Chapter 8
Structural and Functional Adaptations in Plants for Salinity Tolerance

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Abstract Salt tolerance in plants is a multifarious phenomenon involving a variety of changes at molecular, organelle, cellular, tissue as well as whole plant level. In addition, salt tolerant plants show a range of adaptations not only in morphological or structural features but also in metabolic and physiological processes that enable them to survive under extreme saline environments. Morpho–anatomical adaptations include xeromorphic characteristics like thick epidermis and sclerenchyma, well developed bulliform cells, increased density of trichomes and increased moisture retaining capacity by increasing cell size and vacuolar volume. Development of excretory structures like vesicular hairs and salt glands is another major structural adaptation and very crucial for salt tolerance. Physiological adaptations include restricted toxic ion uptake, increased succulence, osmotic adjustment and exclusion of toxic Na^+ and Cl^-.

Keywords Succulence · Osmotic adjustment · Salt exclusion · Ion uptake

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1 Introduction

Soil salinity is among the major abiotic stresses that limits crop productivity worldwide (Hu et al. 2005) since most crops are sensitive to soil salinization (Munns 2002). There are two major processes of soil salinization; geo–historical processes and man–made. Most of the worldwide salt–affected lands are the result of natural causes, i.e., from accumulation of salts over long time period, and this occurs mainly in arid and semiarid zones (Rengasamy 2002). One way of soil salinization is weathering of the rocks that releases soluble salts, which is mainly in the form of sodium chloride and calcium chloride (Szabolcs 1989), other being salt accumulation due to the deposition of salts from oceans by wind or rain (Munns and Tester 2008). Man–made saline soils are mostly found in (semi) arid lands as a result of over-irrigated agriculture, and hence in the rise of water tables. This is the main factor of increasing salinity in agricultural lands (Munns et al. 2002).

Soil salinity is an ever–increasing problem worldwide and it is estimated that the saline soils approach 930 million ha, about 7 percent of the total land worldwide (Szabolcs 1994). Nearly, one third of the total 230 million ha under irrigation is uncultivable due to soil salinity (Oldeman et al. 1991; Ghassemi et al. 1995). Of this total, 15.57% is located in Africa, 5.07% in Australia, 0.57% in Mexico and Central America, 1.80% in North America, 20.21% in South America, 26.70% in North and Central Asia, 24.25% in Southern Asia, and 5.82% in Southeast Asia (Massoud 1974). A large number of plants are found to grow on these areas but tolerance varies greatly not only among species but also within species. Among monocotyledonous crop plants, rice is the most sensitive, bread wheat moderately tolerant and barley the most tolerant. The halophytic tall wheatgrass, a relative of wheat is one of the most salt tolerant of all monocots (Munns and Tester 2008). In dicots, salinity tolerance is even more diverse. For example, some legumes are even more sensitive than rice (Läuchli 1984). Alfalfa is relatively tolerant to salt, and halophytes for example some *Atriplex* spp. grow well at extremely high salinities (Flowers et al. 1977).

There is a wider range of salt tolerance in natural populations, which is reported to be evolved naturally in numerous grass species like *Agrostis*, *Festuca*, *Lolium*, and *Poa* (Humphreys et al. 1986; Acharya et al. 1992). Such plants provide outstanding materials for studying the mechanisms of adaptations they use to tolerate high concentrations of salt (Ashraf 2003). Such adaptations have been evaluated in several grass populations from quite diverse habitats such as estuaries and coastal areas, marine and fresh water salt marshes, and dry–land salinities. Examples are *Sporobolus virginicus* (Naidoo and Mundree 1993), *Cynodon dactylon* (Pasternak et al. 1993; Hameed and Ashraf, 2008), *Spartina patens* (Ashour et al. 1997), *Urochondra setulosa* (Gulzar et al. 2003), *Ochthochloa compressa* and *Aeluropus lagopoides* (Naz et al. 2009), and *Imperata cylindrica* (Hameed et al. 2009).

The main objectives of this chapter are to present the physio–biochemical aspects of salinity tolerance in naturally adapted salt tolerant plants and to correlate them to the structural adaptations found in different plants to cope with highly saline adverse environments.

2 Adaptive Components of Salt Tolerance

Salt tolerance is a complex phenomenon involving a variety of mechanisms. It can be defined as the ability of the plants to complete their growth cycle with an acceptable growth and yield (Flowers et al. 1986; Colmer and Flowers 2008). Three major factors affect the plant growth under salinity, water stress, ion toxicity, and nutrient uptake and translocation, and as a result, disturbance of ionic balances such as K^+ and Ca^{2+}. Physiological drought may play a crucial role, which restricts the water uptake by plants (Table 8.1). On contrary, excess salt uptake by plants interrupts the cellular functions and this damages vital physiological processes, i.e., photosynthesis and respiration (Marschner 1995). Furthermore, mechanisms like increased leaf resistance (fewer stomata, increased cuticle and epidermis thickness, and mesophyll resistance) could prevent turgor loss from leaf and root surface, and hence better water efficiency.

