

# Chapter 7

## Coping with Saline Environment: Learning from Halophytes



Amal Ahmed Morsy, Karima Hamid A. Salama,  
and Mohammed Magdy F. Mansour

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**Abstract** Salt stress is a crucial barrier to crop growth, development, and production and hence negatively affects food security globally. In addition, the current trends of climate change increase the frequencies and severities of drought and heat which accelerate and spread the processes of salt mobilization and accumulation within the upper horizons of arid and semiarid soil. Elevated salinization in arid and semiarid regions necessitates development of economic and environmentally friendly saline agriculture to be comparable with world population increase. As salt stress is a multi-factorial phenomenon caused by various factors or a combination of factors leading to a complex tolerance mechanism, the utilization of suited

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A. A. Morsy (✉) · K. H. A. Salama · M. M. F. Mansour  
Department of Botany, Faculty of Science, Ain Shams University, Cairo, Egypt

halophytes as niche crops is one of the most promising approaches in this regard. Halophytes have the capability to combat various abiotic factors which occur in their surroundings, and they follow different mechanisms to stress adverse effects. Therefore, investigating halophyte can be useful as the processes by which halophytes thrive and sustain productivity in saline water when understood help in modulating adaptation in crop plants. Further, exploring more halophytes to identify additional salt-responsive genes may also lead to the development of transgenic crops with high adaptation to salinity, which are suitable for sustainable salt soil agriculture. This review thus discusses an ecological integrative approach of halophytes, which implies ecological observations in the field that are associated with halophyte development, physiology, and biochemistry. Halophyte utilization in remediation of polluted soils through their sequestration of absorbed harmful ions into their vacuoles as well as other mechanisms of salt resistance is reviewed.

There are also recommendations for current progress and future work on the use of halophytes to enhance crop quality on marginal and irrigated land.

**Keywords** Anatomy · Bioremediation · Ecophysiology · Halophytes · Mineral nutrition · Salinity stress · Tolerance mechanisms · Water relations

## Abbreviations

AKT	K <sup>+</sup> in channels
EC	Electrical conductivity
HKT	High-affinity K <sup>+</sup> transporters
Ksat	Saturated hydraulic conductivity
KUP/HAK/KT	High-affinity K <sup>+</sup> -H <sup>+</sup> symporters
NSSC	Nonselective cation channels
PDD	Predawn disequilibrium
PM	Plasma membrane
ROS	Reactive oxygen species
SOS	Salt overly sensitive
TDS	Total dissolved solids
TSA	Total soluble anions
TSC	Total soluble cations
USEPA	United States Environmental Protection Agency
WUE	Water-use efficiency

## 7.1 Introduction

The world population has doubled in less than 50 years which put a great pressure on world food reserves, fuel, soil, and biological and water resources. The United Nations (2001) predicts about 9.4 billion people worldwide by 2050. Furthermore, the World Health Organization reports 3.7 billion people are undernourished, and the problem of malnourished will be further increasing in the future. Also, food production since 1984 has been declining per capita because of elevating people number, energy shortage in crop production, and freshwater depletion (Pimentel and Pimentel 2008). It is reported that the problem of water supplies for humankind is one of the major threats that we currently have and appears to be more worse in the future (Cosgrove and Loucks 2015). Saline conditions not only reduce most crop production but also affect soil properties and the ecological balance (Hu and Schmidhalter 2002). The salinity effects also include reduced agricultural productivity, low economic yields, and soil erosion. Moreover, soils with low agricultural potential are often saline in the hot and dry regions of the world.

In these regions, most crops are grown under traditional irrigation which exacerbates the problem since this insufficient management of irrigation contributes to secondary salinization in 20% of irrigated land worldwide (Glick et al. 2007). Consequently, both salinity abundance and freshwater depletion are serious environmental problems affecting the food needs of the world's population, and in turn this urges a need to create new productive areas from saline habitats. This situation necessitates development of economically and environmentally sustainable saline farming, which favors the utilization of suited halophytes as niche crops.

