, fruit ripening, senescence and stomatal closure (Wasternack and Hause 2002; Cheong and Choi 2003; Hossain

et al. 2011). Like other phytohormones JA have both synergistic and antagonistic effects. Jasmonate derivatives induce the accumulation of so-called JA-induced-proteins that were found in all plant species tested. However, the role of most of the derivatives of JA is still unclear.

Jasmonates are involved in plant responses to various abiotic stresses and elicit unique responses (Rohwer and Erwin 2008). There are few reports on the role of exogenous JA in plant response to salt stress. It has been reported that jasmonate treatments (or endogenous of these compounds) is accompanied by the synthesis of abundant proteins in response to abiotic stress, called JIPs (Sembdner and Parthier 1993). Pretreatment of *Pisum sativum* seedlings with 10  $\mu\text{M}$  JA counteracted the effect of salt stress by increasing the photosynthesis, RWC and protein content (Fedina and Tsonev 1997). Exogenously supplied JA itself plays the role of a stressor that causes typical stress responses like accumulation of free Pro, high photorespiration, etc. Pretreatment with JA also leads to a decrease of  $\text{Na}^+$  and  $\text{Cl}^-$  accumulation in the shoot. This protection established the involvement of MeJA in osmoregulation or osmoprotection based on increased Pro accumulation and decreased ion accumulation (Fedina and Tsonev 1997). Pedranzani et al. (2003) reported that JA levels in *L. esculentum* cultivars changed in response to salt-stress and JA increase was observed in salt tolerant cultivar from the beginning of salinization, while in salt sensitive cultivar JA level decreased after 24 h of salt treatment. Exogenous JA application after salt treatment may change the balance of endogenous hormones, such as ABA, which provides an important clue for understanding the protection mechanisms against salt stress (Kang et al. 2005). Seo et al. (2005) reported that treatment with JA in the presence of salt stress increased the GAs content. However, endogenous content of bioactive  $\text{GA}_1$  was higher in post-treatment by JA than in pre-treatment by JA. In *G. max*, treatment with exogenous JA mitigated the harmful effect of NaCl (50 mM NaCl). The greatest yield (157% of control) was obtained from soybean plants sprayed with JA (Sheteawi 2007). JA also reduced the salt effects on seed carbohydrates, lipids, proteins, N, P and K. Yoon et al. (2009) observed that pretreatment with MeJA (20 and 30  $\mu\text{M}$ ) counteracted the negative effects of NaCl stress on plant growth, Chl content, leaf photosynthetic rate, leaf transpiration rate, and Pro content of hydroponically grown *G. max* seedlings. Pretreatment with MeJA also significantly increased ABA levels. Kang et al. (2005) reported that post-application with exogenous JA can ameliorate salt-stressed rice seedlings, especially the salt-sensitive rather than the salt-tolerant cultivar. However, there seems to be little information about how salinity affects endogenous JA levels in plants.

#### 2.5.2.5 Salicylic Acid

Salicylic acid (SA) is a common plant-produced phenolic compound and a potential endogenous plant hormone that plays an important role in plant growth and development. The role of SA is intensively studied in plant responses to biotic stress. In recent years the involvement of SA in the response to abiotic stresses has widely

been studied (El Tayeb 2005; Ahmad et al. 2011). However, the actual role of SA in abiotic stresses remains unresolved. Several methods of application (soaking the seeds prior to sowing, adding to the hydroponic solution, irrigating, or spraying with SA solution) have been shown to protect various plant species against abiotic stress by inducing a wide range of processes involved in stress tolerance mechanisms (Horvath et al. 2007).

El Tayeb (2005) found that SA application to barley induced a pre-adaptive response to salt stress, enhanced the synthesis of Chl *a*, Chl *b* and Car, and maintained membrane integrity, leading to improvement of plant growth. SA-pretreated plants exhibited less  $\text{Ca}^{2+}$  and more accumulation of  $\text{K}^{+}$ , and soluble sugars in roots under saline condition (El Tayeb 2005). *Zea mays* treated with SA exhibited increased growth, decreased lipid peroxidation and membrane permeability, which were increased by salt stress (Gunes et al. 2007). In mungbean plants SA alleviates salt-induced decrease in photosynthesis and minimizes the leaf  $\text{Na}^{+}$ ,  $\text{Cl}^{-}$ , and  $\text{H}_2\text{O}_2$  content (Nazar et al. 2011). This was accompanied by increased N and S assimilation through inducing the activity of NR and ATPs. Exogenous SA also improves grain yield under salt stress in *T. aestivum* (Arfan et al. 2007). The application of SA via root drenching protected *Lens esculentum* against NaCl stress and increased photosynthetic rates under salt stress (Stevens et al. 2006; Poór et al. 2011).

It was found that SA treatment caused accumulation of both ABA and IAA in *T. aestivum* seedlings under salinity. However, the SA treatment did not influence on cytokinin content. Thus, protective SA action includes the development of antistress programs and acceleration of normalization of growth processes after removal of stress factors (Sakhabutdinova et al. 2003). Gémes et al. (2011) suggested that, the cross-talk of signaling pathways induced by SA and high salinity may occur at the level of ROS and NO production. They observed that SA-induced generation of  $\text{H}_2\text{O}_2$  and NO are considered to be functional links of cross-tolerance to various stressors. SA-stimulated pre-adaptation state was beneficial in the acclimation to subsequent salt stress in *Solanum lycopersicum* (Gémes et al. 2011). At the whole-plant level, SA-induced massive  $\text{H}_2\text{O}_2$  accumulation only at high concentrations (1–10 mM), which later leads to death of the plant. Torabian (2011) reported that pre-treatment with SA induced adaptive responses in *Medicago sativa* plant under salinity stress and consequently, encouraged protective reactions in biotic membranes which improved the growth of seedlings. SA pre-treatment improved growth and resulted in higher resistance of plants to salinity, so that it increased germination percentage, seed vigor index and growth parameters of the seedlings. Also, salinity intensified electrolyte leakage, while SA decreased it and this decrease was stronger at SA concentration (Torabian 2011).

Erdal et al. (2011) investigated the effects of foliar-application of SA on salt sensitivity of *T. aestivum*. They observed that salt-induced deleterious effect in wheat seedlings were significantly alleviated by the SA treatment. SA can be used as a signal molecule to investigate plant defense to abiotic stress. After the application of SA, increasing tolerance of wheat seedlings to salt stress may be related to increases in antioxidative enzyme activity. Exogenous SA treatment significantly increased the fresh and dry weights in both root and shoots of wheat plants under

salt stress. In parallel to increasing antioxidant activity, SA treatment decreased  $H_2O_2$  content when compared to plants growing under salt stress without SA. In *Brassica juncea*, Yusuf et al. (2012) reported that SA enhanced the level of antioxidant system (SOD, CAT and POX) both under stress and stress-free conditions. However, the influence of SA on antioxidant system was more pronounced under stressful condition, therefore, suggesting that the elevated level of antioxidant system might be responsible for increased tolerance of *B. juncea* plants to NaCl stress.