Plant tolerance to saline environments is of broad spectrum ranging from glycophytes (that are sensitive to salt) to halophytes (that tolerate high concentrations of salt). The acquired salt tolerance may be of hereditary nature in some species (Niknam and McComb 2000), i.e., passed along to offspring. Halophytic or salt tolerant species can adopt multiple strategies to survive under high salinities by controlling the levels of ions their shoots or particularly in leaves. The mechanisms involved are restricting or excluding the ion uptake at root level, and hence minimizing the translocation of salts to the shoot (Flowers and Colmer 2008).

Genkel (1954) divided the halophytes into three groups: euhalophytes, crinohalophytes, and glycohalophytes, but this classification has been modified by Nagalevskii (2001) and Zhao et al. (2002). Salt tolerance in euhalophytes is based on accumulation, as they accumulate salts in their tissues, crinohalophytes depend on excretion of toxic ions like Na^+ and Cl^- as they are capable of excreting salts out of the plant body, and glycohalophytes rely on avoiding mechanism by preventing the accumulation of excess salts (Voronkova et al. 2008). The growth rate can be linked to the accumulation of salts in the plant leaves that plant takes up from the roots, so the continuation of growth under saline environments is an indication of high degree of salt tolerance.

Table 8.1 Physiological and biochemical mechanisms of salt tolerance in some highly salt tolerant or halophytic plant species

Plant species	Ion uptake and transport	Osmotic adjustment	Ion exclusion
Monocots			
Aeluropus lagopoides	Restricted uptake of Na^+ and Cl^- (Naz et al. 2009), and increased uptake of K^+ and Ca^{2+}	Accumulation of Na^+ and Cl^- in shoot, in addition to retention of K^+ and Ca^{2+} (Naz et al. 2009)	Excretion of only Na^+ and Cl^- ions (Naz et al. 2009)
Cymbopogon jwarancusa	Increased uptake of Ca^{2+}, and increased K^+ in shoots	Accumulation of total free amino acids and soluble proteins	
Cynodon dactylon	Restricted uptake of Na^+ accompanied by high uptake of K^+ and Ca^{2+} (Hameed and Ashraf 2008)	Accumulation of soluble sugars, proline and total free amino acids (Hameed and Ashraf 2008)	Excretion of Na^+ and Cl^-
Imperata cylindrica	Increased uptake of Ca^{2+}	Accumulation of total free amino acids and proline	
Lasiurus scindicus	Increased uptake of Ca^{2+}		
Ochthochloa compressa			Excretion of Na^+ and Cl^-
Panicum antidotale		High water use efficiency (Hameed and Ashraf 2009)	
Sporobolus arabicus	Restricted uptake of Na^+ and Cl^-	Accumulation of free amino acids and proline	Excretion of Na^+ and Cl^-
Sporobolus ioclados	Restricted uptake of Na^+ and Cl^-	Accumulation of free amino acids, soluble proteins and soluble sugars	Excretion of Na^+ and Cl^-
Dicots			
Cressa cretica	Restricted uptake of Na^+ and Cl^-		Excretion of Na^+
Fagonia indica		Accumulation of Na^+ and Cl^- in shoot, in addition to retention of K^+ and Ca^{2+}	
Haloxylon recurvum	Increased uptake of Na^+ and Cl^-	Dumping off Na^+	Excretion of Cl^-
Haloxulon salicornicum		Dumping off Na^+ and Cl^-	
Salsola baryosma		Dumping off Na^+ and Cl^-	
Suaeda fruticosa		Dumping off Na^+ and Cl^-	

Morphological features of the plant roots can prevent salts in large quantities. At cellular level, physiological and metabolic features can counteract salts if salts do enter the roots (Winicov 1998). Plants generally use two mechanisms to tolerate high salt concentrations. Firstly, the avoidance, i.e., keeping the salts away from the metabolically active tissues (Munns and Tester 2008). This is through passive exclusion of ions (by a permeable membrane), active expelling of ions (by ion pumps), or by dilution of ions in plant tissues (Allen et al. 1994). Secondly, compartmentalization of accumulated salts in the vacuoles of plant cells (Munns 2002). These two methods are vital for preventing toxic ions to accumulate or causing damage to the plant tissues, and therefore, they could be employed for identifying markers for genetic manipulation of salinity tolerance in plants.

Salt tolerant or halophytic plants can minimize the detrimental effects of salts (i.e., ion toxicity, nutritional disorder, osmotic stress) by modifying morphological, anatomical and physiological mechanisms of salt tolerance (Poljakoff-Mayber 1975; Hameed et al. 2009). Extensive root system (root length and proliferation) and the presence of salt secreting structures (e.g., salt glands) on the leaf surface may prove vital in plants (Marcum et al. 1998; Naz et al. 2009). The salt tolerance of plants may involve: (a) restricted or controlled uptake of salts, (b) tissue tolerance, (c) accumulation of salt in inert areas (e.g., vacuoles), (d) ion discrimination (e.g., uptake and translocation of ions like K^+, Na^+, Cl^- and SO_4^{2-}), (e) production of low molecular weight protective osmolytes like enzymes, hormones, antioxidants, etc. (Gorham and Jones 1990; Munns and Tester 2008). These mechanisms may be responsible for variations in the salt tolerance within plant genotypes or species (Table 8.1).

