

# Chapter 4

## Strategies to Mitigate the Salt Stress Effects on Photosynthetic Apparatus and Productivity of Crop Plants



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**Abstract** Soil salinization represents one of the major limiting factors of future increase in crop production through the expansion or maintaining of cultivation area in the future. High salt levels in soils or irrigation water represent major environmental concerns for agriculture in semiarid and arid zones. Recent advances in research provide great opportunities to develop effective strategies to improve crop salt tolerance and yield in different environments affected by the soil salinity. It was clearly demonstrated that plants employ both the common adaptative responses and the specific reactions to salt stress. The review of research results presented here may be helpful to understand the physiological, metabolic, developmental, and other reactions of crop plants to salinity, resulting in the decrease of biomass

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production and yield. In addition, the chapter provides an overview of modern studies on how to mitigate salt stress effects on photosynthetic apparatus and productivity of crop plants with the help of phytohormones, glycine betaine, proline, polyamines, paclobutrazol, trace elements, and nanoparticles. To understand well these effects and to discover new ways to improve productivity in salinity stress conditions, it is necessary to utilize efficiently possibilities of promising techniques and approaches focused on improvement of photosynthetic traits and photosynthetic capacity, which determines yield under salt stress conditions.

**Keywords** Salinity · Photosynthesis apparatus · Yield · Adaptative response

## Abbreviations

ABA	Abscisic acid
APX	Ascorbate peroxidase
BRs	Brassinosteroids
CAT	Catalase
DW	Dry weight
EBL	24-Epibrassinolide
FW	Fresh weight
GPX	Guaiacol peroxidase
JA	Jasmonic acid
MeJA	Jasmonate
MDHAR	Monodehydroascorbate reductase
MDA	Malonic dialdehyde
NPs	Nanoparticles
Pn	Photosynthetic rate
PAs	Polyamines
RWC	Relative water content
SA	Salicylic acid
SOD	Superoxide dismutase
WUE	Water use efficiency

## 4.1 Introduction

The progressive soil degradation, especially soil salinization, will represent one of the major obstacles to increase the crop production through the expansion of cultivation area in the future (Munns and Gilliam 2015). In many regions of the world, where precipitation is insufficient to leach soluble salts from the root zone, high salt levels in soils or irrigation water represent major environmental concerns for

agriculture, the severity of which can increase in conditions of climate change (Lachhab et al. 2013).

Salinity of soil is one of the main abiotic stresses limiting the growth of crops (Munns and Tester 2008). The high salt concentration in the root zone can be natural or induced by agricultural activities such as irrigation with low-quality water or the use of certain fertilizers (Bartels and Nelson 1994). Nearly 400 million hectares of land is affected by salinization, 80% of which are of natural origin and 20% of anthropogenic origin (FAO 2015).

Globally, no less than 10 million hectares of agricultural land is abandoned annually (Berthomieu et al. 1988) due to the acclimatization over time of small quantities of salts contained in the irrigation water. About 15% of the cultivated land has an excess of salt (Berthomieu et al. 1988), and large quantities of water are of very poor quality (Aissaoui and Reffas 2007). Globally, salinity affects more than 6% of the land; in case of irrigated lands, it is over 40% (Chaves et al. 2009).

In salt zones covering 16 million hectares (Hamdy 1999), plants are often subjected to strong sunlight and low rainfall. In these areas, salinity is not only related to climatic conditions but also to the often poorly controlled use of irrigation. Therefore, the high evaporation demand and low infiltration due to precipitation lead to the accumulation of salt on the soil surface (Gucci et al. 1997). Soils in affected areas contain high concentrations of soluble salts, mainly NaCl, but also  $\text{Na}_2\text{SO}_4$ ,  $\text{CaSO}_4$ , and KCl (Hachicha 2007).

The presence of salts in the soil causes a limitation and decline in yield in many regions, in which the salt concentration of the soil solution exceeds 100 mM, inhibiting the growth of plants (Shahbaz and Ashref 2013). Salt accumulation in soils induces changes in plant physiology and metabolism. It affects germination, seedling growth, vegetative phase, flowering, and fruiting leading to decreased yields and quality of production (Zid and Grignon 1991; Vicente et al. 2004; Parida and Das 2005).

Salt tolerance has been broadly studied in numerous plant species and varieties and in halophytes to understand the mechanisms developed for their adaptation (Abdelly 2006; Messedi et al. 2004; Slama et al. 2017; Ben Hamed et al. 2013; Flowers and Colmer 2015). Salt tolerance is a complex trait that involves a set of mechanisms in plants (Lachhab et al. 2013). Different studies have shown that cultivation of specific plant species or varieties may improve productivity of marginal areas affected by salinity. This can be important, especially in conditions where complementary irrigations are often carried out with water containing high concentrations of soluble ions. In many cases, this has been done without taking into account the tolerance of the different varieties, resulting in poor crop production. Therefore, the breeding for better salt tolerance in crops has become a critical requirement for the future of agriculture in arid and semiarid regions (Owens 2001).

The identification of salt-tolerant genetic resources would certainly contribute to crop improvements, subsequently supporting the agricultural production of salinized areas or areas irrigated with brackish water. In this respect, the knowledge on different adaptative mechanisms, morphological, physiological, biochemical, and other strategies, with which different plants cope with the challenges of the salt

stress is critical for success in crop improvement. Although the topic of salt tolerance is very broad and complex, this chapter will be specifically focused on the mechanisms contributing to the protection of the photosynthetic processes against detrimental effects of the salt stress.

## **4.2 Origin of Soil Salinization**

Salts are composed of the different mineral elements of the soil, and some of them represent the essential nutrients needed for plant life. Their concentrations can become very high due to natural processes and/or poor management. In any part of the world, when evaporation exceeds precipitation, salts tend to be accumulated in soils, leading to increased concentrations (Hachicha 2007). Also, salinity increases due to poor drainage and poor water use in irrigation.

Salty soils are rich in soluble salts that affect plant growth and productivity (Mermoud 2006; Hachicha et al. 2017). Generally, in soils where drainage is weak or absent due to their impermeability, salts accumulate in the superficial horizons.

Salinity is a common phenomenon in arid and semiarid regions. Although identification of the natural processes that lead to salinization is essential for understanding the status of salt in any habitat, identification of the origin of salinity and its progression in the wild is important to cope with this constraint. Soluble salts can have three major sources.

### **4.2.1 Marine Origin**

The salts of marine origin are transported and deposited in the continents in three ways. Cyclic salts, brought to the continents in the form of salty spray, are solubilized by rainwater, then redistributed, and transported to the oceans by drainage. Infiltration salts, brought to coastal habitats by seawater infiltration, are the main local source. Fossil salts, precipitated for a long time in certain localities, are led to the rhizosphere or to the surface of the earth by capillarity.

### **4.2.2 Lithogenic Sources**

Some sedimentary rocks contain high levels of chloride and sulfate. The extent of salinization of groundwater and soils depends on the rate of alteration of these sedimentary rocks, which, in turn, varies considerably by region and climate zone. Generally, these rocks release more sulfate than chloride. The weathering of these rocks also releases significant amounts of carbonates, calcium, and magnesium. It

**Table 4.1** The areas of salt-affected soils in different parts of the world (FAO 2008)

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
<b>Total</b>	<b>12.781</b>	<b>397</b>	<b>3.1</b>	<b>434</b>	<b>3.4</b>

was documented that these rocks may represent important sources for the local formation of saline lands (Siadat et al. 1997; FAO 2000).

### 4.2.3 Anthropogenic Sources

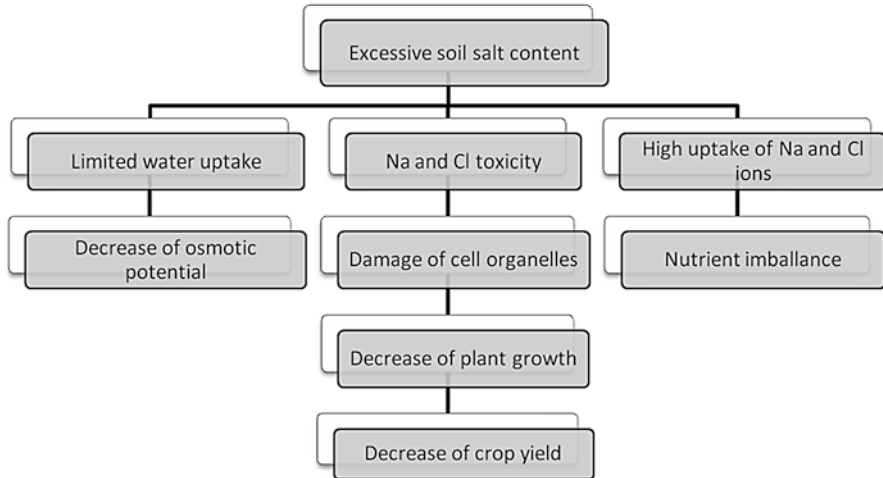
During the last centuries, large quantities of soluble salts accumulated in soils due to human activity. In some areas, poor-quality irrigation with intense evaporation in arid and semiarid regions and the use of inappropriate cultivation practices have led to the accumulation of large quantities of salt in the upper layers of the soil ground (Qadir et al. 2008). Following the development of the industry and the extensive use of fuels, another source of soluble salts has been added. The use of urban water leads to an increase in salinity. Similarly, the reuse of wastewater causes considerable salinization of groundwater (Shakir et al. 2017).

Saline soils are characterized by the predominance of Ca and Mg ions, as well as Na. The presence of salts leads to an increase in the osmotic pressure of the circulating solution, making it difficult for the plant roots to absorb water and nutritive elements and may cause the plasmolysis of the root cells. The excessive presence of certain anions or cations may affect the absorption and development of some plant species, while other ions (Cl, B, and Na) may also be toxic.

In Table 4.1 is the situation presented by FAO about the total area of saline soil in the world (FAO 2008).

## 4.3 Effects of High Salinity on Plants

Accumulation of electrolytic solutes in water and soil in higher concentrations is stressful to many plants. As stated before, saline soils occur in different regions of the world, although the majority of their occurrence is in semiarid and arid regions. There, as a result of insufficient downward percolation and lack of salt leaching, the soluble minerals can accumulate in the root zone. In hot and dry areas, the meager



**Fig. 4.1** Overview of salt stress effects on plants (Adapted from Evelin et al. 2009)

rainfall is accompanied by high temperature and low air humidity, leading to excessive evaporation. Moreover, in many places, such as river valleys, these conditions are associated with the presence of salt-bearing sediments, and shallow, brackish groundwater, resulting in gradual conversion of rich and fertile soils into barren saline soils (Hillel and Vlek 2005).

Presence of high salt concentrations in soil or water leads to osmotic stress, which is one of the most severe stress factors worldwide, with particular importance for numerous regions located in semiarid and arid climate zones. Figure 4.1 briefly illustrates the different ways by which the salinity affects plant functions. In addition to physical (osmotic) effects of soluble particles limiting water uptake by roots, the salinity effects are associated also with toxicity of individual ions and nutritional imbalance or interactions of these factors (Ashraf and Harris 2004).

### 4.3.1 *Effect of Salinity on Germination and Emergence*

Salt stress can limit plant growth, by changing the balance between availability and needs. The scarcity of rains in many regions of the world accentuates salinization of irrigated land and makes them unsuitable for cultivation and abandoned (Yan et al. 2015). Salinity is a limiting factor in agriculture (Qadir et al. 2014). Generally salinity causes a decrease in soil hydraulic conductivity and root aeration and an increase in resistance to root penetration. Moreover, roots meet greater difficulty in suction of water and absorption of nutritional elements.