However, some studies demonstrate that application of SA (0.5 mM) may promote the formation of ROS in the photosynthetic tissues and increase oxidative damage during salt and osmotic stresses. For instance, Barba-Espín et al. (2011) studied the effect of SA treatment on the response of *P. sativum* plants to salinity. NaCl-induced damage to leaves was increased by SA, which was correlated with a reduction in plant growth. The content of AsA and GSH in leaves of salt-treated plants increased in response to SA, although accumulation of the respective DHA and GSSG occurred. An increase in  $H_2O_2$  also occurred in leaves of salt-exposed plants treated with SA. Negative effect of SA in the *P. sativum* plants exposed to NaCl was also correlated with an imbalance in antioxidant metabolism. Generally, deficiency of SA or a very high level of SA increases plant susceptibility to abiotic stresses. The optimal concentration (0.1–0.5 mM for most plants) enhances abiotic stress tolerance.

#### 2.5.2.6 Brassinosteroids

Brassinosteroids (BRs) is the most recent group of phytohormones and is a class of over 40 polyhydroxylated sterol derivatives, ubiquitously distributed in all kinds of plant. Their strong growth-inducing capacity, recognized as early as prior to their identification in 1979, tempted the scientists to visualize the practical importance of this group of phytohormones (Hayat and Ahmad 2011). Recently, the physiological, cellular, and molecular mechanisms by which BRs regulate various aspects of plant development are being discovered (Yang et al. 2011). Although there are different kinds of BR, 24-epibrassinolide (EBR) is one of the most widely used BR. The BRs have a potential application in agriculture to increase yield and to stimulate crop growth under stress (Houimli et al. 2010; El-Mashad and Mohamed 2012; Hayat and Ahmad 2011).

The effect of EBR and 28-homobrassinolide (HBR) on the inhibition of germination and seedling growth of rice (*O. sativa*) induced by salinity stress was studied by Anuradha and Rao (2001). They reported that application of BRs reverse the inhibitory effect on germination and seedling growth. The activation of seedling growth by BRs under salinity stress was associated with enhanced levels of nucleic acids and soluble proteins (Anuradha and Rao 2001). The effect of BR on *H. vulgare* leaf cell ultrastructure was examined under salt stress. Leaf segments were pre-incubated in either BR solution or water and then incubated in 0.5 M NaCl solution in presence or absence of BR. BR had no effect on leaf cell ultrastructure under normal conditions. However, damages imposed by salt stress on nuclei and chloro-

plants were significantly reduced by BR treatment (Krishna 2003). When *Capsicum annuum* seedlings were sprayed with EBR in the presence of NaCl, it significantly ameliorated the adverse effects of salinity by increasing the RWC, photosynthetic pigments and decreasing the electrolyte leakage. Exogenous BR also increased the fresh and dry weight of plant parts under salt stressed condition (Houimli et al. 2010). Another recent study reported the ameliorative effect of EBR and ethylene on germination of *Cucumis sativus* seeds in presence of NaCl (250 mM). The reduction in ethylene evolution from imbibed seeds by salt stress was attenuated by EBR. In maize seedlings, pre-sowing treatments of HBR enhanced the activities of antioxidative enzymes (SOD, GPX, CAT, GR, APX) and minimized the lipid peroxidation thus helps the plants to withstand the oxidative stress induced by salt stress. In *T. aestivum*, exogenous application of EBR increased plant biomass under saline condition, but it had no prominent effect on accumulation of different mineral nutrients (Shahbaz and Ashraf 2007). Foliar application of BRs also increased yield attributes of salt treated *T. aestivum* and significantly overcome the negative effect of salinity on crop productivity and photosynthetic pigments (Eleiwa et al. 2011). Salinity reduced sugar (reducing and non-reducing), total carbohydrate and protein percentage of grains while foliar application with BRs significantly increased gradually all the chemical constituents. Foliar application of BRs also significantly increased the concentration and total uptake of macro and micronutrients (N, P, K, Fe, Mn, Zn and Cu) in straw and grains (Eleiwa and Ibrahim 2011). El-Mashad and Mohamed (2012) also reported that brassinolide enhanced tolerance of *V. sinensis* plants to NaCl. They observed that foliar spray of BR (0.05 ppm) mitigated salt stress by inducing activities of enzymatic and non-enzymatic antioxidants, e.g., SOD, POX, polyphenol oxidase, AsA, tocopherol, and GSH. Recently, Samira et al. (2012) showed that the EBR treated plants had greater relative growth rate compared to untreated plants when exposed to salt stress. Application of EBL increased photosynthesis by increasing stomatal conductance in salt stressed plants and may have contributed to the enhanced growth. The water use efficiency was also improved by the application of EBL.

## 2.5.3 Antioxidants

### 2.5.3.1 Ascorbic Acid

Ascorbate (AsA) or ascorbic acid (Vitamin C) is an important antioxidant in plant tissue which is synthesized in cytosol of higher plants primarily from conversion of D-glucose to AsA. AsA has been shown to have an essential role in several physiological processes in plants, including growth, differentiation, and metabolism. It functions as a reductant for many free radicals, thereby minimizing the damage caused by oxidative stress. Plant with higher amount of AsA content showed better protection against oxidative stress. Ascorbate influences many enzyme activities, minimizing the oxidative damage through synergic function with other antioxidants



(Foyer and Noctor 2005a, b). Ascorbic acid reacts with a range of ROS such as  $^1\text{O}_2$ ,  $\text{O}_2^-$ ,  $\text{HO}\cdot$  and  $\text{H}_2\text{O}_2$ , which is the basis of its antioxidant action (Shigeoka et al. 2002; Foyer 2004). The role of AsA as a cofactor for a range of oxygenase and hydroxylase enzymes is also dependent on its reducing activity (De Tullio 2004). Upon oxidation, by loss of one electron, the monodehydroascorbate (MDHA) radical is formed and this is usually the initial product of AsA oxidation in biological systems (Smirnoff and Pallanca 1996; Noctor and Foyer 1998). AsA can also directly scavenge and regenerate tocopherol from tocopheroxyl radicals, thus providing membrane protection (Li and Jin 2007). AsA also plays a role as a co-factor of violaxanthin de-epoxidase, thus sustaining dissipation of excess excitation energy (Pourcel et al. 2007).