Plants that can withstand increased salinity are called halophytes, whereas agricultural crops have a wide range of responses to salt stress. Halophytes follow different mechanisms to adjust to salinity adverse effects by the accumulation of salts in the vacuoles away from the chloroplast and cytosol, osmolyte biosynthesis, ion homeostasis, and ROS scavenging systems (Flowers and Colmer 2015). Different halophytic species have different strategies for dealing with high salinity. Tolerance to salinity in halophytes is due not only to physiological traits and their genetic modification (Vasquez et al. 2006) but also to compound ecological features in the plant rhizosphere and phyllosphere (Ruppel et al. 2013). Both latter strategies are ascribed to microorganisms inhabiting halophyte roots and leaves, which contribute significantly to halophyte salinity tolerance.

It is also established that inauguration of these mechanisms via short-term treatment with low concentration of salts can enhance salt tolerance of plants (Meng et al. 2018), a process called salt acclimatization. In the current contribution, our goal is to suggest an ecological integrative approach of halophytes, which involves an attempt to correlate ecological observations gathered in the field with halophyte growth, anatomy, and physiological and biochemical data. Also, some halophytes have been shown to have the ability to remove soil pollutants, a strategy termed phytoremediation of contaminated soils (Manousaki and Kalogerakis 2011). We intend therefore in this contribution to get a comprehensive report of the relationships

between halophytes and corresponding environmental factors. Learning from halophyte mechanism to cope with high salt for the purpose of crop plants to withstand high soil salinity is also discussed.

## 7.2 Causes of Soil Salinity

The causes of soil salinity may be natural (primary salinization) or man-made (secondary salinization).

### 7.2.1 Primary Salinization

Primary salinization is a natural process in arid areas which refers to the deposition of salts as a result of lithological heritage or topography (Tanji 2002). Climatic effects and water management can also induce salinization. For example, evapotranspiration mainly contributes to the pedogenesis of saline and sodic soils in arid and semiarid areas. In addition, arid tropical countries are susceptible to high vaporization which is higher than rainfall, and this leads to the rise of  $H_2O$  to the surface soil where solutes accumulate and salinity happens (Smith et al. 1995). Another

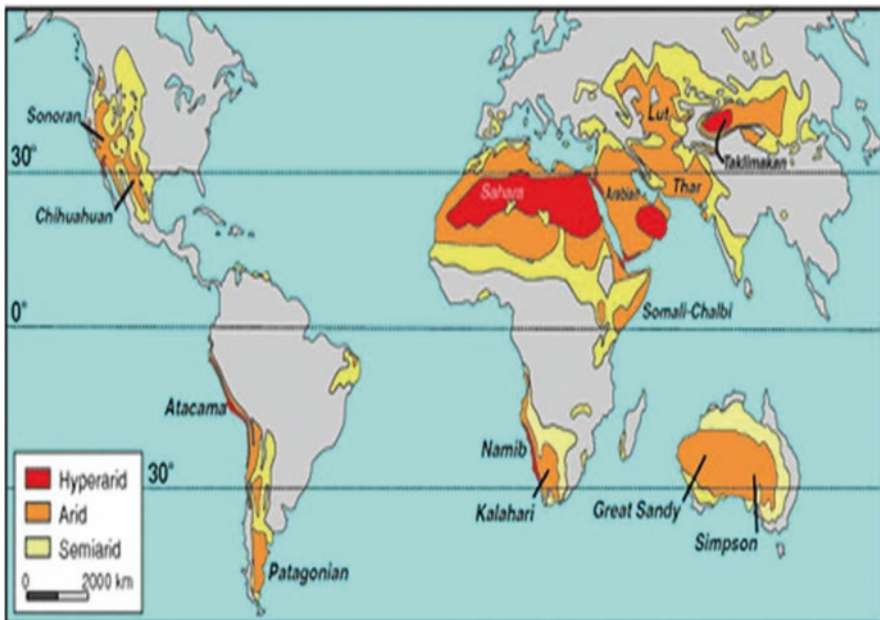


Fig. 7.1 World map of arid and semi-arid regions

form of salinity occurs in marshes where the main cause is the intrusion of saline water into rivers or aquifers (Howard and Mullings 1996). Another natural source of soil salinity may include oceanic salt deposition in the coastal areas.