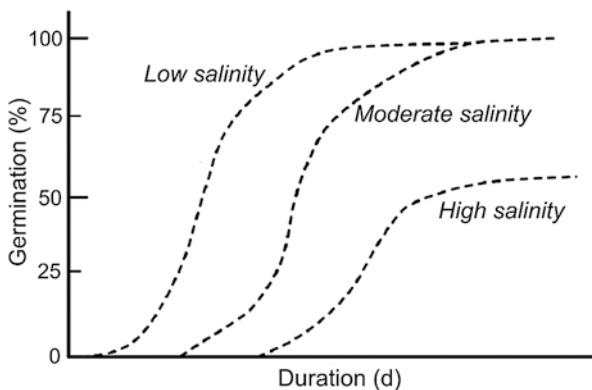
The salinity results in most of plants in reduction of growth and development (Munns and Tester 2008). A large number of alterations occur in plants (e.g.,

osmotic adjustments and various reactions) which affect the various organs from the roots to the stems and leaves and which may actually prevent plant growth. This adverse effect is translated by physiological, morphological, molecular, and biochemical changes which negatively affect plant growth and production (Qadir et al. 2014).

Dynamics of germination depends on genetic predispositions and health status, but it is strongly influenced by environmental conditions, including soil water availability (Gutterman 1993). Abdelly (2006) showed that most plants are more sensitive to salinity during their germination and emergence, when the harmful osmotic or toxic effects of salts are very direct and strong.

Germination of seeds represents often the critical step in the establishment of crop canopy, and thus, it can determinate successful agricultural production. Indeed, under salt stress, a late development favors the accumulation of toxic ions that can kill plants before the end of their development cycle (Munns 2002). Salt tolerance can therefore be evaluated by the precocity of germination.

The response to salt of plant species depends on several variables, starting with the species itself and specific genotypes, but also on salt concentration, growing conditions, and developmental stage of the plant. The decrease of the soil osmotic potential prevents the imbibition of the seed following a decrease in enzymatic activities and a strong absorption of  $\text{Na}^+$  compared to  $\text{K}^+$ , leading to embryonic toxicity and delay in metabolic processes (Pires et al. 2017). Percentage of germination under salt stress depends on the level and duration of salinity applied (Fig. 4.2). In addition to final percentage, the salinity influences also the germination dynamics and vitality of the seedlings (Wang et al. 2011).



**Fig. 4.2** Relationship between rate of germination and time after sowing at different salinity levels (Modified from Ibrahim 2016)

#### 4.3.1.1 Plant Responses on the Different Levels of the Salt Stress

The salinity of soils and waters is induced by the presence of too high concentrations of ions, especially  $\text{Na}^+$  and  $\text{Cl}^-$ . Salinity has three effects, reduces water potential, affects ionic homeostasis, and induces toxicity. At the same time, salt stress affects by different ways different levels of plant organization (Fig. 4.3) and various plant organs (Fig. 4.4).

Excess salt induces osmotic and ionic stress (Yan et al. 2015). The fast response to salt stress is the slowdown of leaf expansion that ceases at high concentrations (Wang and Nil 2000) and affects negatively plant growth (Hernández et al. 1995). The reduction in growth has been shown to be correlated with the salt concentration and the osmotic potential of soils (Flowers and Colmer 2015). The harmful effect of salt is remarkable and causes the death of plants or reduces their productivity. However, growth reduction occurs in most of plant species, but a level of tolerance or sensitivity varies widely among species. For example, for *Raphanus sativus* (radish) plants, 80% of the growth reduction under salt stress is attributed to loss of leaf area (Chartzoulakis and Klapaki 2000).

The action of salinity on the growth leading to both an imbalanced nutritional value of essential ions and a high uptake of toxic ions by the plant (Munns 2002) is connected with stress inducing low osmotic potential of soil solution (Munns and Tester 2008; Yan et al. 2013). Growth reduction in Poaceae can be attributed to an excessive uptake of  $\text{Na}^+$  ions (Tester and Davenport 2003, Gu et al. 2016). In tomato, salinity significantly reduces the mass of aerial parts, the number of leaves, the height of plants, and the plant root area and length (Mohammad et al. 1998).

However, in other obligatory halophytes, growth is increased with the salinity of the medium. These plants require a certain concentration of salt to express their maximum growth potential. In fact, the growth optimum is obtained at 200 mM NaCl in *Salicornia rubra* (Khan et al. 2010) and at 50 mM NaCl in *Alhagi pseudalhagi* (Fabaceae) (Kurban et al. 1999). In a non-excretory mangrove (*Bruguiera parviflora*), optimal growth is obtained at 100 mM NaCl, but 500 mM NaCl may be often lethal for these species (Parida et al. 2004). Optimal growth is achieved at 50% seawater in *Rhizophora mucronata* (Aziz and Khan 2001). The beneficial effect of salt was also observed in *Sesuvium portulacastrum* and *Batis maritima* (Messedi et al. 2004).

Growth of different organs of the same plant does not have the same degree sensitivity to salinity (Negrão et al. 2017). In fact, salt stress reduces the growth of aerial parts by decreased carbon allocation for the foliar growth in favor of root growth (Yeo et al. 1991; Huez-López et al. 2011). On the other hand, other studies (Hajlaoui et al. 2010, Lv et al. 2015) report the opposite; the roots are the most affected.

According to Munns and Rawson (1999), the effect of salinity usually results in a reduction in vegetative growth (reduction in height, number of tillers and leaves) which is a function of division and cell elongation. The growth of shoots is more sensitive to salts than the roots (Fig. 4.4).

Salinity affects the growth of plant roots (Kamiab et al. 2012; Rewald et al. 2012). It has shown that salt stress increases the PR/PA ratio. Indeed, plants main-



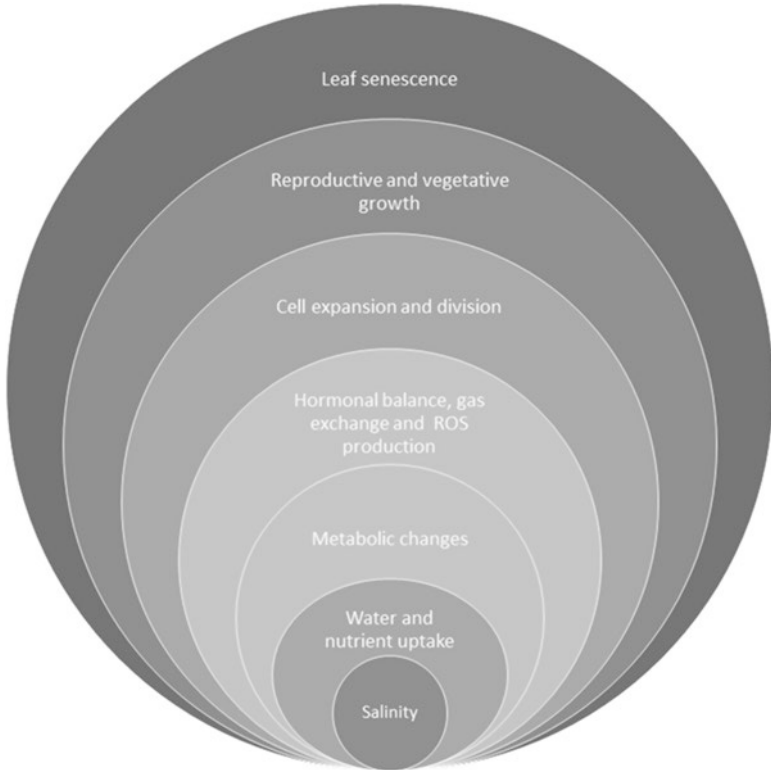
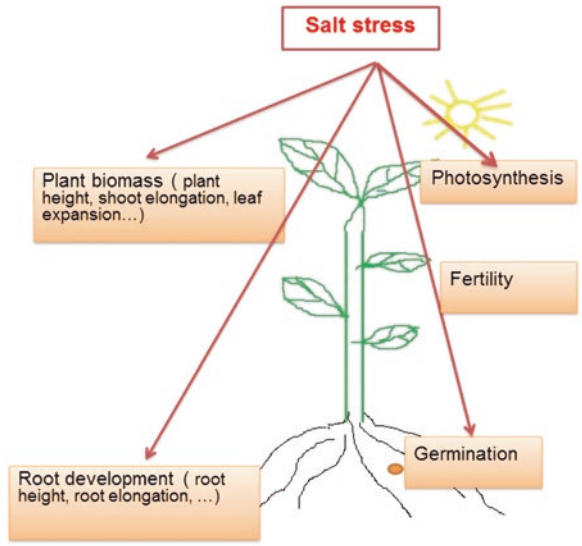
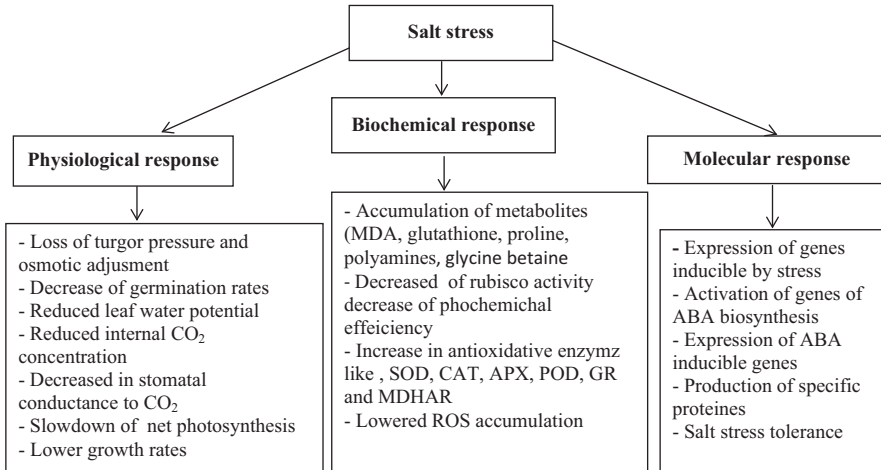


Fig. 4.3 Changes in plant growth under salinity effects (Modified from de Oliveira et al. 2013)

Fig. 4.4 Effect of salt stress on the different organs of plants





**Fig. 4.5** Plant physiological, biochemical, and molecular response to salt stress

tain relatively high root growth under high saline stress; the increase in the PR/PA ratio that follows seems to be associated with an increase of their tolerance to salt.

Kafkai (1991) suggests that under salt stress, the plant spends more photosynthetic energy to maintain high water status and for production of roots for reduction of water loss. In these conditions, it seems that the arrest of leaf growth is triggered by hormones (Munns and Tester 2008) and a significant proportion of assimilates is then relocated to root growth (Fig. 4.5). This is one of the key anatomical responses to osmotic stress in many species, whose adaptative nature is evident since an increase conditions, it seems that the arrest of leaf growth is triggered by of the root mass/mass ratio of the canopy maximizes the water absorption area in decreasing the evaporation surface (Munns 2002).

The mechanisms of salt tolerance include the changes of low as well as of high complexity. The low complex mechanisms are associated with the expression of particular biochemical pathways. On the other hand, the mechanisms of high complexity modify the activities of key processes of energy metabolism, such as photosynthesis and respiration, as well as processes related to water uptake and transpiration and stomatal activity. The highly complex responses involve also the processes related to changes in the cell wall, cytoskeleton, and plasma membrane, related to water use efficiency, and securing the key cell elements (Botella et al. 1994).

### 4.3.2 Effects on the Anatomy of the Leaf

Salinity causes the increased thickness of epidermis, palisade and spongy parenchyma, and mesophyll, cell length, and cell diameter of the leaves of *Atriplex*, *Faba*, and *Gossypium* (Longstreth and Nobel 1979). However, it was shown that in

mangroves (*Bruguiera parviflora*), the thickness of the epidermis and mesophyll, and the intercellular space in the leaves, is reduced (Parida et al. 2004). In wheat, area of flag leaf was significantly lowered in conditions of salt stress, significantly limiting yield (Ahmad et al. 2005). Salt causes increased vacuolation, development of the endoplasmic reticulum and mitochondria, vesicle formation and tonoplast fragmentation, and cytoplasmic degradation by mixing the matrices of cytoplasm and vacuole in the potato leaves (Mitsuya et al. 2000). It induces a reduction in intercellular spaces and number of chloroplasts in potato (Bruns and Hecht-Buchholz 1990) and stoma density in tomato (Romero-Aranda et al. 2001).