AsA plays an important role in plant stress tolerance. Under stressed condition plants showed different capacity of AsA metabolism which is due to the variation of AsA synthesis and regeneration. Different studies showed that AsA content in leaves of stressed plants tends to increase with increasing levels of salt stress (Mohamed et al. 2010). Agarwal and Shaheen (2007) reported that AsA concentration in leaves of *Momordica charantia* increased under NaCl stress as compared to control. Increase in AsA concentration due to salinity was reported by other researchers (Panda and Upadhyay 2004; Parida et al. 2004).

Exogenous application of AsA influences many enzyme activities and minimizes the damage caused by oxidative processes through a synergic function with other antioxidants (Shalata and Neumann 2001; Athar et al. 2008). This multiplicity of functions has led some researchers to suggest that, in addition to being a powerful antioxidant and redox buffer, AsA may be a signaling molecule involved in the regulation of complex processes such as the senescence of plants and their response to  $\text{O}_3$ , photo-oxidative conditions, or pathogen attack (Pastori et al. 2003). Exogenous application of AsA helps the *L. esculentum* seedling to recover from salt stress (Shalata and Neumann 2001). They observed that the addition of exogenous AsA to the root medium remarkably increased seedling survival and decreases lipid peroxidation. Hamada and Al-Hakimi (2009) found that exogenously applied AsA were generally effective partially or completely countering the inhibitory effects of salt stress on net photosynthetic rate, pigments biosynthesis and membrane integrity by exerting a stimulatory action on these parameters, especially in plants subjected to moderate and low salinity levels. The leakage of  $\text{K}^+$  was also reduced by the application of AsA. Khan et al. (2006) applied AsA as foliar spray (0, 50, 100  $\text{mg L}^{-1}$ ) on *T. aestivum* grown in hydroponics. They observed that foliar spray with AsA improved the growth of non-stressed plants of both cultivars, but did not alleviate the adverse effects of salt stress on plants. However, salt-induced reduction in leaf Chl *a* was improved with AsA application. AsA application enhanced the  $\text{Na}^+$  accumulation in the leaves of salt stressed plants of both cultivars, but it did not change the  $\text{K}^+$  accumulation in the leaves and roots of the salt stressed plants. In vitro experiments were performed by Zeid et al. (2008) in *H. annuus* seedling, to determine responses of *T. aestivum* calli to AsA concentrations (0, 250, 500, 1,000 and 2,000 ppm) under different levels of sea water (0%, 15%, 30% and 45%) and to determine suitable concentrations of AsA to enhance tolerance to salinity. Beltagi



(2008) observed significant synergistic effect between NaCl (40 mM) and AsA treatment, where AsA increased the contents of Chl *a* and Chl stability index (CSI %) in *Cicer arietinum*. Khafagy et al. (2009) observed that pre-soaking of *C. annuum* seeds in AsA partially counteracted the harmful effect of NaCl salinity. Chl *a* and *b* concentrations significantly increased in AsA pre-soaked salt-stressed seedlings compared to the seedlings subjected to salt only.

In a recent study, Azzedine et al. (2011) reported that the application of vitamin C was effective to mitigate the adverse effect of salt stress on plant growth due to increased leaf area, improved Chl and Car contents, enhanced Pro accumulation and decreased H<sub>2</sub>O<sub>2</sub> content. Dehghan et al. (2011) reported that exogenously applied AsA counteracts the adverse effects of salt stress on growth of *Glycine max* seedlings which was cultivar specific. AsA induced enhancement in growth of salt-stressed plants coupled with an increase in CAT, POD and SOD activities. Ascorbic acid pretreatment to in vitro-grown sugarcane plants enhance their salt tolerance by enhancing CAT and POD activities soluble protein contents as well as better root length (Munir and Aftab 2011).

### 2.5.3.2 Glutathione

Glutathione (GSH) is a strong antioxidant which prevents damage to important cellular components caused by ROS (Pompella et al. 2003). It also plays an indirect role in protecting membranes by maintaining  $\alpha$ -tocopherol and zeaxanthin in the reduced state. It can also function directly as a free radical scavenger by reacting with  $^1\text{O}_2$ ,  $\text{O}_2^{\cdot-}$  and  $\text{HO}^{\cdot}$ . GSH protects proteins from denaturation caused by oxidation of protein thiol groups under stress. In addition, GSH is a substrate for glutathione peroxidase (GPX) and glutathione-S-transferases (GST), which are also involved in the removal of ROS (Noctor et al. 2002).

Glutathione accumulates to high concentrations, especially in stress situations. Increase in GSH concentrations during stress offsets stress-initiated oxidation of GSH and causes changes in gene expression directly or through interaction with regulatory proteins and/or transcription factors. This increase is equally important in signal transduction and defense against ROS and is through a multilevel control mechanism, which includes coordinate activation of genes encoding GSH biosynthetic enzymes and GR (Srivalli and Khanna-Chopra 2008). Thus, GSH acts as a redox sensor of environmental cues, and increase in GSH helps plants to tolerate oxidative stress. Likewise, GSH also plays a protective role in salt tolerance by maintaining the redox state. Investigation on the enzymatic pathways leading to GSH synthesis in wild type and salt-tolerant *B. napus* plants showed assimilation of sulfur and the biosynthesis of cysteine and GSH in order to mitigate salt-induced oxidative stress (Ruiz and Blumwald 2002; Hussain et al. 2008). Sumithra et al. (2006) found that GSH concentration in the salt-stressed mungbean leaves of cv. Pusa Bold was higher than cv. CO 4, whereas GSSG concentration was higher in the leaves of CO 4 than in those of Pusa Bold, indicating that Pusa Bold was more tolerant than CO 4 as the levels of lipid peroxidation and H<sub>2</sub>O<sub>2</sub> concentration

in Pusa Bold was lower than in CO 4 under salt stress. In addition, maintaining a high ratio of GSH/GSSG plays an important role in salt tolerance (Hasanuzzaman et al. 2011a, b). Salt-tolerant cultivars of cotton had a higher GSH/GSSG ratio than salt-sensitive lines under saline conditions (Gossett et al. 1996).