Soil reclamation is a very expensive and physically difficult process to practice. However, cultivation of salt tolerant species/varieties is the most practical solution, particularly when salinity is relatively low. When a plant is exposed to increased soil salinity, a primary response is decreased plant water potential, and this is due to a decrease in both osmotic and water potentials of the soil. Accumulation of osmotically compatible cellular solutes (e.g., sugars, proteins, free amino acids) is one of the well–characterized responses of plants to such low water potential. In salt tolerant species, accumulation of osmotically compatible solutes directly correlates with Na gradients in soil and thereby reduces the detrimental effect of salt stress (Briens and Larher 1982; Lee et al. 2007). Mechanisms involved in salinity tolerance or adaptations crucial for the plant survival are still not well understood. Therefore, there is a need to identify appropriate morpho-anatomical or physio-biochemical indicators of salinity tolerance in halophytic and other salt tolerant plants (Ashraf and Harris 2004).

2.1 Morphological Traits

Salinity–induced changes in root morphology, anatomy, and ultrastructure as well as some physiological implications of the altered growth patterns have been reviewed earlier at length. Excess salinity has been reported to inhibit both root cell division and cell expansion (Zidan et al. 1990). Generally, in glycophytes, root growth is less affected by salinity than either vegetative shoot growth or fruit and seed production (Maas and Nieman 1978). Depending on the type of plant species, the level of salinity stress and the composition of the external solution, root growth may be stimulated, inhibited or unaffected (Delane et al. 1982, Waisel 1985).

Soil salinity directly affects plant growth and development, especially crop species (Chinnusamy et al. 2005; Ashraf 2009). In general, dicotyledonous halophytes show optimal growth up to 250 m*M* NaCl (Flowers et al. 1986). However, in monocotyledonous halophytes growth is generally not simulated by salts or if so, then it is at 50 m*M* NaCl or less (Glenn 1987; Glenn et al. 1999). Rooting parameters (depth, proliferation and weight) are reported to be associated with salinity tolerance. Root weights increase under salinity in the grasses (Marcum et al. 1998). Shoot biomass production in highly salt tolerant species like *Leptochloa fusca* and *Puccinellia distans* is not affected by salinity. On the other hand, *Pennisetum divisum* has the lowest fresh and dry biomass of both shoots and roots and is very sensitive to salinity stress (Ashraf and Yasmin 1997).

2.2 Anatomical Traits

Both halophytes and non–halophytes exhibit remarkable anatomical changes when exposed to elevated levels of salinity (Maas and Nieman 1978). However, most conspicuous changes are notable in leaf. Longstreth and Nobel (1979) reported a smaller increase in the mesophyll area/leaf area in *Atriplex patula* (halophyte) than that in *Phaseolus vulgaris* and *Gossypium hirsutum* (both glycophytes). This reveals a greater tendency of *Atriplex* to maintain constant mesophyll area, and is an adaptive feature which reflects greater degree of shielding to photosynthetic mechanisms from harmful effects of salts. Zoysiagrass (*Zoysia* spp.) does not show any change in the density of salt glands when grown under salinity (Marcum and Murdoch 1990). Enhanced salt tolerance of *Zoysia* spp. is proportional to a greater density of salt glands in different species (Figs. 8.1 and 8.2) followed by exclusion of shoot ions through leaf glands (Marcum et al. 1998).

Many salt tolerant plants, particularly dicotyledonous halophytes are characterized by xeromorphic characteristics (Table 8.2) such as thick succulent leaves (Fig. 8.3), which apparently aid sufficient water supply (Vakhrusheva 1989). Smaller reduced leaves with dense covering of pubescence are also a characteristic of xerophytes, which accounts for a successful survival of halophytes under dryland salinities (Mokronosov and Shmakova 1978).

Salt secretion by micro-hairs has been detected only in certain Chloridoideae, all having ‘chloridoid type’ micro-hairs with basal cell partitioning membranes. It has not been detected in many species with micro-hairs lacking basal cell partitioning membranes. For example, the ‘chloridoid type’ micro-hairs of *Sporobolus elongatus* and *Eleusine indica* do not secrete salt, despite their possession of partitioning membranes (Amarasinghe and Watson 1988). At leaf level, there are certain appendages which help the plant to secrete excess salts from the main body. Most important