### 7.2.2 Secondary Salinization

Secondary salinization is the term used to distinguish human-induced salinization from naturally salt-affected soils. This type of salinization is mostly found in the semiarid and arid areas where the mean annual precipitation is 25–500 mm (Plasentis 2005). Most of the arid areas globally range from 15 to 30° north and south of the equator (Fig. 7.1, Ustin et al. 2009). The secondary salinity of water and soils in arid regions is rising as a result of growth in mining, industry, and agriculture as well as water resource re-use. Irrigated agriculture is not only participating in the deterioration of water quality, but also it is a key player in the observed water quality deterioration of many rivers. Utilization of such impaired water quality is a future threat for soils with insufficient leaching (FAO 2009). Leaching of mineral salt from the local geology after rainfall and also mining and industrial contamination is considered an important cause for secondary salinization (Stark et al. 2000). FAO (2009) indicated that “although soil salinity is easy to detect, most soil maps, particularly at small scales, show primary salinity because of its association with geological or geomorphological features, which facilitates mapping at such small scales. The mapping of secondary salinization is, however, more complicated because of high spatial and temporal variability and therefore reliable figures are hard to obtain.”

## 7.3 Salinity Composition and Measurement

Soluble salts are those inorganic chemicals that are more soluble than gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ), which has a solubility of 0.241 g per 100 mL of water at 0 °C (Essington 2005). Most soluble salt in saline soil are composed of cations ( $\text{Na}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ) and anions ( $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ,  $\text{HCO}_3^-$ ). Usually smaller quantities of potassium ( $\text{K}^+$ ), ammonium ( $\text{NH}_4^+$ ), nitrate ( $\text{NO}_3^-$ ), and carbonate ( $\text{CO}_3^{2-}$ ) are also found as do many other ions. Among all these salts, the dominant anions are chloride ( $\text{Cl}^-$ ) and sulfate ( $\text{SO}_4^{2-}$ ), and the dominant cations are  $\text{Na}^+$ ,  $\text{Ca}^{2+}$ , and  $\text{Mg}^{2+}$  (Vargas et al. 2018).

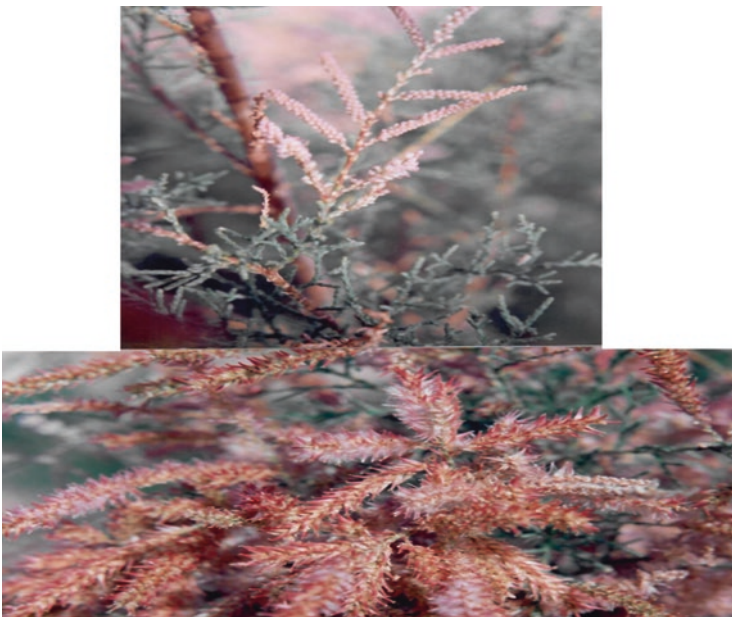
Electrical conductivity (EC) is one of the measurements used to measure soil salinity. Electrical conductivity is reported as decisiemens/m ( $\text{dS m}^{-1}$ ) or millisieimens/cm ( $\text{mS cm}^{-1}$ ); the latter is equivalent to mmhos/cm. Second, total dissolved solids (TDS) are defined as mg/L or g/L, and multiplying the EC by 640 approximated it for solutions up to approximately  $5 \text{ dS m}^{-1}$ . Meanwhile for high salty water and soil solutions, EC is multiplied by 800. Also, salinity could be measured through total soluble cations (TSC) and total soluble anions (TSA). Both TSC and TSA are