Using buthionine sulfoximine (BSO) and exogenous GSH, Gossett et al. (1996) investigated the importance of maintaining sufficient GSH pools. BSO reduced the growth of the control cell line by 94%, whereas the NaCl-tolerant cell line showed significantly less growth reduction (Gossett et al. 1996). When medium containing BSO was supplemented with exogenous GSH, growth was restored in both cell lines; however, when GSSG was added to medium with BSO, growth was almost completely restored in only the NaCl-tolerant cell line. This was most likely due to the elevation of GR activity and an increased ability to convert GSSG to GSH. Kattab (2007) reported that *B. napus* seed priming with GSH improved seedling resistance probably by enhancing the activities of antioxidant enzymes (SOD, GPX, POX and APX). Exogenous GSH (0.5 mM) maintained plasma membrane permeability under NaCl stress and cell viability in *Allium cepa* (Salama and Al-Mutawa 2009). However, this effect could partially alleviate the harmful effect of salinity stress which reflected on growth and yield of *T. aestivum* plant. In *Tagetes erecta*, application of GSH (100 or 200 ppm) was found to be effective in increasing plant height, no. of branches, fresh and dry weight of herb and flowers, no. of flowers, total carbohydrates (%), total phenols, xanthophyll pigment content and mineral ion percentage under saline (1,500 ppm NaCl) conditions (Rawia et al. 2011).

### 2.5.3.3 Tocopherol

Tocopherols belong to Vitamin E family of amphiphilic antioxidants, with the sub-family of tocotrienols. Tocopherols and tocotrienols are synthesized by higher plant plastids and by cyanobacteria. There are four tocopherol and tocotrienol isomers ( $\alpha$ ,  $\beta$ ,  $\gamma$  and  $\delta$ ). Relative antioxidant activity of the tocopherol isomers *in vivo* is  $\alpha > \beta > \gamma > \delta$  and hence  $\alpha$ -tocopherol has the highest antioxidant activity (Garg and Manchanda 2009). Tocopherols contribute to reduce ROS levels (mainly  $^1\text{O}_2$  and  $\text{OH}^\bullet$ ) in photosynthetic membranes and limits the extent of lipid peroxidation by reducing lipid peroxyl radicals ( $\text{LOO}^\bullet$ ) to their corresponding hydroperoxides (Maeda et al. 2005). In addition, tocopherols are part of an intricate signaling network controlled by ROS, antioxidants, and phytohormones, and are therefore good candidates to influence cellular signaling in plants (Munné-Bosch 2007). However, the ability to critically assess the physiological roles of tocopherol has only recently become available with characterization of plant and cyanobacterial mutants affected in its biosynthesis and transgenic plants with increased tocopherol and tocotrienol content.

Several lines of evidence indicate that  $\alpha$ -tocopherol plays a major role in plant stress tolerance, keeping an adequate redox state in chloroplasts (Munné-Bosch 2005). However, studies on tocopherol-deficient plants have recently revealed that  $\alpha$ -tocopherol is not essential for plant survival under optimal conditions, and that  $\alpha$ -tocopherol deficiency leads to only a slightly increased susceptibility to

photooxidative stress (Kanwischer et al. 2005). Rady et al. (2011) presoaked *H. annuus* seeds with exogenous  $\alpha$ -tocopherol and exposed to saline soil with different salinity levels (EC 1.56, 4.68 and 7.83 dS m<sup>-1</sup>). They observed that salinity induced decreased in total soluble sugars content and the activities of CAT, POX, PPO and PAL were significantly altered by exogenous  $\alpha$ -tocopherol. Treatment with  $\alpha$ -tocopherol also improved the mineral nutrient content in the plant with concomitant increase in Pro, free amino acids and total phenol contents in both cultivars. Farouk (2011) reported that  $\alpha$ -tocopherol could minimize salt-induced leaf senescence in *T. aestivum*. Exogenous  $\alpha$ -tocopherol also enhanced the antioxidant enzyme activities under salt stress which rendered the lower level of H<sub>2</sub>O<sub>2</sub> and lipid peroxidation. Salt stressed plants supplemented with  $\alpha$ -tocopherol decreased the Na<sup>+</sup> and Cl<sup>-</sup> content but increased the K<sup>+</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup> contents (Farouk 2011).

## 2.5.4 Signaling Molecules

### 2.5.4.1 Nitric Oxide

Nitric oxide (NO) is a gaseous biological molecule which is involved in physiological responses to various abiotic stresses. Recently, NO has emerged as an important signaling molecule and antioxidant. NO triggers many kinds of redox-regulated (defense-related) gene expressions, directly or indirectly, to establish plant stress tolerance (Sung and Hong 2010). Several reports indicated that the application of exogenous NO donors confers tolerance to various abiotic stresses including salinity (Hossain et al. 2010; Xiong et al. 2010; Hasanuzzaman et al. 2011a; Bai et al 2011; Liu et al. 2011). NO exerts a protective function against oxidative stress mediated by reaction with lipid radicals, which stops the propagation of lipid oxidation; scavenge the O<sub>2</sub><sup>•-</sup> and formation of peroxynitrite (ONOO<sup>-</sup>) that can be neutralized by other cellular processes. It also helps in the activation of antioxidant enzymes (SOD, CAT, APX, GPX, GR, POX, etc.) and functions as a signaling molecule in the cascade of events leading to gene expression. These mechanism together confer enhance protection against oxidative stress (Hasanuzzaman et al. 2010a; Misra et al. 2011). However, whether or not endogenous NO has an antioxidant function is debatable.

Uchida et al. (2002) reported enhanced tolerance to salt stress (100 mM NaCl, 8 days) in rice seedlings pre-treated with NO (1  $\mu$ M SNP, 2 days). This pre-treatment induced the activity of antioxidant enzymes (SOD, CAT and APX). Enhanced seed germination and root growth of *Lupinus luteus* seedlings (Kopyra and Gwóźdź 2003) and increased growth and dry weight of *Z. mays* seedlings (Zhang et al. 2006b) were also observed with the treatment of NO donor under salt stressed condition. Fan et al. (2007) showed that exogenous NO (100  $\mu$ M SNP) significantly alleviated the salt injury to cucumber seedlings and increased seedling growth. In addition, photosynthetic pigment content, Pro as well as the activity of SOD, POD, CAT and APX were also increased. Similarly, net photosynthetic rate, stomatal conductance, and transpiration rate also increased significantly. However, exogenous NO donor