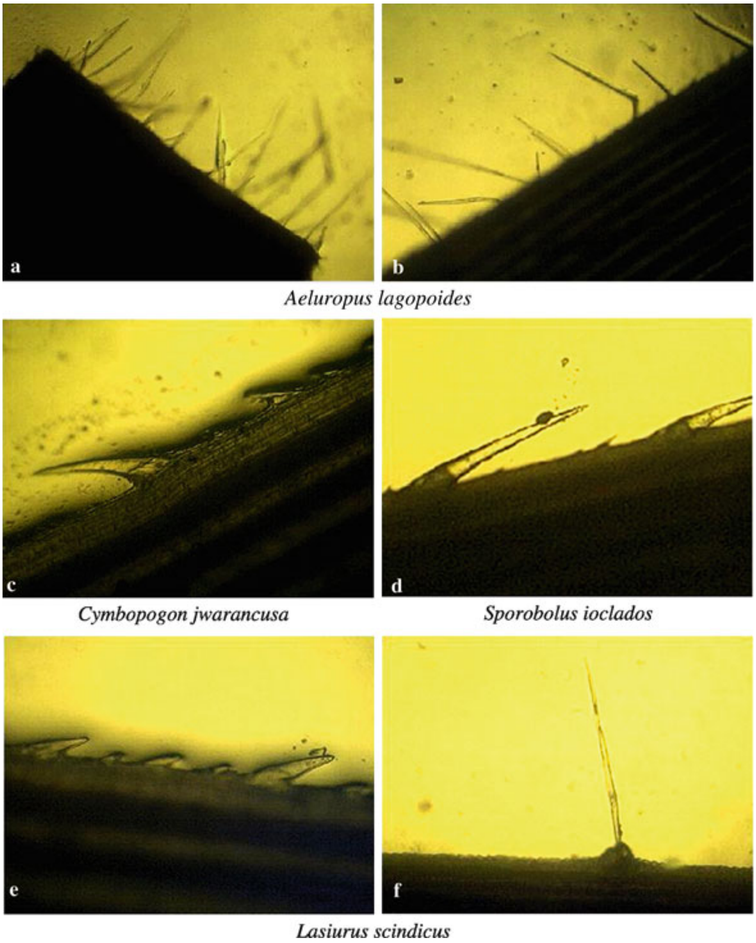
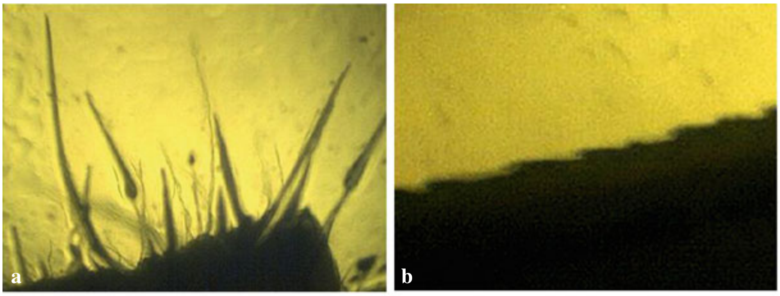
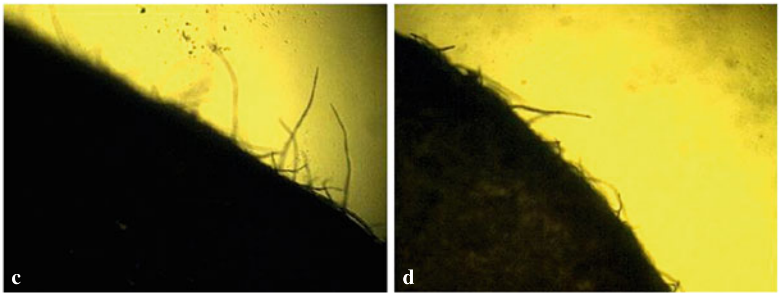


Fig. 8.1 **a** Dense hairiness in *Aeluropus lagopoides* on leaf surface. **b** Glandular and simple hairs on leaf margins in *A. lagopoides*. **c** Marginal hairs in leaf of *Cymbopogon jwarancusa.* **d** Salt secretory hairs on leaf margins. **e** Marginal hairs in leaf of *Lasiurus scindicus*, and **f** Glandular hairs on leaf surface in *L. scindicus*

among these are salt secretory trichomes (e.g., *Atriplex* spp.), second type is multicellular salt glands which occur in many desert and coastal habitat flowering plants, and are confined to the members of families including Poaceae, Aveceniaceae, Acanthaceae, Frankeniaceae, Plumbaginaceae and Tamaricaceae (Mauseth 1988; Thomson et al. 1988; Marcum and Murdoch 1994). In contrast, the stem of halophyte *Salicornia fruiticosa* has a simple cortex and single layered epidermis which is thin–walled and the photosynthetic tissue has palisade and parenchymatous cells for storage of water (Fahn 1990).