### 4.3.3 Plant Mineral Nutrition

In salt stress conditions, the mineral nutrition of the plant is disturbed. Indeed, the  $\text{Na}^+$  ions disrupt cation ( $\text{K}^+$ ,  $\text{Ca}^{2+}$ ) absorption (Haouala et al. 2007). At the root level,  $\text{Na}^+$  moves  $\text{Ca}^{2+}$  from cell walls (Zhu 2002). For example, in the isolated cell walls of barley roots,  $\text{Na}^+$  and  $\text{Ca}^{2+}$  are competing for the same site absorption, while  $\text{K}^+$  is fixed on other sites. As a result, the  $\text{K}^+/\text{Na}^+$  ratio at the surface of cells depends on competition with  $\text{Na}^+/\text{Ca}^{2+}$  (Stassart et al. 1981).

### 4.3.4 Effect of Salinity on Agronomic Yield

Components of crop performance, such as the number of tillers per plant, the number of ears, the number of spikelets per ear, and the grain weight, are usually influenced by the presence of salinity stress. Ahmad et al. (2005) have shown that all performance parameters are reduced under the salinity and that the higher the salinity, the higher yield decrease is observed.

The barley plants under salt stress during heading or differentiation of the ear have shown the reduced plant height and leaf area (Singh et al. 1994), as well as decrease in stem weight, stem length, and shoot dry matter. The number of spikelets per spike is decreased, as well as the number of grains. Salinity has a detrimental effect on the remobilization of reserves during the filling of the grains. Salinity decreases yield more often by reducing the number of spikes bearing the spikelets, ear weight, and 1000-seed weight (Munns and Rawson 1999). Mass and Grieve (1990) observed the changes in the final capacity of spike, associated with lower number of spikelets and grains per spike, as well as a decrease in spike length. Salt stress led to an increase of the phyllochron. In addition, the number of leaves on main stem was lower, and a vegetative period of stem meristem was shorter (Mass and Nieman 1978).

In case of rice, screening of cultivars for salt tolerance has been based mostly on growth rate and grain yield (Kafi et al. 2013). In this respect, it was shown that yield under salt stress was well correlated with panicle weight, number, height, and tiller

number. The significant variability in salt resistance and yields in salt stress conditions was observed among families of rice, providing promising background for salt stress studies and breeding in this crop (Souleymane et al. 2017).

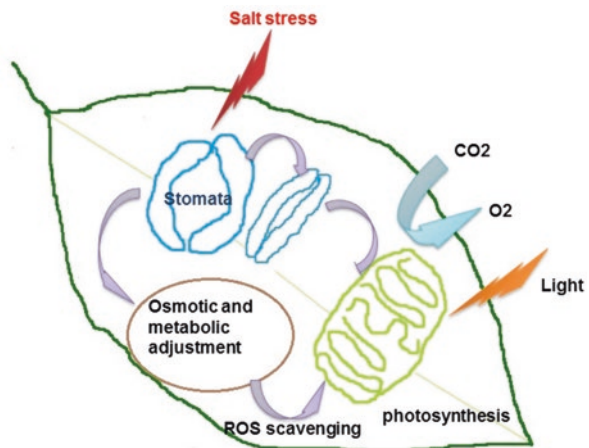
The effect of irrigation with saline water was tested by Lamsal et al. (1999) in wheat, observing decreases of grain yield and of all yield components and growth parameters, including flag leaf area, plant height, grain per spike, number of spikes per plant, grain weight per spike, 1000 grain weight, as well as total dry matter accumulation.

#### 4.3.4.1 Photosynthetic Responses and Acclimations on Salt Stress

Photosynthesis is strongly involved in plant productivity (reduction of production of biomass, leaves) and nutrient flows in plants. Salinity affects the physiological activity of the leaf, particularly photosynthesis, which is the main cause of reduced plant productivity (Alem et al. 2002). The adaptation of photosynthesis under salt stress is presented in Fig. 4.6.

In specific environments, the resistance to drought and salinity are important traits determining the yield of main crops (Munns and Tester 2008; Munns, et al. 2010). The phenotypic effects of these two stresses are often very similar, and, therefore, the similar screening methods and tools can be used for both stresses. Important and relatively fast response to salinity is stomatal closure, associated partly with the osmotic effect of salts on the capacity of roots to absorb the soil water (Munns and Tester 2008). Insufficient uptake of the water due to salinity is denoted as “chemical drought” (Munns et al. 2010). In the early stages of the stress, the decrease of photosynthetic rate is caused by stomatal closure. The standard measurements of stomatal conductance or screening based on photosynthetic parame-

**Fig. 4.6** Photosynthesis adaptation to salt stress



ters are usually quite slow, and the reproducibility is often low (Munns et al. (2010). Therefore, there is still a need for fast and reliable methods of monitoring photosynthesis in salt stress conditions. Chlorophyll fluorescence measurements can be used in plant phenotyping and breeding programs to monitor different biotic and abiotic stresses including mineral deficiencies, soil salinity, and pathogenic diseases (Brestic and Zivcak 2013; Kalaji et al. 2017).

Under moderate salinity, the photosynthetic efficiency can reach the values similar to the control, but under high salinity, photosynthesis is significantly inhibited, as it was found in *Desmostachya bipinnata* (L.) Staph. (Asrar et al. 2017). At high concentrations of salt, the photosynthetic pigments, photochemical quenching, and electron transport rate were significantly decreased, whereas at moderate salt stress, the decrease was not observed. The content of MDA increased at high salinity, documenting excessive accumulation of ROS. Under increasing salinity treatments, a subsequent decrease of Rubisco content was also observed. The proteins of photosynthetic complexes were overexpressed (D1, AtpA, PetD) or remained unaffected (PsbO) under moderate salinity but decreased at higher concentrations, except of AtpA. Severe salt stress caused damages to PSII photochemistry and downregulation of chloroplast proteins connected with biochemical limitations in *D. bipinnata* (Asrar et al. 2017). The rate of photosynthesis increases for low levels of salinity and decreases in high level, without modification on stomatal conductance *Bruguiera parviflora* (Parida et al. 2004).

Salinity stress induces for the majority of plants a reduction in production of biomass essentially due to a decrease in photosynthesis (Kalaji et al. 2018). These changes are mostly connected with changes of carboxylation processes, but not photophosphorylation, which are most affected by salt stress. The response of plants to salt stress is heavily dependent on genotype. The salt stress has both short- and long-term effects on photosynthetic processes. The early effects can be observed after a few hours or days of exposure of the plants to salinity, and there can be a full cessation of carbon uptake for a few hours. The long-term effect appears after several days of salt treatment. The reduction of photosynthesis is caused by the accumulation of salt in the leaves (Munns and Termaat 1986). Whereas some studies indicate a reduction in photosynthesis by salinity (Chaudhuri and Choudhuri 1997; Soussi et al. 1998; Romero-Aranda et al. 2001; Kao et al. 2001), others show that carbon assimilation is not affected by salt stress or, in some cases, also enhanced by moderate salt concentrations (Rajesh et al. 1998; Kurban et al. 1999).

In the mulberry tree, the net assimilation of CO<sub>2</sub> (PN), the stomatal conductance (gs), and the rate of transpiration (E) are reduced under salt stress, whereas the intercellular concentration of CO<sub>2</sub> (Ci) is increased (Agastian et al. 2000). In *Bruguiera parviflora*, PN increases at low salinity but decreases at high salinity, whereas at low salinity, it remains comparable to that of control plants and falls at high concentrations (Parida et al. 2004).

Many studies showed, however, a major role of salt stress in limiting osmotic conductance and reducing reactive oxygen species (ROS) and main enzymes of detoxification of ROS. According to Munns and Tester (2008), the reduction in photosynthesis is related to the decrease in leaf water potential, which is responsible for

the closure of stomata (Allen et al. 1985), which causes the reduction of photosynthesis and stomatal conductance (Orcutt and Nilsene 2000).

Salt stress reduces chlorophyll content and increases respiration, but has no significant effect on carotenoid levels in alfalfa (Khavari-Nejad and Chaparzadeh 1998). In *Atriplex lentiformis*, uptake of CO<sub>2</sub> and the ratio of Rubisco to phosphoenolpyruvate carboxylase (PEPC) activity decreased under salt stress. Phosphoenolpyruvate carboxylase (PEPC) activity increases linearly with salinity, whereas that of ribulose biphosphate carboxylase/oxygenase (Rubisco) is not changing significantly (Zhu and Meinzer 1999). The reduction in photosynthesis is caused also by a decrease in stomatal conductance which restricts the access of CO<sub>2</sub> for Calvin-Benson cycle (Brugnoli and Bjorkman 1992). Stomata closure minimizes transpiration and affects light capture by chloroplasts and photosystems leading to impaired activity of these organelles (Iyengar and Reddy 1996).

In the process of photosynthesis, two key complex events occur: light reactions, in which light energy is converted into ATP and NADPH and oxygen is evolved, and light-independent, dark reactions, in which CO<sub>2</sub> is fixed into carbohydrates by utilizing both of the products of light reactions (Allakhverdiev et al. 2002).

Pigment analysis showed that salt stress resulted in a significant decrease in chlorophyll *a* content, whereas the content of chlorophyll *b* remained unaffected. It appeared that chlorophyll *b* tolerated more the salinity than chlorophyll *a*. However, total carotenoid contents were increased. For some crops carotenoid concentration can be increased in conditions with low salinity and on the other hand under high salinity can be significantly decreased.

CO<sub>2</sub> assimilation rate (Chaves et al. 2011; Kalaji et al. 2011; Kanwal et al. 2011; Chen et al. 2015; Hniličková 2017; Dąbrowski et al. 2017) and photosynthetic oxygen evolution can be also inhibited (Dąbrowski et al. 2016). Increases in *F<sub>o</sub>* have been attributed to physical separation of the PSII from associated pigment antennae and decreases in the number of active RCs (Strasser et al. 2010). In the present study, the salt-induced increase in *F<sub>o</sub>* indicates that some active RCs were inactivated by salt stress. This inactivation of RCs by salt stress was further evidenced by the increase in the ABS/RC value and the decrease in the values of RC/CSO and TRO/ABS after salinity treatment. Specific chlorophyll *a* fluorescence transient parameters derived from OJIP test ( $\phi E_o$ ,  $\phi P_o$ ,  $\psi O$ , RC/CS, RC/ABS, PIABS, and PICS) were decreased under salt stress, while  $dVo/dto(Mo)$ ,  $V_j$ , and  $\phi Do$  were increased. The decrease of ETRmax and yield and the change of chlorophyll *a* fluorescence transients showed that salt stress had an important influence on photosynthesis. These results indicated that the effects of salinity stress on photosynthesis may depend on the inhibition of electron transport and the inactivation of the reaction centers, but this inhibition may occur in the electron transport pathway at the photosystem II (PSII) donor and acceptor sites (Mehta et al. 2010). Salt stress can damage active reactive centers of PSII and destroys the oxygen-evolving complex (OEC) and impairs the electron transfer capacity on the donor side of PSII (Misra et al. 2001; Mehta et al. 2010; Sun et al. 2016; Kan et al. 2017; Kalaji et al. 2018).

The major consequences of salt stress on the main photosynthetic parameters in the various crop plants are presented in Table 4.2.