markedly decreased membrane permeability, rate of  $O_2^{\cdot -}$  production, the contents of MDA and  $H_2O_2$ , and intercellular  $CO_2$  concentration. Treating *H. vulgare* leaves with exogenous NO (50  $\mu$ M SNP), Li et al. (2008) observed that NO could alleviate the damage of salt stress (50 mM NaCl) which was reflected by decreased ion leakage, MDA and  $H_2O_2$  content. Additionally, the presence of the NO donor enhanced the activities of SOD, APX and CAT. David et al. (2010) reported that NO enhanced biochemical adaptation during the seedling growth of *H. annuus* under salinity conditions (40–120 mM NaCl). They found an increased  $Na^+/K^+$  ratio (4-fold) in roots, and  $Na^+$  was rapidly transported to the cotyledons, which registered a concomitant increase in this ratio. They also concluded that the origin of this endogenous generation of NO appears to be mediated by NO synthase (NOS) activity (David et al. 2010). Exogenous NO supplementation as SNP has significant ameliorating effect against NaCl induced oxidative damage in *Cicer arietinum* leaves as observed by Sheokand et al. (2010) who exposed 5-day-old plants to NaCl treatment (250 mM) alone and in combination with two concentrations of SNP (0.2 and 1 mM) for 2, 4 and 6 days. Both the SNP treatments had a positive effect on antioxidant enzymes SOD, CAT, APX, GR and DHAR under salt stress. NaCl treatment resulted in a decline in the GSH/GSSG and AsA/DHA ratio; however, SNP treatments increased the reduced form of both the metabolites thus elevating the ratio of GSH/GSSG and AsA/DHA. Exogenous NO partially decreased MDA and  $H_2O_2$  content. When exposed to NO donors, NO-associated salt priming action was evident in halophytes in tolerating high salinity during germination and early growth stages (Molassiotis et al. 2010) which was due to the better induction of antioxidant enzyme activity in response to high salinity conditions. Recently, Corpas et al. (2011) reported that under salt stress the osmotic stress-activated protein kinase (NtOSAK) is activated by NO and confer stress signals. While studying with *L. esculentum* cv. Hufan1480 and Hufan2496, Wu et al. (2011) observed notable improvement of growth and enhanced antioxidant defense in salt-stressed (100 mM NaCl) plants when treated with exogenous NO (100  $\mu$ M SNP). They observed that in presence of 100  $\mu$ M SNP under salt stress, the reduction in shoot and root dry mass declined to 16% and 3%, respectively in Hufan1480, and to 21% and 6%, respectively in Hufan2496. The MDA content of Hufan1480 and Hufan2496 decreased significantly by 22% and 12% over the salt treatment, respectively. The rate of  $O_2^{\cdot -}$  production in Hufan1480 and Hufan2496 decreased significantly by 20% and 17%, respectively by application of 100  $\mu$ M SNP under salt stress. A remarkable increase in the activities of SOD, POD, CAT, APX, AsA and GSH were recorded by NO treatments under stress condition. In our recent study, we observed that exogenous NO modulated the ROS detoxification systems in *T. aestivum* seedlings (Hasanuzzaman et al. 2011a). The seedlings pretreated with NO donor (1 mM SNP, 24 h) when exposed to salt (150 and 300 mM NaCl, 4 days) showed an increase in the AsA and GSH contents and the GSH/GSSG ratio as well as the activities of monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), GR, GST and GPX as compared to the seedlings without NO pretreatment, which ultimately decreased the contents of MDA and  $H_2O_2$ .

### 2.5.4.2 Hydrogen Peroxide

It is generally thought that  $H_2O_2$  is a ROS and for many years and it was viewed as the inevitable but unwanted by-product of an aerobic respiration. But recent studies have shown that it has important role in redox signaling in regulating normal processes, including oxidative stress and thus it has been established as a 'necessary evil for cell signaling' (Rhee 2006). The function of  $H_2O_2$  as a signaling molecule in transduction of stress signals to the alteration of expression profiles of target genes was also studied in plants (Hung et al. 2005; Hernandez et al. 2010). The connection between  $H_2O_2$  and signaling networks has been extensively documented for a number of stress responses (Larkindale and Knight 2002; Apel and Hirt 2004; Cheeseman 2007).

Recent studies have demonstrated that pretreatment of plants with exogenous  $H_2O_2$  confers abiotic stress tolerance including salinity. Azevedo Neto et al. (2005) reported that addition of  $H_2O_2$  to the nutrient solution induces salt tolerance by enhanced activities of antioxidants and reduced peroxidation of membrane lipids in leaves and roots of maize as an acclimation response. Wahid et al. (2007) reported that *T. aestivum* seeds soaked in 1, 40, 80 and 120 mM  $H_2O_2$  and subsequent growing in saline condition (150 mM NaCl) showed that the level of  $H_2O_2$  in seedlings arising from  $H_2O_2$ -treated seeds grown under salinity was markedly lower than the salinized controls, suggesting the operation of antioxidant system in them. These seedlings also exhibited better photosynthetic capacity, particularly the stomatal conductance (gs), thus improving the leaf gas exchange due to stomatal component of photosynthesis. Moreover,  $H_2O_2$  treatment improved leaf water relations and maintained turgor. Although  $Na^+$  and  $Cl^-$  content increased due to salinity,  $H_2O_2$ -treated seedlings displayed greater tissue  $K^+$ ,  $Ca^{2+}$ ,  $NO_3^-$   $PO_4^{3-}$  levels and improved  $K^+ : Na^+$  ratio. Exogenous  $H_2O_2$  treatment enhanced the membrane properties, as revealed from greatly reduced relative membrane permeability (RMP) and less altered ion leakage pattern (comparable to water controls). Fedina et al. (2009) reported that pretreated *Hordeum vulgare* seedlings with 1 and 5  $\mu M$   $H_2O_2$  for 2 days followed by exposure to 150 mM NaCl for 4 and 7 days showed higher rate of  $^{14}CO_2$  fixation with lower MDA,  $H_2O_2$  and Pro contents in comparison to the seedlings subjected NaCl stress only. In addition,  $Cl^-$  content in the leaves of NaCl treated plants considerably less in pre-treated plants. These results clearly indicated that  $H_2O_2$  metabolism is involved as a signal in the processes of salt tolerance. Recently, Yadav et al. (2011) observed that seeds of *C. annuum* primed with  $H_2O_2$  (1.5 mM) showed enhance tolerance to salt stress (NaCl, 200 mM, 10 days). The plants grown from primed seeds flowered earlier and also produced more number of fruits.