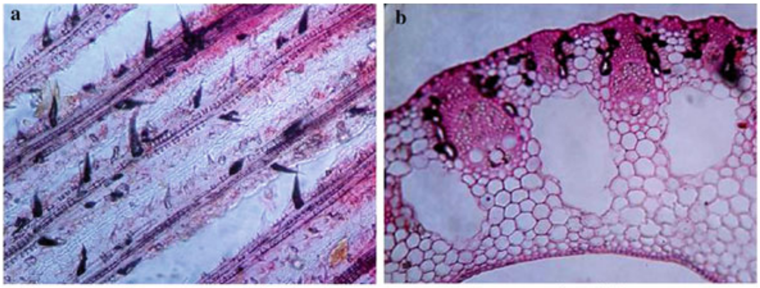


Ochthochloa compressa

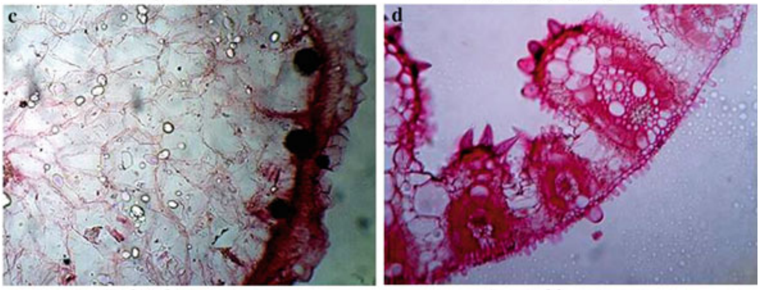


Cressa cretica

Fig. 8.2 **a** Dense hairiness in *Ochthochloa compressa* on leaf surface with a mixture of glandular and simple hairs and trichomes. **b** Marginal hairs on leaf in *O*. *compressa*. **c** Dense hairiness in *Cressa cretica* on leaf surface, and **d** Leaf margins



Aeluropus lagopoides *Desmostachya bipinnata*



Haloxylon recurvum *Leptochloa panicea*

Fig. 8.3 **a**, **e** Dense cover of leaf trichomes in *Aeluropus lagopoides.* **b** Aerenchyma in leaf sheath in *Desmostachya bipinnata*. **c** Leaf succulence in *Haloxylon recurvus*, and **d** Dense cover of microhairs on both leaf surfaces and trichomes on adaxial surface in *Leptochloa panicea*

Table 8.2 Anatomical mechanisms of salt tolerance in some highly salt tolerant or halophytic plant species

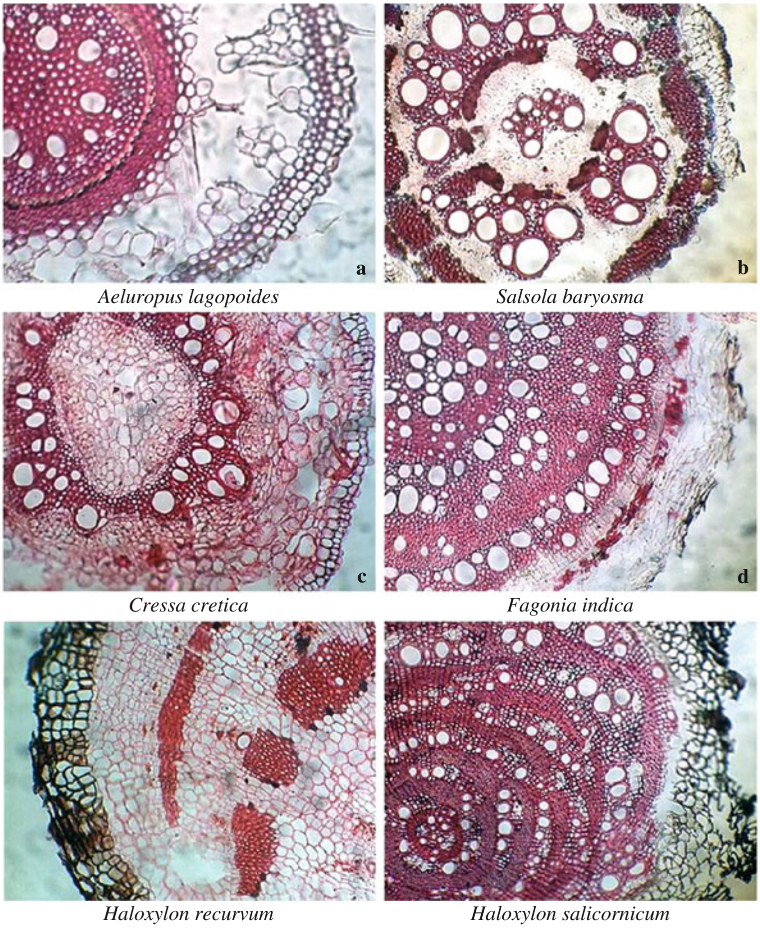
Plant species	Development of xeromorphic characteristics	Structural modifications to salt stress	Salt excretory structures
Monocots			
Aeluropus lagopoides	Dense hairiness on both leaf surfaces as well as leaf margins, and increased sclerification in stems	Increased sclerification in root outside endodermis	Ion exclusion through micro hairs
Cymbopogon jwarancusa	Increased sclerification in stem and leaf and increased trichome density		
Cynodon dactylon	Increased hairiness (trichomes)		Ion exclusion through micro hairs
Imperata cylindrica	Succulence in leas midrib, highly developed bulliform cells, increased sclerification in leaf and root, and reduced stomatal density and pore area (Hameed et al. 2009)	Formation of aerenchyma in leaf sheath, increased area of vascular tissue, and enlarged bulliform cells (Hameed et al. 2009)	
Lasiurus scindicus	Increased sclerification in stem and development of bulliform cells	Increased sclerification in roots	
Ochthochloa compressa	Dense hairiness on adaxial leaf surface and leaf margins		Ion excretion through salt glands and micro hairs
Panicum antidotale	Development of bulliform cells and extensive leaf rolling, and reduction in stomatal density and size (Hameed and Ashraf 2009)		