**Table 4.2** Salt stress photosynthetic adaptive responses of different plant species

Plant species	Salt stress	Photosynthetic parameters measured	Adaptative response to salt stress	References
<i>Cakile maritima</i>	0, 100, 200, 300, and 500 mM NaCl	RGR, ROS, $\Phi_{PSII}$ , DW, $F_m$ , $F_o$ , $F_s$ , $F_v/F_m$ , NPQ, qP	Adaptative response to salt stress Net photosynthetic rate, stomatal conductance, maximum quantum efficiency of PSII, and quantum yield were stimulated in the 100–200 mM NaCl range Higher salinity adversely affected gas exchange and changed PSII functional characteristics, resulting in a reduction of net photosynthetic rate per leaf area unit	Debez et al. (2008)
<i>Atriplex portulacoides</i>	0, 200, 400, 800, and 1000 mM NaCl	RGR, ROS, SOD, APX, $\Phi_{PSII}$ , DW, $F_m$ , $F_o$ , $F_s$ , $F_v/F_m$ , NPQ, qP	The maintaining photosynthetic activity, photosynthetic pigment contents, and preserving PSII functional integrity, in conjunction with the accumulation of natural bioactive compounds (e.g., polyphenols, anthocyanins, and proline) and the active contribution of enzymatic antioxidant defenses	Benzarti et al. (2012)
<i>Atriplex hortensis</i>	0, 5, 15 g/l NaCl	The plant height, root system length, leaf area, Chl content	Improved tolerance to salt stress may be accomplished by decline in growth and photosynthetic activity	Sai Kachout et al. (2009)
<i>Suaeda salsa</i>	2, 4, 6, and 8 g/kg NaCl	FW, DW, height, total nitrogen (TN), and total carbon (TC)	FW, DW, and height were promoted at lower salinity treatments but reduced at higher salinity treatments, while TN and TC contents were kept stable with increasing salinity level Nitrogen addition could significantly mitigate the deleterious effects of salt stress	Jia et al. (2017)
<i>Aeluropus litoralis</i>	0, 200, and 400 mM NaCl	Proteomic analysis	The reduction of proteins related to photosynthesis and induction of proteins involved in glycolysis, tricarboxylic acid (TCA) cycle, and energy metabolism	Azri et al. (2009)
Mediterranean <i>Linonium</i> sp. <i>L. santapolense</i> , <i>L. girardinianum</i> , <i>L. narbonense</i> , <i>L. virgatum</i>	0, 200, 400, or 800 mM NaCl	DW, ion content, pigment content-free proline, glycine betaine, total soluble sugars, analysis of soluble carbohydrates	The efficient transport of $Na^+$ and $Cl^-$ to the leaves and their compartmentalization in vacuoles The accumulation of fructose and proline, as the main physiological osmolytes responsible for cellular osmotic adjustment The activation of $K^+$ transport from the roots to the leaves in the presence of high salt concentrations	Al Hassan et al. (2017)

(continued)



Table 4.2 (continued)

Plant species	Salt stress	Photosynthetic parameters measured	Adaptative response to salt stress	References
<i>Limonium bicolor</i> (bag.) Kuntze	0, 100, 200, and 300 mM NaCl	DW, water content, net CO <sub>2</sub> assimilation rate (PN), stomatal conductance (gs), transpiration rate of MDA, content of total phenolic and flavonoids	Adaptation resistance mechanisms involving an increased number of salt glands, enhanced activities of antioxidant enzymes, and an accelerated accumulation of secondary metabolites	Wang et al. (2016)
<i>Zea mays</i> L. Maize	0, 100, 200, 300 mM NaCl	Prompt Chl fluorescence (PF), delayed Chl fluorescence (DF), modulated 820 nm reflection	Decreasing the number of active PSII reaction centers Impaired the connectivity between independent PSII units, destroyed the oxygen-evolving complex, and limited electron transport beyond the primary quinone acceptor Q <sub>A</sub> <sup>-</sup> . The photochemical activity of PSII is higher in salt stress than that of PSI	Kan et al. (2017a, b)
<i>Paulownia</i> sp.	Saline soils (EC = 1.6; 6.3; 14 mS.m <sup>-2</sup> )	Chlorophyll pigments Chlorophyll <i>a</i> fluorescence (PAM fluorimeter)	The Q <sub>A</sub> reoxidation and photochemical quenching increase The stimulation of the linear electron transport Increased ETR and qP in presence of salt enhanced the ability of the photosynthetic apparatus to maintain QA in the oxidized state and an increase in the proportion of the "open" PSII reaction centers	Stefanov et al. (2016)
<i>Paspalum vaginatum</i> Swartz cv.	0, 75, 150, 300, and 600 mM NaCl	FW, DW, Chl fluorescence (mini-PAM)	Maximum efficiency of PSII photochemistry declined only in the highest salinity. A full recovery of the fluorescence parameters upon rewetting. The rapid osmotic adjustment capacity was associated with higher sugar levels	Pompeiano et al. (2016)



According to Munns and Tester (2008), the reduction of photosynthesis is related to decreased leaf water potential, which is responsible for stomatal closure (Price and Hendry 1991; Allen et al. 1985), which causes the reduction of stomatal conductance (Orcutt and Nilsen 2000). The diffusion of CO inside the stomata then becomes limited, and its binding at the chloroplast level consequently decreases; the regeneration of RuBP (ribulose biphosphate) becomes limited.

### 4.3.5 Effects of Salt Stress on Ultrastructure of Chloroplasts

The diffusion of CO<sub>2</sub> inside the stomata then becomes limited, and its binding at the level of chloroplasts decreases (Graan and Boyer 1990); consequently the regeneration of RuBP (ribulose biphosphate) becomes limited (Gimenez et al. 1992). Stomatic control and regulation involve cell turgor but also root signals, such as abscisic acid (ABA) (Zhang and Davies 1989). Cellular turgor occurs more or less directly in the chloroplast: directly by maintaining the volume of the chloroplast and indirectly by its effect on the stomatal opening, which controls the conductance and conditions the use of energy photochemical (ATP, NADPH) in chloroplasts (Gupta and Berkowitz 1987).

Salt causes disorganization of the thylakoid structure, increases the number and size of plastoglobules, and reduces starch ranges (Hernández et al. 1995, 1999). In mesophyll potato cells, thylakoid membranes are distended, and most are altered under severe salt stress (Mitsuya et al. 2000). Salinity reduces the number and thickness of the stack of thylakoids by grana (Bruns and Hecht-Buchholz 1990a, b). In NaCl-treated tomato plants, chloroplasts are assembled, cell membranes are deformed and wavy, and the structure of grana and thylakoids is affected (Khavari-Nejad and Mostofi 1998). Ultrastructural changes of chloroplasts under salt stress are well studied in *Eucalyptus microcorys*. These changes include the appearance of large starch grains, dilation of thylakoid membranes, almost complete absence of grana, and development of mesophyll cells (Keiper et al. 1998).

#### 4.3.5.1 Effect of Salinity on Reproduction Process

Salinity reduces the growth rate of the plant and its reproductive organs (Hu et al. 2017). They studied the effect of salinity on the physiology of reproduction; they found that the number of pollen in two different types of barley cultivars was reduced from 24 to 37%. Studies by Munns and Rawson (1999) on the effect of salt accumulation in the meristem of barley on reproduction and development show that short periods of salt stress during organogenesis may have irreversible consequences on the fertility of the ear; it causes the abortion of the ovaries.

It was observed higher floret fertility contributed to higher seed set and grain yields in tolerant genotypes, whereas higher spikelet sterility led to poor seed set and lower grain yields in sensitive to salt stress genotypes. It is important to do

screening at reproductive stage for morphological traits like floret fertility are thus more useful to identify plant genotypes tolerant to salinity stress (Rao et al. 2008).

Floral phenology, pollen quality, and seed set of *Plantago crassifolia* plants were optimal in plants grown in non-saline conditions. Same positive tendency was observed in the presence of 100 mM NaCl. But progressive reduction of pollen fertility, seed set, and seed viability has been observed by higher salt concentrations (Boscaiu et al. 2005).

#### 4.3.5.2 Symptoms of Toxicity Connected with Ionic and Nutritional Balance in Plants

Saline solutions impose ionic and osmotic stress in plants. The effects of this stress can be observed at different levels. In sensitive plants, the growth of aerial parts and to a lesser extent that of roots is rapidly reduced. This reduction phenomenon appears to be independent of the tissue Na<sup>+</sup> concentration but would rather be a response to the osmolarity of the culture medium (Munns 2002). The specific toxicity of Na<sup>+</sup> ions is related to the accumulation of these ions in the leaf tissues and leads to necrosis of the aged leaves. Generally, this necrosis begins with the tip and the edges to finally invade the entire leaf. The reduction in growth is due to a reduction in leaf life, and thus there will be a reduction in growth and productivity (Munns 1993 and 2002). In saline soils, Na<sup>+</sup> ions induce deficiency in other elements (Silberbush et al. 2005). The effects of Na<sup>+</sup> are also the result of deficiency in other nutrients and interactions with other environmental factors, such as drought, which increase the problems of Na<sup>+</sup> toxicity. The excess of Na<sup>+</sup> ions inhibits the uptake of other nutrients either by competition at the sites of the root cell plasma membrane transporters or by inhibition of root growth by an osmotic effect. Thus, the absorption of water and the limitation of the nutrients essential for the growth and the development of the microorganisms of the soil can be inhibited.

Leaves are more sensitive to Na<sup>+</sup> ions than roots because these ions accumulate more in the aerial parts than in the roots. These can regulate the concentration of Na<sup>+</sup> ions by their export either to the aerial parts or to the ground. The metabolic toxicity of Na<sup>+</sup> is mainly related to its competition with K<sup>+</sup> at sites essential for cell function. Thus, more than 50 enzymes are activated by K<sup>+</sup> ions; Na<sup>+</sup> ions cannot replace K<sup>+</sup> in these functions (Bhandal and Malik 1988; Tang et al. 2015; Gu et al. 2016). For that, a high concentration of Na<sup>+</sup> can affect the functioning or the synthesis of several enzymes. In addition, protein synthesis requires high K<sup>+</sup> concentrations for tRNA binding on ribosomes (Blaha et al. 2000) and probably for other ribosome functions (Wyn Jones et al. 1979). The disruption of protein synthesis by the high concentration of Na<sup>+</sup> represents the major toxic effect of Na<sup>+</sup> ions. Osmotic stress could occur following an increase in Na<sup>+</sup> concentration at leaf apoplasm (Oertli 1968). This result was verified by microanalyses (R-X) of Na<sup>+</sup> concentration in apoplasm of rice leaves (Flowers et al. 1991). The presence of high concentrations of Na<sup>+</sup> in the cells allows the plant to maintain its water potential lower than that of the soil to maintain its turgor and water absorption capacity. This leads to an increase in osmotic concentration either by absorption of solutes from the soil or by synthesis of compatible

solutes. The former, usually  $\text{Na}^+$  and  $\text{Cl}^-$ , are toxic, while the latter are compatible but energetically expensive for the plant.

#### 4.4 Specific Adaptative Strategies of Plants Under Salt Stress

Several studies have shown that plants adapted to salt stress use one or more mechanisms to mitigate the effect of  $\text{NaCl}$  such as (i) the  $\text{Na}^+$  reabsorption by transfer cells or vascular parenchyma (Karray-Bouraoui 1995); (ii) the compartmentalization of ions between the organs (roots/aerial parts), tissues (epidermis/mesophyll), or cellular compartments (vacuole/cytoplasm) (Cheeseman 1988); and (iii) the dilution of  $\text{Na}^+$  by the material produced growing leaves (Tester and Davenport 2003).

The mechanism by which a plant tolerates salt is complex, and it differs from species to species (Munns and Tester 2008; Bueno et al. 2017). The main effects of salt stress and development of plant adaptation of various crop plants are presented in Table 4.3.

Salt affects seed germination through osmotic effects (Khan et al. 2000), ion toxicity, or a combination of the two (Khan and Ungar 1998; Munns and Tester 2008). Osmotic stress can result in inhibition of water uptake that is essential for enzyme activation, breakdown, and translocation of seed reserves (Ashraf and Foolad 2007; Munns and Tester 2008). Furthermore, ionic stress can inhibit critical metabolic steps in dividing and expanding cells and may be toxic at high concentrations (Munns and Tester 2008). The excess  $\text{Na}^+$  and  $\text{Cl}^-$  have the potential to affect plant cell enzymes, resulting in reduced energy production and some physiological processes (Munns and Tester 2008; Morais et al. 2012). The degree of salt tolerance varies among plant species and, for a given species, also at different developmental stages (Ahmad et al. 2013; Bueno et al. 2017). Some plants have adapted to grow in high-salinity environments due to the presence of different mechanisms in them for salt tolerance, such plants are known as salt-tolerant plants or halophytes (Ahmad et al. 2013), but a large majority of plant species grown in non-saline areas are salt-sensitive (glycophytes). Glycophytic and halophytic species differ greatly in their tolerance to salt stress (Munns and Tester 2008).