### 2.5.5 Polyamines

Polyamines (PAs) are ubiquitous low-molecular-weight aliphatic amines that are involved in regulation of plant growth and development. PAs are also implicated in a wide range of environmental stress tolerance in plants. New roles are being

discovered every day for these interesting molecules in the plant world. In higher plants, the most common PAs are spermidine (Spd), spermine (Spm) and their diamine obligate precursor putrescine (Put). Like PAs displaying high biological activity are involved in a wide array of fundamental processes in plants, such as replication and gene expression, growth and development, senescence, membrane stabilization, enzyme activity modulation and adaptation to abiotic stresses (Kuznetsov and Shevyakova 2007; Gill and Tuteja 2010; Hussain et al. 2011b; Shu et al 2012; Alet et al. 2012). However, the precise physiological function and mechanism of action of PAs still remain unclear. In contrast to the reliable works on the role of PAs in plants defense against biotic and abiotic stresses, few reports recently indicated that PAs may act as cellular signals in intrinsic talk with hormonal pathways including ABA (Alcazar et al. 2010a, b; Gill and Tuteja 2010). Additionally, PAs like Spm and Spd are regarded as potent inducers of NO in plants which is another potent signaling molecule (Tun et al. 2006).

Changes in plant PA metabolism occurs in response to a variety of abiotic stresses (Alcazar et al. 2006; Gill and Tuteja 2010). These changes in cellular PA under stress only provide clues on its possible implication in stress response, but they do not provide evidence of its role in counteracting stress. Hence, to understand whether PA actually protect cells from stress-induced damages, exogenous application of PA, which is expected to increase endogenous PA, has been investigated before or during stress (Velikova et al. 2000; Navakouidis et al. 2003; Wang et al. 2007). It has been reported that exogenous application of PAs could alleviate salt-induced reduction in photosynthetic efficiency, but this effect is strongly depended both on PAs concentration or types and stress levels (Duan et al. 2008). The efficiency of PSII (Fv/Fm) measured in leaves of salt-stressed *Cucumis sativus* seedlings was not much influenced by 1 mM Spd application, although Spd could ameliorate plant growth and increase net photosynthetic rate ( $P_N$ ),  $G_s$ , intercellular  $CO_2$  concentration (Ci), actual efficiency of photosystem II ( $\Phi PSII$ ) and the coefficient of photochemical quenching (qP) of *C. sativus* seedlings subjected to salinity (Li et al. 2007). In another study, 10 mM Put alleviated the reduction of salt stress on  $P_N$ . However, Put had no effect on gas exchange and transpiration rate (Tr), and aggravated the reduction of salt stress on Ci. The result obtained by Zhang et al. (2009) suggested that Put strongly affects photosynthetic apparatus involving in enhancement of photochemical quenching rather than regulation of stomatal closure or opening. Several publications have reported that changes of endogenous PA level and forms are involved in regulating the photochemical efficiency of salt-stressed plants, and PAs metabolism-related enzymes are closely correlated with photosynthesis. Exogenous PAs increased bound Spd contents in chloroplasts to enhance the photosynthetic capacities of *Z. mays* exposed to salt stress (Liu et al. 2006). Yamaguchi et al. (2006) reported specific role of Spm during high salt stress using an *Arabidopsis* double knockout mutant plant (*acl5/spms*) which cannot produce Spm. The mutant showed higher sensitivity to high salt than wild type plants. This phenotype was cured by exogenous Spm but not by other PAs, i.e. Put and Spd, suggesting a strong link between Spm-deficiency and NaCl-hypersensitivity. Duan et al. (2008) applied exogenous Spd to salinized nutrient solution which resulted in alleviation of the



salinity-induced membrane damage, growth and photosynthesis inhibition, together with an increase in PA and Pro contents as well as antioxidant enzyme activities in the roots of *C. sativus*. Seedlings of *Sorghum bicolor* were subjected to salt stress (180 mM NaCl, 7 days) supplemented with 0.25 mM Spm, showed improved growth and partial increase in activities of POX and GR with concomitant decreased in MDA content. However, Spm had no effects on soluble protein and Pro content in response to salt stress (Chai et al. 2010).

Quinet et al. (2010) found that Put differently influences the effect of salt stress on PA metabolism and ethylene synthesis in *O. sativa* cultivars differing in salt resistance. Exogenous Put reduced Na<sup>+</sup> accumulation in shoots and roots of salt-treated plants of susceptible cultivar while no change was obtained in tolerant one. Amri et al. (2011) showed that the use of different degrees of exogenous PA can reduce the effects of salt stress on growth of *Punica granatum*. PA treated seedlings under salt stressed condition did not show clear differences in plant growth, however it significantly reduced the Na<sup>+</sup> and Cl<sup>-</sup> content and increased Pro content. Application of Put reduced the membrane injury index and increased RWC, photosynthetic rate, and pigments content of *Citrus karna* under saline conditions compared to plants exposed to NaCl in the absence of Put (Sharma et al. 2011). Application of Put alone or in combination also improved the activities of SOD, POD and Pro content under saline conditions. More importantly, application of Put increased K<sup>+</sup> and reduced Na<sup>+</sup> and Cl<sup>-</sup> concentrations in leaf tissues which indicated that Put could improve the tolerance of salt-susceptible Karna khatta by regulating absorption and accumulation of ions as well as improving antioxidant enzyme activities (Sharma et al. 2011). In *C. sativus* seedlings, exogenous Put regulated ion distribution in salt-stressed plants, especially, by preventing the accumulation of Na<sup>+</sup> and Cl<sup>-</sup> in the leaves which were associated with an improvement of the actual PS II efficiency which rendered the plants more tolerant to salt stress (Shu et al. 2010). The photosynthesis of salt-stressed *C. sativus* was enhanced by exogenous Spd that mitigates the decreased stomatal conductance under salt stress as reported by Li et al. (2007). Spd had better effects on the growth and photosynthesis in leaves of salt-stressed seedlings than roots. Recently, Zhang et al. (2011) observed that exogenous Put concentrations significantly increased growth, photosynthesis and decreased lipid peroxidation of *C. sativus* seedlings under salt stress. Improved photosynthesis in plants due to Put application was due to its modulation capacity of photosynthetic proton circuit as recently reported by Ioannidis et al. (2012). Gupta et al. (2012) found a Ca<sup>2+</sup> independent auto regulatory cytoplasmic protein which is phosphorylated in root cytosolic fraction during NaCl/ABA/Spd treatment indicating its importance in salinity mediated signal transduction. Anjum (2011) reported that application of Spd (0.1 or 0.5 mM) to the saline nutrient solution and its weekly sprays (1 or 5 mM) on NaCl-stressed plants improved leaf number, Chl content, Fv/Fm, net photosynthetic rate, and N content; increased total Spd and Spm contents; and reduced Na<sup>+</sup> contents in Troyer citrange (*Poncirus trifoliata* × *Citrus sinensis*). In *O. sativa* seedlings, exogenous PAs (Spd and Spm) reversed the inhibitory effect of salinity which was conferred by preventing growth inhibition or various forms of cellular damages, maintaining proper K<sup>+</sup>/Na<sup>+</sup> balance or triggering the level of

osmolytes and activity of antioxidant enzymes and thus led the plants to tolerate the salt stress (Roychoudhury et al. 2011). Saleethong et al. (2011) investigated the effects of exogenously supplied Spd in two rice cultivars differing in salt tolerance. The major effect of exogenous Spd offered protective roles on salinity-stressed plants by stabilizing membrane, scavenging free radicals and maintaining  $K^+/Na^+$  status. These results indicated that exogenous PAs can be applied as short-term pretreatment prior to introduction of salt stress to increase salt tolerance.