Table 8.2 (continued)

Plant species	Development of xeromorphic characteristics	Structural modifications to salt stress	Salt excretory structures
Sporobolus arabicus	Increased succulence and sclerification in stem	Development of aerenchyma in leaf sheath	Ion exclusion through micro hairs and leaf sheath
Sporobolus ioclados	Increased sclerification below exodermis and increased leaf hairiness	Increased endodermis thickness	Ion exclusion through micro hairs
Dicots			
Cressa cretica	Increased sclerification in stem and increased cuticle and epidermis thickness in leaves		
Fagonia indica	Increased succulence in leaves		
Haloxylon recurvum	Increased succulence and sclerification in stem, and increased succulence in leaves		
Haloxulon salicornicum	Increased sclerification in stem		
Salsola baryosma	Increased succulence in stem		
Suaeda fruticosa	Increased succulence in leaves		

Stomatal features like density and size are critical for controlling transpirational loss from leaf surface and even more critical under physiological droughts (Hameed et al. 2009). The importance of stomatal characteristics in avoiding water loss through leaf surface has been reported several species like *Distichlis spicata* (Kemp and Cunningham 1981), barley (Gill and Dutt 1982), and wheat (Akram et al. 2002).

The roots of saline desert plants have reduced cortex to shorten the distance between epidermis and stele. The casparian strip is much wider in the highly dry and salt marsh habitat plants, as compared to mesophytes. In saline habitat plants, the endodermis and exodermis (hypodermis with casparian band) represent barriers (Fig. 8.4) of variable resistance to the radial flow of water and ions from cortex



Aeluropus lagopoides *Salsola baryosma*

Cressa cretica *Fagonia indica*

Haloxylon recurvum *Haloxylon salicornicum*

Fig. 8.4 Roots **a** Sclerification surrounding vascular region above endodermis and in vascular region in *Aeluropus lagopoides,* **b** Sclerification in patches in vascular regions with unusually large metaxylum vessels in *Salsola baryosma* and **e** *Haloxylon recurvum*, **c** Sclerification of vascular region with highly developed storage parenchyma in pith and cortical regions in *Cressa cretica,* Highly sclerified central region in **d** *Fagonia indica* and **f** *Haloxylon recurvum* to the stele under prevailing conditions (Hose et al. 2001; Taiz and Zeiger 2002). Such adaptation is advantageous for efficient functioning of endodermis, when the protoplasts are attached to the large portions of the radial and transverse walls of endodermal cells (Fahn 1990).

Drought avoidance is a vital adaptive strategy against salt stress. Modifications like highly developed bulliform cells (important for leaf rolling) can play an important role in avoiding water loss during physiological drought caused by salinity (Abernethy et al. 1998; Alvarez et al. 2008). Thick epidermis is a characteristic feature of many salt tolerant terrestrial species (Ristic and Jenks 2002) and this is one of the most valuable mechanisms relating to xeric adaptation to prevent water loss (Jenks and Ashworth 1999; Zhao et al. 2000).

Root aerenchyma is reported to be a distinctive attribute of waterlogged plants. Colmer and Flowers (2008) summarized characteristics of aerenchyma in halophytic species, but this is exclusively under waterlogged conditions. Aerenchyma formation in halophytes may aid in efficient solute transport in addition to oxygen (Hameed et al. 2009). Increased sclerenchyma under salinity stress not only provides rigidity to the tissues or organs, but also vital for reducing water loss through plant surface. Increased sclerification has been reported by several researchers in salt tolerant or halophytic plants, e.g., *Spartina alterniflora* (Walsh 1990), *Puccinellia tenuiflora* (Zhao et al. 2000), and *Prosopis strombulifera* (Reinoso et al. 2004).

2.2.1 Succulence

Succulence (both leaf and stem) is one of the most noticeable features in halophytes, which provides not only more space for dumping off toxic ions in the plant body, but also increasing the total plant water content (Waisel 1972; Drennan and Pammenter 1982), and this is crucial for balancing out ion toxicity. Leaf succulence is very rare in monocots (Hameed et al. 2009), but relatively common in dicots, such as *Kandelia candel* (Hwang and Chen 1995) and many other halophytes (Flowers and Colmer 2008). It is not very much clear as succulence is simply a response to salinity or is the response of adaptive value of halophytic plants (Waisel 1972).