With the degree of salinity of soil solution, glycophytes in general are exposed to changes in their morphophysiological (Bennaceur et al. 2001) and biochemical (Grennan 2006) behavior. So the plants react to these variations in salinity in the biotope to set off resistance mechanisms. Among these mechanisms, the osmotic adjustment plays a vital role in the resistance or the tolerance of the plant to stress (Munns 2002). The plant will have to synthesize organic solutes to adjust its water potential. A salinity adaptation strategy consists of synthesizing osmoprotective agents, mainly amino compounds and sugars, and to be accumulated in the cytoplasm and organelles (Ashraf and Foolad 2007; Chen et al. 2010; Sengupta and Majumder 2010; Yan et al. 2013). Identification and understanding of plant tolerance mechanisms to salinity therefore have a clear interest in varietal improvement. The objective of this study is to determine certain morphological and physiological criteria allowing early identification of saline-tolerant plants.

**Table 4.3** Salt stress adaptive responses of different plant species

Plant species	Conditions of salt stress	Parameters measured	Adaptive response to salt stress (mechanism implicated in salt tolerance)	References
<i>Cakile maritima</i>	50, 100, 200, 300, 400, or 500 mM NaCl which progressively adjusted with increasing NaCl concentrations 50 mM step per day	Germination rate, RGR, fresh weight (FW), dry weight (DW), ionic status (K <sup>+</sup> , Na <sup>+</sup> , Cl <sup>-</sup> , K <sup>+</sup> /Na <sup>+</sup> , Mg <sup>+</sup> , Ca <sup>+</sup> )	Growth activity maintained up to 500 mM NaCl Preservation of the biomass production Ability to maintain the tissue water status The efficiency of selective K <sup>+</sup> uptake Na <sup>+</sup> utilization by the plant for osmotic adjustment	Debez et al. (2004) Megdiche et al. (2007)
<i>Crithmum maritimum</i>	0, 50, and 200 mM which progressively adjusted with increasing NaCl concentrations 50 mM step per day	Growth parameters, MDA, POD, SOD, catalase, peroxidase	Keeping of convenient tissue water supply Selective accumulation of K <sup>+</sup> versus Na <sup>+</sup> High antioxidant enzyme activities (SOD-CAT-POD), preventing toxic accumulation of AOS	Ben Amor et al. (2005) Ben Hamed et al. (2007)
<i>Gypsophila oblancoolata</i> Bark.	0, 50, 100, 150, 300 mM NaCl	Germination, antioxidant activities of enzymes/ isoenzymes (SOD, CAT and POX, MDA)	Different antioxidant metabolism to the different salt concentration	Sekmen et al. (2012)
<i>Cakile maritima</i> (halophyte) <i>Arabisidopsis thaliana</i> (glycophyte)	100 mM and 400 mM NaCl (daily increase by 50 mM NaCl or 10 mM)	DW, H <sub>2</sub> O <sub>2</sub> , antioxidant enzyme activities, MDA	Increase in H <sub>2</sub> O <sub>2</sub> , antioxidant activities and MDA in halophyte compared to the glycophyte plant	Ellouzi et al. (2011) Ellouzi et al. (2014)
<i>Limonium latifolium</i> , <i>Marricaria maritima</i> , <i>Crambe maritima</i>	0, 100, 200, or 400 mM NaCl	H <sub>2</sub> O <sub>2</sub> assay, MDA, Na accumulation in plant tissues, CAT activity, APX activity, GR activity	Results showed that <i>L. latifolium</i> , <i>M. maritima</i> , and <i>C. maritima</i> used different antioxidant enzymes to cope with salinity The most tolerant species ( <i>L. latifolium</i> ) uses GR to protect from stress-induced ROS	Ben Hamed et al. (2014)
<i>Triticum aestivum</i> L. (wheat) <i>Hordeum vulgare</i> L. (barley)	100 mM NaCl	K, Ca, Na, DW	Na <sup>+</sup> uptake and transport increased under NaCl presence Specific osmotic adjustment of barley is distinguished by a good ability to sequester Na <sup>+</sup> inside the vacuole	Ben Ahmed et al. (2010)

<i>Sesuvium portulacastrum</i>	0, 100, 200, 300, 400, and 500 mM NaCl incorporated with Hoagland's nutrient solution	PN, transpiration rate (E), water use efficiency (WUE), antioxidant enzyme activity (CAT, GR, SOD, APX, and GPX)	Na <sup>+</sup> uptake and transport increased under NaCl presence	Muchate et al. (2016)
<i>Hordeum vulgare</i> L. (barley)	0, 50, 100, 150, and 200 mM NaCl	Germination, the radicle breaching, and the coleoptile's emergence	NaCl, at doses up to 200 mM, slows the rate of barley germination without affecting their ability to germinate. During the phase of coleoptile's emergence, barley cultivars show greater sensitivity to NaCl than during radicle breaching.	Abdi et al. (2016)
<i>Sarcocornia frutescens</i> (L.)	10 (control), 60, 100, 200, and 300 mM NaCl	DW, biomass allocation, tissue water content	Increase Cl <sup>-</sup> and Na <sup>+</sup> uptake used instead of organic osmolytes Increase of succulence in shoots at higher salt concentrations and the ability to maintain a lower K <sup>+</sup> /Na <sup>+</sup> ratio and higher K-Na selectivity in all organs	García-Caparrós et al. (2017)
<i>Barbarea verna</i> , <i>Capsella bursa-pastoris</i> , <i>Hirschfeldia incana</i> , <i>Lepidium densiflorum</i> , <i>Malcolmia triloba</i> , etc.	Starting 25 days after sowing (DAS), plants watered with 150 mM NaCl for 30 days	Germination, root elongation, leaf water relation, Na <sup>+</sup> , K <sup>+</sup> , stomatal size and density	The control of transpirational water flux (i.e., via stomatal and/or aquaporin regulation) that is associated with ion loading and accumulation	Orsini et al. (2010)
<i>Plantago crassifolia</i> L.	100, 200, 300, 400, or 500 mM NaCl	Germination, seedling recovery, plant growth, proline content, soluble sugar fraction	Proline may still play an important role in the protection against high salinity "Osmolytes" work primarily through oxidative detoxification	Vicente et al. (2004)
<i>Atriplex halimus</i> L., <i>Atriplex nummularia</i> L.	0, 300, 600, 800, and 1000 mM NaCl; 0, 300, 600, 800, and 1000 mM KCl	Leaf tissue water, leaf area, (Na <sup>+</sup> , Ca <sup>2+</sup> , K <sup>+</sup> , Mg <sup>2+</sup> ), proline concentration	High absorption and transport of Na <sup>+</sup> to shoots and its use for osmotic adjustment The efficiency of the vacuolar compartmentalization of Na <sup>+</sup> ions The salt tolerance depends upon the chemical composition of the salts in the soil solution	Belkheiri and Mulas (2013)
<i>Matricaria recutita</i> L.	0, 6, 9, and 12 dS m <sup>-1</sup> NaCl	POX activity, oil and chamazulene content, flavonoid compounds	Increasing of POX activity, flavonoid content, and chamazulene content Root growth stimulation at 9 ds m <sup>-1</sup> NaCl Na compartmentation in root at 12 dS m <sup>-1</sup> NaCl	Askari-Khorasgani et al. (2017)

#### 4.4.1 *Morphological and Anatomical Adaptations of Plants*

Native plants in saline and desert environments have developed, over time, certain traits that give them the ability to develop in these stressful conditions. These traits are often of morphological and anatomical types. However, scientific studies have been done on the development and role of these morpho-anatomical features and also studies with other adaptative reactions of plants to the salt stress.

The most obvious morphological adaptations of plants in saline desert habitats are the reduction in leaf size and the number of stomata per unit leaf area, the increase in succulence and cuticle thickness of the leaf, and the formation of a layer of wax (Gale 1975; Mass and Nieman 1978). These adaptations play a crucial role in the conservation of water for the development of the plant in saline conditions. More recently, it has been shown that there is variability among the *Cenchrus ciliaris* ecotypes that allows it to withstand severe salinity conditions especially during drought periods (Hameed et al. 2015).

These are the most visible adaptations found throughout the plant (Dickison 2000). At the leaf level, there are certain structures that allow the plant to secrete excess salt. The most important are the secretory trichomes (*Atriplex* spp.) and the salt glands found in many plants of desert flora and coastal habitats. The latter are characteristic of a few families, including Poaceae, Avicenniaceae, Acanthaceae, Frankeniaceae, Plumbaginaceae, and Tamaricaceae (Mauseth 1988; Thomson et al. 1988, Marcum and Murdoch 1994).

Desert plants have usually succulent stems characterized by a well-developed water storage tissue in the cortex and marrow (Lyshede 1917; Dickison 2000). A multilayered epidermis may have thick walls, covered with thick cuticle surmounted by wax. For example, at *Anabasis* sp. the epidermis is formed of 8 to 11 layers. The stem of *Salicornia fruticosa* consists of a single cortex and an epidermis with a single thin-walled cell base. The palisadic and parenchymal tissue of photosynthetic organs is used for water storage (Fahn 1990).

The roots of xerohalophytes reduced the cortex to shorten the distance between the epidermis and the stele (Wahid 2003). The Caspari band is larger in dry-habitat plants than in mesophytes (Wahid 2003). In saline environment plants, the endoderm and exoderm represent barriers of variable resistance to the radial flow of water and ions, from the cortex to the stele (Hose et al. 2001; Taiz and Zeiger 2002).

#### 4.4.2 *Salt Tolerance Mechanisms*

The physiological characterization of plant tolerance to salinity results from processes that allow the plant to absorb water and mineral salts from substrates with low hydric potential but also to live by accepting the important presence of the sodium in its tissues; halophytes, which accumulate the most sodium (Elzam and Epstein 1969, Guerrier 1984a), are distinguished by a strong capacity development

of organic compounds (Briens and Larhe 1982), these two factors allowing the maintenance of a high internal osmotic pressure which favors the water exchange between the external and cellular compartments (Guerrier 1984b).

All plants do not react in the same way to salt stress; according to their production of biomass in the presence of salt, four main trends have been discerned: The first is true halophyte, whose production of biomass is stimulated by the presence of salt. These plants (*Atriplex* sp., *Salicornia* sp., *Sueda* sp.) present extensive adaptations and are naturally favored by soil salinity. Optional halophytes can show a slight increase in biomass at levels low in salts: *Plantago maritima* and *Aster tripolium*. Nonresistant halophytes can support low concentrations of salts: *Hordeum* sp. Glycophytes or halophytes can be sensitive to the presence of salts: *Phaseolus vulgaris* (Cheeseman 2015).

The adaptation reaction of various glycophytes to different salt stress treatments is presented in Table 4.4.

According to Munns et al. (2006), tolerance of cereals to salinity depends on variability genetics such as some species that resist this type of abiotic stress than others. In particular, the toxic effect of salts is less pronounced in common wheat than in durum wheat. This character is conferred by the presence of *Kna1*, a gene responsible for the exclusion of sodium. In addition barley can grow normally under conditions considered as limiting. Indeed, in addition to the exclusion of sodium, the barley plant uses another salinity tolerance mechanism that manifests itself by the imprisonment of salts in a very specific compartment in the leaf. This not only spares their effects toxic but also counteracts the osmotic pressure of the soil (Munns and Tester 2008).

#### **4.4.3 Ion Exclusion and Compartmentalization Mechanisms of Plant Tolerance to Salinity**

According to Berthomieu (1988), the plant prevents salt from rising up to leaves. A first barrier exists at the level of the endoderm, an inner layer of the root. However, this barrier can be interrupted, especially during emergence ramifications of the root. Other mechanisms limit the passage of salt from the roots to leaves, but the genes that govern them are still largely unknown.

It is also indicated that the exclusion capacity of  $\text{Na}^+$  and/or  $\text{Cl}^-$  stems is good correlated with the degree of salt tolerance. Maintaining a low concentration of Na in the leaves may be due to an exclusion mechanism that causes an accumulation of Na in the roots, avoiding excessive translocation to the stems; but it can also be linked to a high mobility of this element in the phloem. However, some physiological measures concord to suggest the existence of an active expulsion of cytoplasmic sodium apoplasm or to the vacuole, thus protecting enzymatic equipment from the cytoplasm in aerial organs (Greenway and Munns 1980).