### 2.5.6 Trace Elements

Selenium (Se), and silicon (Si) are considered as beneficial elements for plants: they are not required by all plants but can promote plant growth and may be essential for particular taxa. These beneficial elements have been reported to enhance resistance to abiotic stresses such as drought, salinity, and nutrient toxicity or deficiency (Hasanuzzaman et al. 2010a, b; Hasanuzzaman and Fujita 2011b; Tahir et al. 2012). In case of Se, the beneficial effects of low doses of Se have received little attention compared to toxic effects that typically occur at higher concentrations. Better understanding of the effects of beneficial elements is important to improve crop productivity and enhance plant nutritional value for a growing world population.

#### 2.5.6.1 Selenium

During last two decades the physiological roles of Se in plants have been studied by many researchers although Se has not been confirmed to be an essential micronutrient in higher plants. There are several evidences on its positive effect on plant growth and productivity at low concentrations (Turakainen et al. 2004; Hasanuzzaman et al. 2010a, b; Hasanuzzaman and Fujita 2012; Hasanuzzaman et al. 2012b). However, the specific physiological mechanisms underlying the beneficial role of Se in plants have not been clearly elucidated. It is already established that the plants supplemented with Se have shown enhanced resistance to certain abiotic stresses including salinity (Djanaguiraman et al. 2005; Filek et al. 2008; Hawrylak-Nowak 2009; Cartes et al. 2010; Chu et al. 2010; Djanaguiraman et al. 2010; Hasanuzzaman and Fujita 2010; Hasanuzzaman et al. 2010b; Yao et al. 2010a, b; Hasanuzzaman and Fujita 2011b; Hasanuzzaman et al. 2011b). One of the major effects of Se on abiotic stress tolerance is associated with its antioxidative capacity (Djanaguiraman et al. 2005; Hasanuzzaman et al. 2011b; Hasanuzzaman and Fujita 2011a).

A plenty of research results have shown the ability of Se to protect plants from salt stress-induced damages when applied at low concentration. The interaction of Se with soil salinity has been studied earlier by Terry et al. (2000). Kong et al. (2005) reported that at low concentrations (1–5  $\mu\text{M}$ ), Se tends to stimulate the growth, the activities of SOD and POD, as well as the accumulation of water-soluble sugar in leaves of sorrel (*R. patientia*  $\times$  *R. tianshanicus*) seedlings. However, at higher concentrations (10–30  $\mu\text{M}$ ), Se exerted diminished beneficial effects on



growth and enzyme activities. Results revealed that SOD and POD activity of salt-stressed seedlings increased when exposed to concentrations ranging 1–5  $\mu\text{M}$  Se. At concentrations between 10 and 30  $\mu\text{M}$ , there were adverse effects on both enzymes compared with that at 5  $\mu\text{M}$  Se. In *C. sativus* leaves, Se treatments at 5 and 10  $\mu\text{M}$  significantly improved the growth rate and increased the photosynthetic pigments and Pro contents when subjected to salt stress (Hawrylak-Nowak 2009). Additionally, Se enhanced the salt tolerance of *G. max* seedlings by protecting the cell membrane against lipid peroxidation (Djanaguiraman et al. 2005). Se-treated plants have also increase Pro content (Djanaguiraman et al. 2005). However, the mechanisms and the reasons for Pro accumulation in Se-supplied plants have not been fully investigated. Walaa et al. (2010) observed that NaCl-induced lipid peroxidation which led to increase the percentage of electrolyte leakage, were effectively minimized when the seedlings were pretreated with Se. Se-supplemented seedlings also showed enhanced antioxidant activities and Pro content. In our recent study, we investigated the regulatory role of exogenous Se in the antioxidant defense systems in *B. napus* seedlings exposed to salt stress (Hasanuzzaman et al. 2011b). Twelve-day-old seedlings, grown in Petri dishes, were supplemented with Se (25  $\mu\text{M}$   $\text{Na}_2\text{SeO}_4$ ) and salt (100 and 200 mM NaCl) separately and in combination, and grown for 48 h. The AsA content of the seedlings decreased significantly with increased salt stress, while the amount of GSH and GSSG increased. In addition, the APX and GST activity increased significantly with increased salt concentration (both at 100 and 200 mM NaCl), while GPX activity increased only at moderate salt stress (100 mM NaCl). Glutathione reductase activity remained unchanged at 100 mM NaCl, while it decreased under severe (200 mM NaCl) salt stress. The CAT, MDHAR and DHAR activities decreased with increasing concentration of salt stress, whereas a sharp decrease of these activities was observed under severe salt stress (200 mM NaCl). Concomitant increases in the levels of  $\text{H}_2\text{O}_2$  and MDA were also measured. However, further investigation revealed that Se treatment had a synergistic effect: in salt-stressed seedlings, it increased the AsA and GSH contents, and the activities of CAT, APX, MDHAR, DHAR, GR, GST and GPX. As a result, addition of Se in salt-stressed seedlings led to a reduction in the levels of  $\text{H}_2\text{O}_2$  and MDA as compared to salt stress alone.