recorded as charge/L or meq/L. Osmotic potential in MPa can be calculated by taking the product of EC multiplied by 0.00364. Further, if EC is multiplied by 0.0127, ionic strength in  $\text{ML}^{-1}$  can be calculated (Tanji 2002). For plant response to salt stress, the USDA National Resources Conservation Service characterizes plant salinity tolerance as none ( $0\text{--}2\text{ dS m}^{-1}$ ), low ( $2.1\text{--}4\text{ dS m}^{-1}$ ), medium ( $4.1\text{--}8\text{ dS m}^{-1}$ ), and high (greater than  $8\text{ dS m}^{-1}$ ) when plant growth is reduced by no more than 10% when plant presents in soil of the indicated soil salinity range.

## 7.4 Halophytes

Halophytes are specialized plants which have been developed over a long period to tolerate salinity in their substrate than glycophytes can do (Flowers and Muscolo 2015). They can also complete their life cycle under high salinity which is usually toxic to other plant species and causes damage to almost 99% of their population (Flowers and Colmer 2008). Halophytes are highly evolved organisms that can maintain their morphological, anatomical, and physiological characteristics even under high saline conditions (Flowers et al. 1977; Flowers and Colmer 2008).

The term halophyte derives from halophilous (salt-loving), which describes plant species that grow well under saline conditions like salt marches (Yense 2000). Although over 1400 genes are known to be involved in salt tolerance mechanism in