**Table 4.4** Adaptive responses to salt stress in different glycophytes

Plant species	Salt stress	Photosynthetic parameters measured	Adaptive response to salt stress	References
<i>Matricaria chamomilla</i> L. (German chamomile)	0, 50, 100, 150 mM NaCl	Na, K, Fe, soluble carbohydrates, proline	The difference in growth at the salinity treatments can be attributed to differences in ion transfer rates to the leaves and proline and carbohydrate accumulation	Heidari and Sarani (2012)
<i>Amaranthus cruentus</i> L.	5 g L <sup>-1</sup> NaCl	DW, pigment content photosynthesis rate, transpiration, antioxidant enzyme activities	5 g L <sup>-1</sup> of NaCl does not affect the yield as well as its pigment content, photosynthesis, transpiration rate, stomatal conductance, or antioxidant enzyme activities	Quin et al. (2013)
<i>Brassica rapa</i> L.	0, 50, 100, and 150 mmol NaCl	DW; FW; shoot length; root length; chlorophyll <i>a</i> , <i>b</i> , <i>a + b</i> ; proline contents; relative water content (RWC)	Increasing proline content in leaves Low plant dry mass at high salt concentrations High salinity levels decrease normal photosynthetic and other biological processes	Jan et al. (2017)
Tomato landrace	0, 300, 450, and 600 mM NaCl	FW, DW, leaf gas exchange, CO <sub>2</sub> assimilation rate, transpiration rate, stomatal conductance (g <sub>s</sub> ), intercellular CO <sub>2</sub> concentration (C <sub>i</sub> ), total soluble sugars, total antioxidant capacity	Changes in total antioxidant capacity and leaf pigment content that emphasized the occurrence of modifications in the photosynthetic apparatus according to salt gradient The more efficient assimilate supply and an integrated root protection system provided by sugars and antioxidants can explain the significantly higher root/shoot ratio	Moles et al. (2016)
<i>Triticum aestivum</i> L. (wheat)	200 mmol NaCl	RWC photosynthetic rate (Pn) and stomatal conductance (gs)	Under salt stress, the salt-resistant cv. YN19 had higher efficiency in photosynthetic electron transport, hence maintaining higher photosynthetic rate under salt stress, compared with the salt-sensitive cv. JM22	Sun et al. (2016)
<i>Lolium perenne</i> L. (ryegrass)	0, 0.15, and 0.30 M NaCl	JIP test parameters	JIP test estimated higher potential photosynthetic efficiency (vitality) during salt stress conditions in the most tolerant variety	Dąbrowski et al. (2016)



<i>Glycine max</i> L. (Merr.) (soybean)	0.59% NaCl kg <sup>-1</sup> 1.29% NaCl kg <sup>-1</sup> soil	Gas exchange parameters (PN, gs, Ci, E, Fv/Fm, and ETR)	Regression analysis indicated that there has been found extremely significantly positive correlation between GY and P <sub>N</sub> in field condition P <sub>N</sub> parameter can be used as physiological index for field resistance of soybean to salt stress	He et al. (2016)
<i>Beta vulgaris</i> sp. L. (sugar beet)	50 mM NaCl applied in 50 mM increments each day over 6 days until a final level of 300 mM	ΦPSII, Rubisco activity, chlorophyll and protein contents, enzyme activities, phosphoenolpyruvate carboxylase (PEPC) activity, chloroplast metabolite level	The contribution of chloroplasts and the extra-chloroplast space to salinity tolerance via metabolic adjustment	Hossain et al. (2017)
<i>Amaranthus cruentus</i> L.	0, 25, 50, 75, and 100 mM of NaCl. NaCl was added gradually (25 mM of NaCl day <sup>-1</sup> ) to avoid osmotic shock	Plant height, DW, proline, sugar, amino acid, carbohydrates	Reduction in the relative water content and membrane integrity suggest a low ability of experimental cultivar to adjust osmotically under salt stress The K <sup>+</sup> /Na <sup>+</sup> ratio abruptly decreased in 25 mM of NaCl, suggesting an ionic imbalance, which may partially explain the salt-induced growth reduction	Menezes et al. (2017)
<i>Chrysanthemum patulosum</i>	0, 50, 100, 150, and 200 mM NaCl	Plant growth parameters, ion leakage, leaf relative water content (RWC), leaf chlorophyll concentration (SPAD-502)	The water content and cell turgor may relatively be preserved under saline conditions An increase in ion concentrations (Na <sup>+</sup> and Cl <sup>-</sup> ) induced from salinity largely contributed to a decrease in leaf osmotic potential, and this adaptation allows plants to keep cell turgor by continuing water uptake	Yasemin et al. (2017)
<i>Oryza sativa</i> subsp. indica cv	200 mM NaCl	Cytokinin oxidase activity	Previous studies have shown that an enhanced CK content improves stress tolerance ability. Previous studies have shown that an enhanced CK content improves stress tolerance ability. Enhanced cytokinin activities improves stress tolerance ability of rice	Joshi et al. (2017)

(continued)

Table 4.4 (continued)

Plant species	Salt stress	Photosynthetic parameters measured	Adaptative response to salt stress	References
Matricaria Recutita L. (chamomile)	2, 6, 9, and 12 dS m <sup>-1</sup> NaCl	Nutrient uptake, plant productivity, essential oil and chamazulene percentage	The difference responses to productivity and salt resistance were attributed to the genetic variation, higher root-to-shoot ratios, and compartmentalization of sodium in roots of the Shiraz and Ahvaz genotypes, leading to better nutrient uptake and balance, while the nutrient composition was relatively in the same range for all genotypes. The differential responses to productivity and salt resistance were attributed to the genetic variation, higher root-to-shoot ratios, and compartmentalization of sodium in roots, leading to better nutrient uptake and balance	Askari-Khorasgani et al. (2017)

An organism can hardly exclude the  $\text{Na}^+$  completely of its tissues. At the plants, one of the best-known salinity tolerance strategies is compartmentalization ions ( $\text{Na}^+$ ,  $\text{Cl}^-$ ) in excess in the tissues. This controlled redistribution is mainly in vacuoles (Niu et al. 1995) and possibly at the whole-plant scale, in the oldest or least sensitive organs (Cheeseman 1988a, b; Munns 1993).

To be controlled, the movement of ions through the membranes involves an active transport, energy consumer, who uses different carriers (in variable density) to the surface of cell membranes (Orcutt and Nelen 2000; Tyerman and Skerret 1999; Al-Khateeb 2006). Once vacuolated, the excess  $\text{Na}^+$  contributes to the osmotic adjustment without altering the process metabolic rate (Levitt 1980; Yeo 1983, 1998).

The best way to maintain a low cytoplasmic concentration in  $\text{Na}^+$  is to compartmentalize this ion in the vacuole. This intracellular compartmentalization can be associated with succulence, which increases the volume of vacuoles in which  $\text{Na}^+$  ions accumulate. These ions are pumped into the vacuole before being concentrated in the cytoplasm. Ion pumping is provided by  $\text{Na}^+/\text{H}^+$  antiports. The difference in pH is restored by  $\text{H}^+$ -ATPase and pyrophosphatases (Blumwald 2000). Anti- $\text{Na}^+/\text{H}^+$  activity was increased following the addition of  $\text{Na}^+$  in wheat roots (Garbarino and DuPont 1989), tomato (Wilson and Shannon 1995), and sunflower (Ballesteros et al. 1997). Stimulation of activity is greater in the tolerant species, *Plantago maritima*, than in susceptible species, *Plantago media* (Staal et al. 1991). In sensitive rice, however, salinity does not induce the activity of anti- $\text{Na}^+/\text{H}^+$  antibodies in tonoplasts (Fukuda et al. 1998). Salinity also induces the activity of  $\text{H}^+$  vacuolar pumps in tolerant and sensitive plants (Hasegawa et al. 2000). To maintain the osmotic balance between the vacuole and the cytoplasm, there will be synthesis of compatible organic compounds. Generally these compatible compounds protect the biochemical reactions against high concentrations of inorganic compounds (Shomer et al. 1991). These compatible compounds are neutral and highly soluble and contain secondary metabolites such as glycine betaine, proline, and sucrose (Hu and Schmidhalter 2000). There is a close correlation between the synthesis of these organic compounds and tolerance to salinity or drought. This correlation has been noted in maize (Saneoka et al. 1995). These compounds appear to be very effective in maintaining a negative osmotic potential in the cytoplasm and in protecting proteins and ribosomes against the deleterious effects of  $\text{Na}^+$  ions. Although organic compounds give the plant some tolerance to salinity, they need to be accompanied by strong regulation of  $\text{Na}^+$  pumps.

#### 4.4.4 Tolerance of Halophyte Plants to Salinity

Plants in salt-exposed (e.g., coastal) environments have certainly acquired characteristics to adapt to soils whose chemical composition varies in time and space, depending on salinity and associated stress (Ben Hamed et al. 2013). Therefore, the adaptations of these coastal plants are complex and different. Nowadays, many

authors study halophytes as plant object with developed mechanisms of salt resistance. Halophytes are plants which can be productive under stress (Ben Hamed et al. 2013; Llanes et al. 2013; Slama et al. 2015).

Salinity tolerance reflects the ability of plant halophytes to grow and complete their life cycle in environments containing soluble salts at high concentrations. Halophytes are characterized by low morphological and taxonomic diversity. At the same time, halophytes require salt for optimal growth. The high concentrations of the ions in the tissues of halophytes suggest that their metabolic process may be more tolerant to salt stress compared to the glycolytic metabolism.

#### **4.4.5 Regulation of Salt Loads in Aerial Parts**

##### **4.4.5.1 Salt Release in Aerial Parts**

Soluble substances pass from the inside of the leaves to the outside where they are accumulated. These substances are released from the leaves through the epidermis and stored in the cuticle. It is called pseudo-secretion (Klepper and Barrs 1968). The sodium is the most flexible element among osmotic cations. However, chlorine is the most flexible element among anions (Tukey et al. 1958; Tukey and Morgan 1962). The release of electrolytes is highly dependent on the plant water status. The salts released from the leaves of *Atriplex* sp. normally present half of the leaf contents. The phenomenon of salt release in coastal areas where mangroves and other native halophytes grow is based on the desalination process with halophyte participation.

##### **4.4.5.2 Guttation**

Salt glands are not the only structures through which salt is removed from the plant. Hydathodes are structures which can also eliminate water. Guttation is a common phenomenon in young leaves. The liquid obtained is not a direct secretion of the xylem sap. In fact, the content of nutrient ions in the xylem sap liquid is much lower compared to the sap liquid from the other plant tissues.

Guttation liquid contains mainly calcium, carbonate, sodium, and silicate. In some plant species, hydathodes can function as salt glands and participate in the selective removal of ions. The secretion of salt in this way may be important in young halophytes that develop under humid conditions.

##### **4.4.5.3 Elimination of Organs Saturated with Salt**

It is a phenomenon that can eliminate a large amount of salt in halophytes. In some species such as *Juncus maritimus* or *Juncus gerardii*, leaves fall after being loaded with unwanted ions. Some succulent plants such as *Halocnemum* or *Salicornia* get

rid of part of the cortex. This part of the cortex released large amount of salt, which allows the plant to survive (Chapman 1960).

#### 4.4.5.4 Remobilization of Salt

The substances accumulated in the aerial parts can be transported by the phloem vessels to the roots and after into the rhizosphere. This has been verified for sodium (Cooil et al. 1965). A similar process has been observed for *Suaeda monoica* and *Salicornia europaea* (Von Willert 1968). Salt recirculation also exists in non-excretory mangroves (Scholander et al. 1962; Atkinson et al. 1967).

#### 4.4.5.5 Accumulation of Salt in Secretory Epidermic Hairs

In some species, epidermic hairs remove salt from sensitive sites of leaf mesophyll. The epidermic hairs work for a short time, but they are very effective. Salt accumulation by vesicle traffic under salt stress is widely known in semi-halophytic and halophytic species of the family Chenopodiaceae. For example, in *Atriplex*, salt hairs or trichomes are formed by two cells: a small basal cell and a large vesicle (Osmond et al. 1969, Mozafar and Goodin 1970). The basal cell has a high structural similarity with the cells of the salt glands. It is characterized by a dense cytoplasm rich in mitochondria, endoplasmic reticulum, and numerous small vesicles. It differs from glandular cells by the presence of chloroplasts.