Increased succulence in halophytes in response to increasing salinity is presumed to be of adaptive nature (Waisel 1972). Succulence is very much greater in halophytic dicotyledonous species than in monocotyledonous ones (Flowers et al. 1986). There is also evidence of a rapid increase in vacuolar volume and in the concentration of Na^+ (Mimura et al. 2003) in the cells of mangrove *Bruguiera sexangula*, which is a potential mechanism to cope with a rapid increase in external salt concentration.

2.2.2 Salt Excretion

Halophytes utilize salts in osmotic adjustment, which lowers water potentials of their tissues. Accumulation of toxic ions in large quantities in leaves, while avoiding their toxic effects seems to be an important strategy for growth and survival under harsh climates (Greenway and Munns 1980). Balancing of growth and ion accumulation is the major phenomenon of salt tolerance in some species, while in others excess of toxic ions is secreted via secretory structures like salt glands and micro-hairs (Drennan and Pammenter 1982; Flowers and Yeo 1986). *Spartina* spp. are the example where shoot mineral content is regulated by the ionic secretion through specialized salt glands. Salts are also released by the leaf surface through cuticle or in guttation fluid; but they also become concentrated in salt hairs (Stenlid 1956).

Many species exude Na salts onto the leaf surface (Drennan and Pammenter 1982; Marcum et al. 1998; Naidoo and Naidoo 1998), which is effective in reducing Na concentration in plant tissues, i.e., *Sporobulus* spp. (Lipschitz and Waisel 1974; Marcum and Murdoch 1992). Salt secretory trichomes, characteristic of *Atriplex* spp., are bladder–like hairs projecting out of leaf surface. They consist of a large secretory or bladder cells on the top and a stalk consisting of one or sometimes a few cells (Samoui 1971; Dickison 2000). All these cells contain mitochondria, dictyosomes, ribosomes, endoplasmic reticulum and a large flattened nucleus. The chloroplasts are rudimentary or partially developed. The only difference lies in that a single large vacuole is present in bladder cell and many small vacuoles in the stalk cell (Osmond et al. 1969). A symplastic continuum exists from the mesophyll cells to the bladder cells for the movement of ions. The external walls of bladder and stalk cells are cutinized, while inner primary walls are not (Thomson and Platt-Aloia 1979).

In grasses, the glands are generally bi–celled, i.e., an outer cap cell and a subtending basal cell. They may be sunken, subsunken, extending out of epidermis (Lipschitz and Waisel 1974; Marcum and Murdoch 1994) or lie in bands or ridges (Marcum et al. 1998). In dicotyledonous species, the salt glands are multi–cellular, consisting of basal and secretory cells. The number of cells may vary from 6 up to 40 in different genera (Fahn 1990). For example, in *Tamarix* spp. the salt glands consist of two basal collecting cells and outer six highly cytoplasmic secretory cells (Mauseth 1988). However, the glands of *Avicennia* and *Glaux* comprise several secretory cells positioned above a single disc–shaped basal cell (Rozema et al. 1977). The position of the epidermal glands may be lateral (*Tamarix*), present in epidermal depression (*Glaux*) or projecting out of abaxial surface of leaf–like trichomes in *Avicennia* (Thomson et al. 1988).

2.3 Physiological/Biochemical Traits

Salinity causes many adverse effects on plant growth which may be at physiological or biochemical levels (Munns 2002; Munns and James 2003), or at the molecular level (Mansour 2000; Tester and Davenport 2003). In order to assess the tolerance of plants to salinity stress, growth or survival of the plant is measured because it integrates up– or down–regulation of a variety of physiological mechanisms (Niknam and McComb 2000). Cell growth rate depends on cell wall extensibility as well as turgor (Lockhart 1965).

2.3.1 Osmotic Adjustment

Accumulation of exceptionally high concentrations of inorganic ions as well as organic solutes is an important physiological adaptation in both halophytic and salt tolerant species (Pitman 1984). In salt excretory plants, salt is kept away from photosynthesizing or meristematic cells. In these plants, osmotic balance is generally achieved via extensive accumulation of organic solutes and/or inorganic ions. However, in plants where salt inclusion is the prime mechanism, accumulation of some inorganic ions (predominantly Na^+ and Cl^-) regulates the osmotic adjustment (Wyn Jones and Gorham 2002; Ashraf 2004). Both organic and inorganic solutes are essential for osmoregulation in plants, especially under saline environments. However, their relative contribution to osmotic adjustment varies from plant to plant or species to species, or even within different tissue of the same plant (Ashraf 1994; Ashraf and Bashir 2003; Hameed and Ashraf 2008).

There is a variety of compatible osmolytes in higher plants. Important among these are soluble sugars, organic acids, and soluble proteins. The important amino acids that accumulate in the plants are alanine, arginine, glycine, leucine, serine, and valine, along with the imino acid proline, citrulline and ornithine (Rabe 1990; Mansour 2000; Ashraf 2004). Osmoregulation via accumulation of free amino acids and in particular, glycinebetaine is the principal strategy in many plant species to tolerate salt stress (Martino et al. 2003). Amides such as glutamine and asparagine (Dubey 1997; Mansour 2000), and proline (Ashraf 1994; Abraham et al. 2003) have also been reported to accumulate in large amounts in higher plants in response to salt stress.