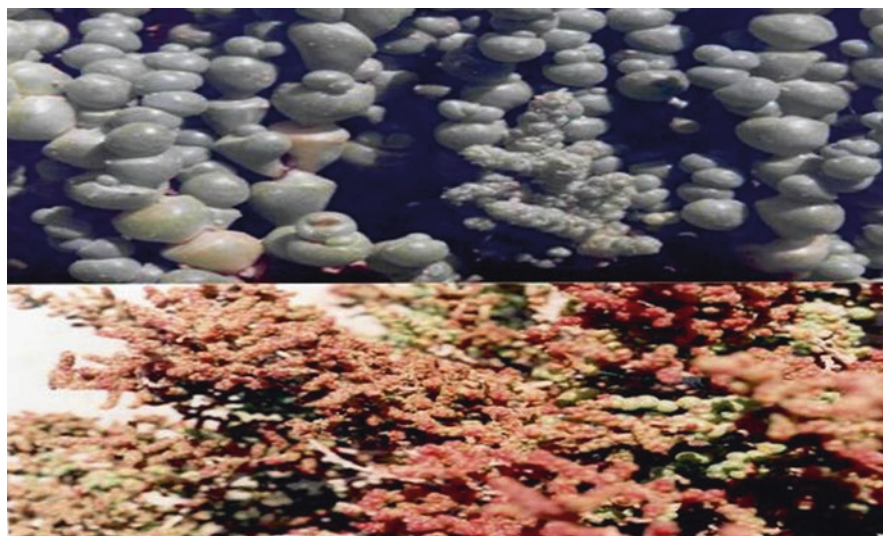


**Fig. 7.2** True close up views showing *Tamarix passerinoides* Del





**Fig. 7.3** Upper photo showing *Suaeda vermiculata* Forssk., the lower one of *Sevada schimperi* Moq.



**Fig. 7.4** Early flowering *Halopeplis perfoliata* (Forssk.) Bge. ex Schweinf

some halophytes, the exact mechanism whereby wild plants cope with saline environments is not very well understood despite the new genetic engineering approaches (Yancey et al. 1982). Such genes and other enzyme systems as well most likely operate in concert not in a solo, and each halophytic species supposedly has its own orchestra to match its tolerance mechanism requirements (Flowers and Muscolo 2015). Halophytes (Figs. 7.2, 7.3, and 7.4) mainly belong to the Tamaricaceae (*Tamarix* spp.), Aizoaceae (total 52 species; *Mesembryanthemum*), Avicenniaceae (total 19 species; *Avicennia*), Brassicaceae (total 19 species; *Thellungiella*), Chenopodiaceae (total 281 species; *Atriplex*, *Halopeplis*, *Sevada*, *Suaeda*), Plumbaginaceae (total 60 species; *Limonium*), Poaceae (total 143 species; *Distichlis*, *Leptochloa*, *Puccinellia*, *Thinopyrum*, *Spartina*, *Hordeum marinum*), Rhizophoraceae (total 31 species; *Rhizophora*), and Zosteraceae (total 18 species; *Zostera*) families (Aronson 1989; Flowers and Colmer 2008).

### 7.4.1 Classification of Halophytes

Halophyte classification depends on many factors such as ecological behavior, distribution, growth, and salt intake (Waisel 1972). Based on the interaction between salt and plant in different environments, Steiner (1934) classified halophytes to (a) salt-regulating types, which include managing by increasing succulence and diluting the concentration of salt in the cell sap (e.g., *Haloxylon recurvum*, *Salsola baryosma*, *Sesuvium sesuviodes*, *Trianthema triquetra*, *Zygophyllum simplex*); (b) salt excretion, which occurs through the salt glands in the desalting halophytes (e.g., *Aeluropus lagopoides*, *Chloris virgata*, *Cressa cretica*, *Sporobolus helvolus*, *Tamarix* spp.); and (c) regulation absent, which occurs in those leading to a constant but slow increase in the salt concentration during the vegetative periods (e.g., *Juncus* sp.). Another system of classification depending on the internal salt of the halophyte species where Ashraf et al. (2006) classified halophytes into (a) excluders: where salt concentration in the above ground plant parts are constantly low under various soil concentrations, and (b) includers: where salts are concentrated in above ground plant parts from low or high soil levels and (c) includers: where salts are concentrated in the shoots either in low or high soil salt contents. Furthermore, Walter (1961) classified the halophytes into (a) facultative halophytes, plants that grow and develop in natural soils (i.e., lacking salts) but can withstand certain levels of soil salinity (Cyperaceae, Juncaceae, and Gramineae), and (b) euhalophytes, plants that show optimum growth with certain salt levels but do not grow in a vigorous way (Mangroves). One more system of halophytes classification is adopted by Weber (2009) where halophytes are classified into (a) excretive (excretive plant species possess an excretive option called glandular cells which enable plants to excrete excess salt from their body in the form of salt crystals), and (b) succulents (in succulent halophytic plants, leaf surfaces have salt bladder which enable the plant to have high water content and thus avoid salt injurious impacts). Most of succulent halophytes inhabiting deserts belong to this category. Depending on the



different habitat of halophytic plants, Youssef (2009) classified halophytes into (a) hydro-halophytes (they are those which can grow in both aquatic and wet soils, such as salt marsh species and mangroves that inhabit coastal lines), and (b) xero-halophytes (they are mostly succulent plants where the soil is saline with low water content due to evaporation).