#### 4.4.5.6 Excretion of Salt

Salt excretion is the most important mechanism which supports halophyte resistance to salinity (Waisel 1972). It allows plants to eliminate excess salt and prevents excessive buildup without reaching toxic levels inside the tissues. It is typical for several halophyte species: Convolvulaceae, Frankeniaceae, Poaceae, Primulaceae, Tamaricaceae, Avicenniaceae, and Plumbaginaceae.

### 4.4.6 Salt-Secreting Structures

#### 4.4.6.1 Trichomes

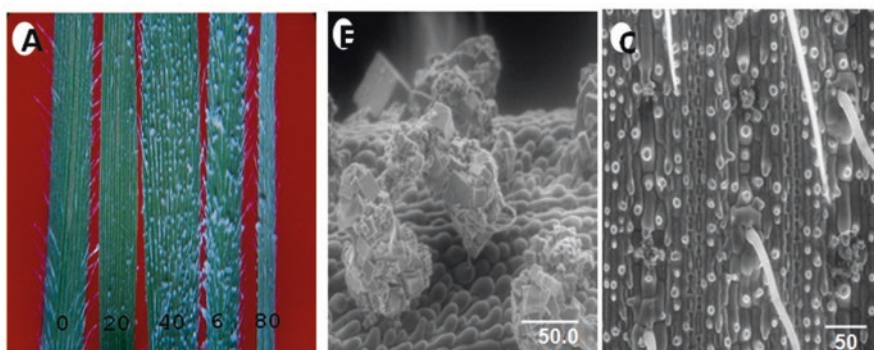
The secretory trichomes of salt are typical for *Atriplex* spp. These are vesicles that emerge at the leaf surface. They consist of a large secretory cell or vesicle at the apex or vesicle from one or a few cells on a pedicel (Smaoui 1971; Dickison 2000). These cells have mitochondria, dictyosomes, ribosomes, endoplasmic reticulum, and a large flattened nucleus. Chloroplasts are found also but rudimentary or

partially developed. In the secretory cell or vesicle is present a large vacuole, while the cell on the pedicle contains the several small vacuoles (Osmond et al. 1969). A symplasmic continuity exists between the mesophyll cells and the secretory cell, for the movements of the ions. The outer walls of vesicular and pedicellar cells are cutinized, while the inner walls are not (Thomson and Platt-Aloia 1979). The salts are externally released by the removal of the leaf.

#### 4.4.6.2 Salt Glands

The glands of herbaceous plants are usually bicellular and formed of an apical and basal cell. They can be submerged, semi-sunken, extended outside the epidermis (Lipshitz and Waisel 1974; Marcum and Murdoch 1994), or lying on the leaf surface in parallel lines on the ridges (Marcum et al. 1998). In dicotyledons (Fig. 4.7), salt glands are multicellular, consisting of basal cells and secretory cells. The number of cells can vary from 6 to 40 depending on the plant genus (Fahn 1990). For example, in *Tamarix* spp., salt glands are composed of two basal and internal collecting cells and six external secretory cells (Mauseth 1988). The glands of *Avicennia* and *Glaux* contain several secretory cells surmounting a discoidal basal cell (Rozema and Riphagen 1977).

At the ultrastructural level, glandular cells in dicotyledonous herbaceous plants contain some lipid bodies, a large flattened nucleus, an endoplasmic reticulum, ribosomes, several mitochondria, rudimentary plastids, and small vacuoles (Thomson 1975). The glands are covered with an elongated cuticle at the level of the excretory cell to form a collecting chamber, in which the salt accumulates before being excreted outside. There is continuity between the basal cell and the apical cell and between the basal cell and the mesophyll cells, thanks to plasmodesmata (Zeigler and Lüttge 1967).



**Fig. 4.7** Salt excretion on adaxial leaf side of *Aeluropus littoralis* plants treated with 0, 200, 400, 600, and 800 mM NaCl observed with a magnifying glass ( $\times 4$ ) (a). Note that leaves were more or less rolled. SEM micrographs of salt crystals observed on adaxial leaf surface from 400 mM NaCl-treated plants (b). Adaxial leaf surface of 400 mM NaCl-treated plant which was washed and observed 2 h later. The appearance of salts indicates location of salt glands (c)

#### **4.4.7 Osmotic Adjustment**

The one of the main physiological traits of tolerance to environmental stress is the osmotic adjustment. This one is realized, thanks to an accumulation of osmoregulatory compounds that may be ions such as  $K^+$  and  $Cl^-$  or organic compounds such as soluble sugars (fructose, glucose, trehalose, raffinose, fructans) and certain amino acids (proline, glycine betaine,  $\beta$ -alaninebetaine, proline betaine) leading to a reduction of the osmotic potential, thus allowing the maintenance of the turgor potential (Zivcak et al. 2016). The accumulation of these compounds has been evident in several plant species subjected to salt stress. It varies in large proportions depending on the species, the stage of development, and the degree of salinity. The differences in solute accumulation (free amino acids, proline, and total soluble sugars) between control plants and plants subjected to salt stress are very important. This phenomenon allows the maintenance of many physiological functions (photosynthesis, transpiration, growth, etc.) and can intervene at all stages of plant development. It allows protection of membranes and enzymatic systems especially in organs where proline appears to play a role in maintaining cytosol-vacuole pressures and pH regulation (El Hassani et al. 2008).

#### **4.4.8 Regulation of Growth by Phytohormones Under Salt Stress**

They have been shown to have physiological responses to various stresses such as drought or salinity and have similar characteristics. They cause a whole increase in the ABA concentration in the aerial part or a reduction in concentrations in cytokinin (Itai 1999). According to Zhu (2001), the reduction of growth is an adaptative capacity necessary for survival of a plant exposed to abiotic stress. Indeed, this delay in plant development can support energy accumulation and resources to limit the effects of stress before that the imbalance between the inside and outside of the plant body does not increase until a threshold where the damage is irreversible. To illustrate this trend, in nature, growth is inversely correlated with salt stress resistance of a species or variety (Zhu 2001). In more control of growth by hormonal signals, the reduction of growth results from the expenditure of resources in adaptation strategies and cytosol-vacuole and pH regulation (Hassani et al. 2008).

#### **4.4.9 Mechanism of Membrane Control Under Salt Stress**

Adaptation to salt stress is also taking place at the level of membrane cell (plasma membrane, tonoplast). The qualitative and quantitative modification of aquaporins (transmembrane proteins) is, for example, a process capable of modifying the water

conductivity of the plant and promoting restricting water movements (Yeo 1998). In terms of ion transport, the salinity resistance strategy is qualitative and quantitative. The selectivity of the ions at the input constitutes the component which is defined from the different recent membrane transporters ( $\text{Na}^+/\text{H}^+$ ). In the diffusion facilitated as in the active transport, the membrane proteins can be very specific to certain solutes. Nevertheless, several solutes can compete for the same transport protein ( $\text{Na}^+$  and K). From a point of quantitative view,  $\text{Na}^+$  membrane permeability and activity, quantity, and sensitivity of the membrane  $\text{Na}^+/\text{H}^+$  antiports evolve to adapt to sodium stress at long term (Niu et al. 1995; Tyerman and Skerrett 1999).

#### ***4.4.10 The Biological Compounds, Trace Elements Useful for Mitigation of Salt Stress Effects***

##### **4.4.10.1 Jasmonic Acid and Salicylic Acid**

Generally, under stressful conditions such as salinity stress, plants employ multiple mechanisms to increase their tolerance (Borsani et al. 2003). One of the adaptive plant responses to salt stress is the production of phytohormones such as abscisic acid, salicylic acid (SA), and jasmonates that might be involved in the alleviation of salinity stress (Wang et al. 2001; Yoon et al. 2009). It was observed that SA reduced salt stress injuries via enhancing antioxidant enzyme activities. Antagonistic effects of abscisic acid and jasmonates on salt stress-inducible transcripts have been found (Moons et al. 1997).

Plant hormones such as methyl jasmonate (MeJA) and jasmonic acid (JA) have an ameliorating effect on different plant species under salt stress (Yoon et al. 2009; Manan et al. 2016). Jasmonates play a role of cellular regulators in the response to stress factors, such as salt, drought, and heavy metal (Anjum et al. 2011; Poonam et al. 2013; Qiu et al. 2014).

Jasmonic acid (JA) and methyl jasmonate (MeJA), which is the methyl ester of JA, are natural plant growth regulators, involved in regulation of the morphological, biochemical, and physiological processes in plants. Their exogenous plant treatment under conditions of high salinity can support the development of biomass yield (Sheteawi 2007).

The several studies have shown that methyl jasmonate can diminish the inhibitory effect of NaCl on photosynthesis rate and can enhance the growth and development of plants (Hristova and Popova 2002; Javid et al. 2011). Application of JA after the stress decreased the adverse effect of high salinity on photosynthesis and growth of barley (Tsonev et al. 1998). In addition, exogenous pretreatment of JA could ameliorate salt-stressed rice seedlings, particularly in salt-sensitive cultivars, and could decrease sodium concentration remarkably (Kang et al. 2005).



#### 4.4.10.2 Brassinosteroids

One of the promising options to mitigate the detrimental effects of salt stress is the exogenous application of plant protectants such as brassinosteroids (BRs) (Vardhini and Anjum 2015). BRs belong to plant polyhydroxysteroids, which are important for the regulation of plant growth and development.

The ability to protect the cellular structures was documented for 24-epibrassinolide (EBL), which reduced damage to membrane lipids, and hence a low MDA concentration. MDA, a product of polyunsaturated fatty acid decomposition, is used as a marker to assess the lipid peroxidation in plasmalemma or organelle membranes, which typically occurs in stress conditions (Sharma et al. 2012). The peroxidation of lipids disturbs the bilayer structure, affecting the membrane fluidity, permeability, bilayer thickness, and other membrane properties due to oxidative damage of lipids and membrane proteins. This may alter ion gradients, strongly influencing the metabolic processes. The lipid peroxidation caused by salt stress is probably one of the major reasons inhibiting plant growth.

In perennial ryegrass exposed to salt stress, it was observed that the treatment by exogenous brassinosteroids led to higher  $K^+$ ,  $Ca^{2+}$ , and  $Mg^{2+}$  content and lower  $Na^+/K^+$  ratio (Sun et al. 2015). The exogenous brassinosteroid application led also to upregulation of antioxidant enzyme (SOD, CAT, and APX) activity, keeping the level of plant hormones at a physiologically favorable level and an increase of proline and ion content ( $K^+$ ,  $Ca^{2+}$ , and  $Mg^{2+}$ ). Exogenous brassinosteroids could prevent the nutritional imbalance and ion toxicity under salt stress (Wu et al. 2017). The main effects of brassinosteroid use have been presented in Table 4.5.

#### 4.4.10.3 Amino Acids: Glycine Betaine and Proline

Amino acids glycine betaine and proline are effectively used for exogenous treatment to mitigate salt stress effects on plants (Sobahan et al. 2012; Li et al. 2014). Improvements of salt tolerance can be partly attributed to more favorable water status, as well as to activity of antioxidative enzymes in leaves, especially of peroxidase. It was found that mitigative effects of exogenous proline in salt stress conditions are more efficient than exogenous application of betaines (Hoque et al. 2007). The proline compared to the betaine can directly scavenge superoxide ( $O_2^{\cdot-}$ ) or hydrogen peroxide ( $H_2O_2$ ) and induce an increase of antioxidant enzyme activities (Demiral 2004; Ashraf and Foolad 2007; Nawaz and Ashraf 2010). At the same time, the unequal reaction of antioxidative enzymes has been observed under different level of salt concentrations. Treatment of 5 mM proline significantly reduced POX3 activity, which resulted in modulating salinity stress compared to 200 mM concentration (Varjovi et al. 2016). Therefore, it is obvious that the effect of proline in plants exposed to salinity is specific, at least to some extent.