2.3.2 Ion Selectivity

A major feature of the solute transport by plants in saline conditions is the degree of selectivity, particularly between potassium and sodium (Ashraf et al. 2005). One of the most important physiological mechanisms of salt tolerance is the selective absorption of K^+ by plants from the saline media (Ashraf et al. 2006). Halophytic or salt tolerant species differ from salt–sensitive ones in having restricted uptake or transport of Na^+ and Cl^- to the leaves despite an effective compartmentalization of these ions. This is critical in preventing the build–up of toxic ions in cytoplasm (Munns 2002; Ashraf 2004). Ion imbalance, particularly that caused by Ca^{2+} and K^+ is the most important and widely studied phenomenon affected by salt stress, which is directly influenced by the uptake of Na^+ and Cl^- ions (Munns 2002 Munns et al. 2006). Maintaining better concentrations of K^+ and Ca^{2+} and limiting the Na^+ uptake are vital for the salt stress tolerance in plants (Karmoker et al. 2008). Higher K^+/Na^+ or Ca^{2+}/Na^+ ratios are characteristic to the tissue salt tolerance, and are often used as a screening criteria for the salt tolerance (Munns and James 2003, Ashraf 2004; Song et al. 2006).

2.3.3 Salt Exclusion

Halophytes or highly salt tolerant plants have both types of mechanisms that enable them to survive and grow for long times in saline soils. They exclude salts efficiently in addition to effective compartmentalization of the salts in vacuoles. Glycophytes, on the other hand, exclude the salts but they are unable to compartmentalize them. The mechanism of salt exclusion involves transport of salts to the leaves and subsequently excreted out of the plant body thereby reducing salt concentration in plant tissues. Salts translocated in the transpiration stream are deposited and their concentration increases with time. This results in much higher salt concentrations in older leaves than those in younger leaves. Mechanisms conferring salt exclusion (both at cellular and whole plant levels) have been reviewed by many authors (Greenway and Munns 1980; Storey and Walker 1999; Jeschke 1984). Salt exclusion is the most important adaptive strategy regulating the internal salt load of halophytes. As an example, about 98% of salt was reported to be excluded in the mangrove species *Avicennia marina* growing in 500 m*M* NaCl (Ball 1988). In perennials, exclusion is particularly important and it is more vital to regulate the incoming salt load in the plant body (Amtmann and Sanders 1999; Hasegawa et al. 2000).

2.3.4 Intracellular Ion Compartmentation

Sequestering of Na^+ and Cl^- in the vacuoles of the plant cells is ideal situation for plants under salt stress. Exceptionally, high concentrations of salts are found in leaves, which still function normally. Concentrations well over 200 m*M* are common in halophytic or highly salt tolerant species, and such concentrations will severely inhibit the activity of several enzymes in vivo (Munns and Tester 2008).

2.3.5 Stomatal Responses

Although there are few data available on stomatal responses of different plant species, it is possible to identify two types of stomatal adaptations to increasing salinity (Flowers et al. 1997): the guard cells can utilize sodium instead of potassium to achieve their normal regulation of turgor (Ashraf 1994), or the ionic selectivity of the guard cells that use potassium and are capable of limiting the sodium intake (Robinson et al. 1997). This mechanism may be very important in non-secretory halophytes that lack secretion mechanisms, and it may therefore be of particular interest as a potential contributor to the development of salt tolerance in crops. Sodium can substitute for potassium in the stomatal mechanism (Flowers and Colmer 2008). In *Suaeda maritima*, sodium is the major cation under salinity in the guard cells of closed stomata (Flowers et al. 1989). Stomatal regulation by sodium provides a vital regulatory mechanism for the control of excessive salt translocation in the shoot, when a plant capacity to compartmentalize increases. In glycophytes, accumulation of sodium ions damages the stomatal function, and this disruption supports their lack of survival under saline conditions (Robinson et al. 1997).

3 Conclusion

Salt tolerant plants adapt specific structural and physiological modifications to cope with high salinities. Morpho–anatomical adaptations include the prevention of undue water loss from the plant by the development of thick epidermis and sclerenchyma, well developed bulliform cells for extensive leaf rolling, and increased density of trichomes, and this is vital in water limiting environment under high salinities. Increased moisture retaining capacity is the other adaptive feature which is critical under physiological drought due to salinity stress. Development of excretory structures like vesicular hairs and salt glands is a major structural adaptation and very crucial for salt tolerance. Physiological adaptations include restricted toxic ion uptake at root level. At cell level, succulence is crucial for dumping off toxic ions in relatively inert areas like vacuoles. Toxic ions like Na^+ and Cl^- are important for osmotic adjustment in highly salt tolerant species. Lastly, the most important point is that ion exclusion which is one of the most vital phenomena for high salt tolerance in plants.

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