## 7.4.2 *Ecophysiological Characteristics of Halophytes*

### 7.4.2.1 **Plant Growth, Morphology, and Anatomy**

In the tropical and subtropical areas, a large number of halophytes are shrubs. However, a small percentage of them are annuals like *Acanthus ilicifolius*. As a result of their cymosely branching, most of halophytic shrubs have a dome-shaped appearance. The majority of species examined had most biomass increase under low salinity conditions, while their growth was slow down by high seawater concentration (Kelly et al. 1982; Glenn and O'Leary 1984; Gorham 1996). Other works report this growth trend of halophytes: as the salt concentration in the growth milieu increases above a critical threshold, depending on halophytic species, the growth decreases gradually in most species (Harrouni et al. 1999, 2001; Daoud et al. 2001). One important indicator that reflects the effect of the growing conditions in the root system is the growth parameter root/shoot ratio. Under moderate drought stress conditions, the growth of the root system increases in order to enable the plant to increase its capacity for water uptake from the growing medium (Harrouni 1989). In saline environments up to a specific limit, the impact of the salinity on root system growth can be matched to that of water stress as salt behaves more like an osmoticum rather than a toxic substance. Increased large root system would therefore seem to be of adaptive significant for plants and their yields as such root system is capable to penetrate more soil layers and thus can absorb greater amount of water and nutrients (Vamerli et al. 2003; Franco et al. 2011). Conversely, another study has demonstrated that halophytic species with other root characteristics, e.g., small roots, can be highly beneficial for greater shoot growth and development as few roots in moist soil can easily uptake enough water independent of the root number (Ma et al. 2010). A consequent response is the root hydraulic conductance in plants irrigated with poor-quality water decreases because the root length and surface area are reduced by such low water quality (Ma et al. 2010).

In mangrove species, root proliferation varies with species and growth conditions such as soil compaction, water capacity, wind speed, and wave direction, which have impacts on the tree stability (Mickovski and Ennos 2003; Ong et al. 2004; Alongi 2009).

To avoid such deleterious conditions, some mangrove species modify to aerial roots, stilt roots/prop roots, and buttress roots instead of tap root systems (Ong et al. 2004; Duke 2011). Such root modifications improve the mangrove tree stability in poor mud along shorelines, which supports them to withstand tides and winds.

For example, *Rhizophora mangle* has prop roots and trunk originated flying buttresses, and both adaptations protect the trees against storm waves (Bayas et al. 2011; Ohira et al. 2013; Mendez-Alonzo and Moctezuma 2015). Besides the supporting function of buttress roots, they act as a conducting system for the transport of water, nutrients, and metabolites for long distances (Tomlinson 1986; Day et al. 2010). Also, the root shape tends to become more oval in weaker soils, which helps them to spread horizontally and ultimately cover a large area of the soil and in turn collect more nutrients from the soil surface (Nicoll and Ray 1996; Clair et al. 2003; Dupuy et al. 2005; Mendez-Alonzo and Moctezuma 2015). However, Srikanth et al. (2015) indicate that other species of mangrove trees that grow in drier soils do not need such root adaptations for their support.

Concerning stem growth in halophytes, several halophytes have been shown to develop succulent stems, which is associated with plant salt tolerance, and the succulence degree is a good indicator of the plant ability to live in saline conditions (Repp et al. 1959). For instance, *Salicornia herbacea* and *Suaeda maritima* are familiar examples for succulence feature where their succulence is developed after ion accumulation in their organs is elevated above a threshold (Joseph et al. 2013). It is noteworthy that salinity stress has been shown to enhance conditions which are suited for succulence: salts inhibit cell division and cell elongation which are typical features for succulence. On the contrary, submerged marine angiosperms are of few halophytes that do not develop succulence, and temperate halophytes are herbaceous, while the tropical halophytes are mostly bushy and exhibit heavily cymosis (Khan and Qaiser 2006). As for the halophyte leaves, they are mostly small, succulent, thick, entire, and glassy in appearance, whereas some species have no leaves (Parida et al. 2016). Additional mode of adaptation is found in arohalophytes where their stems and leaves are heavily covered with trichomes (Parida et al. 2016). Furthermore, submerged marine halophyte leaves are thin, with green epidermis, and their vascular system is not well developed, and hence they can directly absorb water and nutrients from their growth medium directly (Srikanth et al. 2015).