The role of proline and also betaine in maintaining the plant water status under salt stress is important, as the initial slowdown of plant growth after salt imposition is a result of salt osmotic effects (Munns and Tester 2008; Yang and Lu 2006). The

**Table 4.5** Use of exogenous brassinosteroids to mitigate the salt stress effects on plants

Plant species	Mitigation effects on development of salt stress	References
<i>Cucumis sativus</i> L.	Increasing the contents of free proline and soluble sugar Increasing the activity of antioxidative enzymes (SOD, POX, CAT) Effective protection of membrane from salt stress	Shang et al. (2006)
<i>Pisum sativum</i> L.	Increasing FW and DW, seedling height, enhanced photosynthesis rate (Pn), stomatal conductance (gs), total chlorophyll contents (Chl), proline contents Increasing the activity of antioxidative enzymes (SOD, POX, CAT) Increasing the activity of nitrate reductase activity (NRA) and nitrite reductase activity (NiRA)	Shahid et al. (2011)
<i>Oryza sativa</i> L.	Improvement in the growth, level of protein, and proline content Increasing the activity of antioxidative enzymes (SOD, APX, CAT, GPX, and MDHAR)	Sharma et al. (2012) Özdemir et al. (2004)
<i>Brassica juncea</i> L.	Enhancing level of pigments and photosynthetic parameters Improving membrane stability index and relative water content Increasing the activity of antioxidative enzymes (SOD, POX, CAT)	Ali et al. (2008)
<i>Capsicum annuum</i> L.	Increasing relative growth rate and water use efficiency Improving photosynthesis by increasing stomatal conductance	Samira et al. (2012)
<i>Lolium perenne</i> L.	Decrease of electrolyte leakage (EL), malondialdehyde (MDA), and H <sub>2</sub> O <sub>2</sub> contents Enhancing the leaf relative water content (RWC), proline, soluble sugar, and soluble protein content Reducing the accumulation of Na <sup>+</sup> and increased K <sup>+</sup> , Ca <sup>2+</sup> , and Mg <sup>2+</sup> contents	Sun et al. (2015)

water-retaining ability can enhance salt tolerance by preventing too high concentration of ions (Romero-Aranda et al. 2006).

In rice, it was found that exogenous application of glycine betaine and proline may suppress the Na<sup>+</sup> uptake from the apoplast, preventing the detrimental effects of salts (Yang and Lu 2005; Sobahan et al. 2012). Proline inhibits opening of stomata, which keeps the transpiration and Na<sup>+</sup> uptake low. Moreover, in rice treated with betaine, the cells of the root tip and root cap produced numerous vacuoles, playing a role of storage vessels for Na<sup>+</sup> (Rahman et al. 2002). Thus, the specific functions of proline and betaine can contribute to improvements of salinity tolerance.

The use of exogenous proline can balance grain and straw yields under increased salinity levels. The production of grain and straw yields under salt stress conditions after the use of exogenous proline was kept on the significant level. Foliar application of proline and betaine decreased the sodium content and uptake by plants. Thus, it can be concluded that the exogenous application of proline and betaine may mitigate significantly the salt stress effects in crop plants (Siddique et al. 2015; Athar et al. 2015).

#### 4.4.10.4 Polyamines

Polyamines (PAs) are abundant compounds, present in plant cells in concentrations from 10  $\mu\text{M}$  to 10 mM (Roychoudhury et al. 2011). They represent low-molecular-weight, straight-chain, aliphatic amines, including the diamine putrescine ( $\text{Put}^{2+}$ ), triamine spermidine ( $\text{Spd}^{3+}$ ), and tetramine spermine ( $\text{Spm}^{4+}$ ), and are involved in various biochemical and physiological processes related to the regulation of plant growth and development (Puyang et al. 2015). Thanks to their polycationic nature at physiological pH, these compounds can interact with membrane phospholipids, proteins, nucleic acids, and constituents of cell walls, which stabilize these molecules (Roychoudhury et al. 2011).

In the last period, the role of polyamines as second messengers was investigated, especially in response to environmental stresses like osmotic stress, salinity, drought, heat, mineral nutrient deficiency, heavy metals, pH variation, UV irradiation, etc. (Liu et al. 2015). It was documented that exogenous spermidine application diminished the oxidative stress induced by salinity, leading to lower MDA,  $\text{H}_2\text{O}_2$ , and  $\text{O}_2^-$  concentrations in cultivars of bluegrass. Results indicated that exogenous spermidine treatment is able to improve quality of turfgrass, thanks to promoting the tolerance to salinity by eliminating the oxidative damages and upregulating activities of antioxidative enzymes directly or through gene expression (Puyang et al. 2015).

Spermidine efficiently alleviated the inhibitory role of alkaline ions on plant growth and inhibited related oxidative stress (Zhang et al. 2015). At the same time, the exogenous spermidine treatment had positive effects on nitrogen metabolism and activity of its enzymes in tomato seedlings under salt stress (Zhang et al. 2013). Exogenous spermidine application helps tomato seedlings to overcome salinity stress by regulation of protective mechanism of plant cells, including activating of detoxification, which may protect the cellular structures from oxidative damage under salinity stress. Exogenous spermidine is also able to increase salt tolerance of *Panax ginseng* by upregulation of scavenging enzyme activities, which eliminates the oxidative impairment (Parvin et al. 2014).

#### 4.4.10.5 Paclobutrazol

The enhancement of salt tolerance in plants can be achieved through exogenous application of plant growth regulators with specific effects on the content of key plant phytohormones and signal molecules (Kishor et al. 2009; Hu et al. 2017). Paclobutrazol [(2RS,3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1,2,4-triazol-1-yl)pentan-3-ol] is a triazole fungicide which regulates the plant growth mostly by antagonizing the hormone gibberellin (Hajihashemi et al. 2006; Kishor et al. 2009). Paclobutrazol and other triazole compounds are synthetic plant growth regulators, which cause different physiological responses in plants, such as increasing content of chlorophylls, promoting net photosynthesis, regulating cytokinin biosynthesis, inhibiting ABA biosynthesis, reducing free-radical damage, and enhancing the

peroxidase and SOD activities and proline content (Kishor and Sreenivasulu 2014; Khunpon et al. 2017).

Paclobutrazol has also morphological effects on the leaf thickness, cuticle and epidermis, palisade layer, and spongy layer. It can reduce the diameter of xylem vessels; however the phloem elements had shown an increased diameter (Tehranifar et al. 2009). Exogenous treatment has also stimulated effect on root growth and decreasing shoot growth (Banon et al. 2003; Nivedithadevi et al. 2012). Some authors suggest that the paclobutrazol minimizes the absorption of toxic ions such as  $\text{Na}^+$  and  $\text{Cl}^-$ , which eliminates the negative effects of NaCl. Moreover, the experimental results supported the role of paclobutrazol in upregulating the  $\text{K}^+$  uptake (Kishor and Sreenivasulu 2014; Hu et al. 2017). We can conclude that paclobutrazol can improve important plant responses and increase crop production with a consequent benefit to saline agriculture.

#### 4.4.10.6 Trace Elements and Nanoparticles

During the last few years, rapid advances of nanotechnology are associated with release of different types of nanoparticles. Some of them may be accumulated in soil or natural environment with negative effects on biota (Alharby et al. 2016; Yassen et al. 2017). The authors have reported the detrimental effects of nanoparticles (usually at relatively high concentration) on plant health. However, there is an evidence about the positive effects of nanoparticles, which is achieved at relatively low concentrations. This provides the scope for possible agricultural applications of nanoparticles (Siddiqui et al. 2014; Siddiqui and Al-Whaibi 2014; Askary et al. 2016).

One of the promising ways is the use of nanofertilizers. Applying the nutrients in the form of nanoparticles improves the nutrient use efficiency, with low risk of toxicity for soil microbiota and roots. Moreover, such a way of application reduces the frequency of the application and prevents the risk of overdosage. Hence, the potential of nanotechnology to support the sustainable farming is high, including developing countries (Naderi and Danesh-Shahraki 2013; Yassen et al. 2017).

The second way of application relates to exogenous use of trace elements and nanoparticles to mitigate stress effects by influencing some specific plant processes (Zhao et al. 2012; Rico et al. 2013; Rossi et al. 2016). For example, the zinc treatment led to lower MDA and  $\text{H}_2\text{O}_2$  concentration in tissues in the experimental plants under salt stress, which was associated with upregulation of total APX, CAT, POD, and PPO activities under salt stress (Weisany et al. 2012). Decreasing of lipid peroxidation and proline contents under salinity by applying  $\text{Fe}_2\text{O}_3\text{NPs}$  has been found in the peppermint plants. The appropriate concentration of iron nanoparticles can be used for stress resistance of the peppermint (Askary et al. 2017). Fathi et al. (2017) and Soliman et al. (2015) have demonstrated the positive influence of Zn and Fe and their NPs in stress conditions. Nanoparticles were more efficient than other tested forms of these micronutrients. It can be caused by their size, shape, distribution, and other physical characteristics. Latef et al. (2017) reported that priming of

seeds with ZNPs is a useful strategy to increase the salt tolerance of lupine plants. The most efficient was concentration of ZnO NPs 60 mg L<sup>-1</sup>.

It has been also shown that exogenous nanoparticles such as cerium oxide nanoparticles (CeO<sub>2</sub>-NPs) positively influence plant growth and production under normal growth conditions. Depending on soil moisture content, CeO<sub>2</sub>-NPs supported photosynthesis, which led to increase of water use efficiency (WUE), especially in water-restricted conditions (Cao et al. 2017). Under salinity, it was found that CeO<sub>2</sub>-NPs application led to improved plant growth and physiological responses of canola, improving the salt stress responses. However, the stress effects were not fully alleviated by CeO<sub>2</sub>-NPs (Rossi et al. 2016).

Adding SiO<sub>2</sub> nanoparticles was found to be able to improve germination and seedling early growth under salinity stress (Sabaghnia and Janmohammadi 2014; Siddiqui and Al-Whaibi 2014). In similar, nano-silicon (N-Si) was shown to improve seed germination, plant growth, and photosynthesis under environmental stresses in tomato (Almutairi 2016a, b).

Also in the case of application of AgNPs, the alleviative effects in conditions of salt stress were found, including positive influence on seed germination, growth of roots, and thus the overall growth and dry mass increase in tomato seedlings under NaCl stress (Almutairi 2016a). The combined application of AgNPs and salinity increased the soluble sugars and proline contents. On the other hand, it decreased catalase activity and increased peroxidase activity compared to the respective AgNP treatments alone. AgNPs enhanced the salt tolerance in wheat, but the long-term response of AgNPs under salt stress needs further investigation.

El-Sharkawy et al. (2017) have demonstrated that application of K nanoparticles in alfalfa may be more efficient than the use of conventional fertilizers, as the nutrition can be more adequate and this way of application may prevent the negative effects of salt stress in some specific conditions.

The abovementioned results suggest that the application of different nanoparticles is a promising strategy to stimulate the plant tolerance to salt stress. According to the many researchers, engineered nanoparticles have a great chance of getting into agricultural lands (Delfani et al. 2014; Benzone et al. 2015; Liu et al. 2015; Liu and Lai 2015; Mastronardi et al. 2015; Rastogi et al. 2017). We report that a common industrial nanoparticle could in fact have a positive impact on crops. Modern nanofertilizers are expected to contribute to the improvement of crop growth, photosynthesis, and tolerance to environmental stress, which will result to better nutrient and water use efficiency and yield increase.

## 4.5 Conclusion

Nowadays, the advances in research aimed at salt stress effects on plants at different levels, described broadly in this chapter, provide great opportunities to develop effective strategies to improve crop tolerance and yield in different environments affected by the soil salinity. It was clearly demonstrated that plants employ both the

common adaptative responses and the specific reactions to salt stress. Presented data may be helpful to understand the physiological, metabolic, developmental, and other reactions of crop plants to salinity, resulting in the decrease of biomass production and yield. In addition, the chapter provides an overview of modern studies on how to mitigate salt stress effects on photosynthetic apparatus and productivity of crop plants with the help of phytohormones, glycine betaine, proline, polyamines, paclobutrazol, trace elements, and nanoparticles. Plant production in saline agriculture can avoid or, at least, diminish the negative salt effects with use of different approaches and tools, which can have an economic impact worldwide but, especially, in most endangered developing countries.

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