### 2.5.6.2 Silicon

Silicon (Si) is the second most abundant element on the earth crust after oxygen and it is accumulated in plants at a rate comparable to those of macronutrient elements like Ca, Mg and P (Epstein 1999). Although Si is a major constituent of plants, to date its essentiality has not been completely established. It may be considered a 'quasi essential' element for plants because its deficiency can cause various dysfunction in regards to plant growth, development and reproduction. In addition, supplementation with Si exerts a number of beneficial effects on growth and yield of several plant species (Richmond and Sussman 2003; Pilon-Smits et al. 2009). Over last two decades, numerous studies have been performed to understand the

possible mechanism(s) for Si-enhanced resistance and/or tolerance of higher plants to abiotic stresses as well as the mechanism of Si uptake and transport in higher plants (Liang et al. 2007). It was found to stimulate enzymatic and non-enzymatic antioxidant under stressful condition (Liang et al. 2007). The possible mechanisms of Si-mediated protective effects under salt stress may include increased plant water status (Romero-Aranda et al. 2006), enhanced photosynthetic activity and maintenance of ultra structure of leaf organelles (Shu and Liu. 2001), Dismutation of ROS (Zhu et al. 2004), immobilization of toxic  $\text{Na}^+$  (Liang et al. 2003), reduced  $\text{Na}^+$  uptake in plants and enhanced  $\text{K}^+$  uptake (Liang et al. 2005; Tahir et al. 2006) and higher  $\text{K}^+$ :  $\text{Na}^+$  selectivity (Hasegawa et al. 2000). In particular, Si was recently proven to mitigate salinity stress by enhancing  $\text{Na}^+$  exclusion and decreasing lipid membrane peroxidation through stimulation of enzymatic and non-enzymatic antioxidants (Saqib et al. 2008; Hasanuzzaman and Fujita 2011b). The protective effect of Si on salinity has been examined in *O. sativa* (Lekklar and Chaidee 2011), *T. aestivum* (Tuna et al. 2008; Tahir et al. 2012), *Z. mays* (Moussa 2006), *H. vulgare* (Liang et al. 2005), *B. napus* (Hashemi et al. 2010), *L. esculentum* (Romero-Aranda et al. 2006), and *C. sativus* (Zhu et al. 2004).

In *B. napus*, exogenous Si ameliorated the deleterious effects of salinity on the growth through lowering tissue  $\text{Na}^+$  contents, maintaining the membrane integrity of root cells as evidenced by reduced lipid peroxidation and lignifications; and increased ROS scavenging capacity (Hashemi et al. 2010). While studying with *Z. mays*, Parveen and Ashraf (2010) reported that under saline condition exogenously applied Si significantly increased growth of plant. Exogenously applied Si also improved some key plant gas exchange characteristics such as net  $\text{CO}_2$  assimilation rate ( $A$ ), stomatal conductance ( $g_s$ ), transpiration ( $E$ ), and leaf sub-stomatal  $\text{CO}_2$  concentration ( $C_i$ ) and thus acted as beneficial elements for improving salt tolerance of *Z. mays* plants. Applying Si to *Medicago sativa* could alter the activity of antioxidative enzyme of one or several organs of plants to improve the salt tolerance (Wang et al. 2011b). The plants under NaCl stress supplemented with Si significantly increased APX activity in root, shoot and leaves, and CAT activity in leaves, and POD activity in shoots, but decreased the SOD activity in roots under salt stress (Wang et al. 2011b). Ali et al. (2011) found that Si supplementation into the root medium significantly improved the  $\text{K}^+$  and  $\text{K}^+:\text{Na}^+$  ratio, leaf water potential and stomatal conductance, but reduced the  $\text{Na}^+$  in *T. aestivum*. These plants also showed a concomitant increase in number of tillers, number of grains per spike, grain and straw yield with Si application both under optimal and stressful conditions which suggested that Si application in soil medium is beneficial in profoundly affecting physiological phenomena and improving wheat growth under salt stress. Lima et al. (2011) reported that Si application in the nutrient solution significantly increased growth parameters and decreased ion leakage in *Z. mays* seedlings, whereas this response was not observed in *Vigna unguiculata*. In *Glycine max*, an addition of Si to salt stressed plants substantially alleviated the adverse effects of NaCl on growth, as it enhanced endogenous  $\text{GA}_3$ , while reducing the levels of ABA and Pro (Lee et al. 2010). In *Saccharum officinarum*, Si-enhanced tolerance to salt which was ascribed to decreased  $\text{Na}^+$  concentration and increased  $\text{K}^+$  with a resultant improvement

in  $K^+/Na^+$  ratio (Ashraf et al. 2010). Recently, we investigated the beneficial role of exogenous Si (1 mM  $SiO_2$ ) in the antioxidant defense and MG detoxification systems of rapeseed seedlings exposed to salt stress (100 and 200 mM NaCl). We observed that Si treatment had a synergistic effect on salt-stressed seedlings by increasing the AsA and GSH contents, the GSH/GSSG ratio, and the activities of APX, MDHAR, DHAR, GR, GST, GPX, CAT, Gly I, and Gly II. The addition of Si also showed reduced levels of  $H_2O_2$  and MDA in salt-stressed seedlings compared to salt stress alone. Our results suggested that the exogenous application of Si rendered the plants more tolerant to short-term salt stress-induced oxidative damage by enhancing their antioxidant defense and MG detoxification systems (Hasanuzzaman and Fujita 2011b). Tahir et al. (2012) reported that application of Si increased shoot and root dry weight and plant water contents in both normal and saline conditions. Shoot  $Na^+$  and  $Na^+:K^+$  ratio also decreased with Si application under stress conditions. Improved growth of salt-stressed wheat by Si application was mainly attributed to improved plant water contents in shoots, chlorophyll content, decreased  $Na^+$  and increased  $K^+$  concentrations in shoots as well as maintained membrane permeability (Tahir et al. 2012).

## 2.6 Conclusion and Future Perspectives

Based on a plenty of research findings, it is clear that salt stress has devastating effect on the growth, development, physiology and yield of plants. However, the response to salinity differs greatly among various plant species, the levels of stress as well as the environmental condition. In recent years, the biochemical responses of plants to salt stress have been studied intensively. Information on the tolerance mechanism is useful for developing new cultivars that are adaptable in salinity environments although defining salt tolerance is quite difficult because of the complex nature of salt stress and the wide range of plant responses. The use of exogenous protectants under salt stress condition has been found to be very much effective to alleviate salt-induced damages. Phytohormones are thought to be the most important endogenous substances involved in the mechanisms of tolerance or susceptibility of plants. However, the exact mechanism of protection and signal transduction pathways are still unclear. The appropriate dose and duration of treatment of the exogenous protectants and the proper methods of application should be studied more precisely. In addition, further investigations considering molecular approaches are needed to reveal the underlying mechanisms of protection under stressful condition.

**Acknowledgements** We express our sincere thanks to Md. Iqbal Hosen, Key Laboratory of Biodiversity and Biogeography, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, Yunnan, China for providing several supporting document regarding salt stress. We also thank Md. Mahabub Alam, Faculty of Agriculture, Kagawa University, Japan for his continuous support during manuscript preparation. We apologize to all researchers for those parts of their work that were not cited in the manuscripts because of the page limitation.

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Ecophysiology and Responses of Plants under Salt Stress

Ahmad, P.; Azooz, M.M.; Prasad, M.N.V. (Eds.)

2013, XVI, 512 p., Hardcover

ISBN: 978-1-4614-4746-7