Other adaptive mechanisms and features in the morpho-anatomy have been developed in plants inhabiting coastal areas to help them to survive under unfavorable conditions (Grigore and Toma 2007; Hameed et al. 2009; Ashraf and Harris 2013). For example, salinity increases the epidermal thickness to improve the plant water-use efficiency (WUE) and provide more space for  $\text{Na}^+$  sequestration in the leaf epidermis as well (Shabala et al. 2012). At high salinity (750 mM NaCl), however, the thickness of the epidermis decreased to the value observed in the leaves treated with 250 mM NaCl, which was attributed to the decline in cell division as well as growth under high saline condition (Carcamo et al. 2012). Also, at 250 mM NaCl, the thickness of palisade tissue of *Salvadora persica* leaves raised; meanwhile, at 500 mM NaCl, it declined to the control level and disappeared when plants were treated with 750 mM NaCl (Parida et al. 2016). The significance of palisade tissue decline at high salinity might be of an adaptive value to this halophyte to reduce the use of photosynthetic energy under extreme salinity. In contrast, in semi-mangrove *Myoporum bontioides*, a rise in the palisade tissue thickness was observed under high salinity (Xu et al. 2014). Furthermore, in *Spartina species*, the spongy

tissue thickness also elevated with increasing salinity which might help in leaf water content, succulence, and turgor maintenance under high salt stress (Maricle et al. 2009). The study of Maricle et al. (2009) also illustrated that the stomatal density and stomatal aperture diameter declined on lower and upper leaf surfaces by salinity. The decrement in the stomatal number under saline conditions has been similarly indicated in other halophytes such as *Bruguiera parviflora* (Parida et al. 2004), *Nitraria retusa* and *Atriplex halimus* (Boughalleb and Denden 2011), and *Chenopodium quinoa* (Shabala et al. 2012, 2013). Conversely, stomatal index in *Salvadora persica* did not change significantly under saline conditions, which was interpreted to be due to elevated both leaf succulence and pavement cell size, thus improving its WUE and offering extra space for sequestration of  $\text{Na}^+$  in the leaf epidermis (Shabala et al. 2012, 2013; Adolf et al. 2013). Based on the above results, it seems that these changes are fundamental mechanisms to enable halophytic species to survive and cope with saline conditions.

Salinity also induces significant alternations in the stem anatomy of halophytes. In *S. persica*, anatomical alterations have been reported: in response to high salinity, the epidermal cells' diameter and thickness of cortex were lowered, whereas thickness of hypodermal layer, diameter of hypodermal cell, pith area, and pith cell diameter were raised (Parida et al. 2016). Also, salt stress impacts root anatomy where an increase in epidermal thickness and a decrease in the epidermal cell diameters and conducting tissues were observed, which may have an adaptive significance under salinity (Parida et al. 2016). This decrease in cortical cell thickness was also demonstrated in several halophytes mainly due to degradation of the cortical cells, the feature that might be adaptive to conserve essential energy for survival in response to severe salinity (Alam et al. 2015; Nawaz et al. 2016). Although xylem vessel diameters in the stem of *S. persica* did not significantly change, they were declined in many other plants which results in a reduction in water and mineral absorption under high salinity (Sandalio et al. 2001; Ortega et al. 2006; Rewald et al. 2012; Atabayeva et al. 2013). It is therefore proposed that in *S. persica* this response may be an adaptive mechanism to maintain continuous water and mineral ion absorption and transport to the shoot.

As plant roots are the first structure directly faced with soil salinity, they may have a dual mechanism acting as the first line of defense or damage (Rewald et al. 2012). Opposite to the shoot system, the root vascular bundle diameter reduced with salinity, an adaptation to decrease the hydraulic conductivity in order to protect the vessel with considerable conductivity during the stress period (Junghans et al. 2006). It appears that the reduction in the root vessel diameter leads to water uptake declining and consequently decreases plant growth and metabolism under high salinity. Also, a decrease in the size of the vascular cylinder of *Prosopis tamarugo* was reported by Serrato-Vlenti et al. (1991), while Hajibagher et al. (1985) found an increase in the root stelar diameter of the halophyte *Suaeda maritima* in response to salinity. The reduced conducting tissues might explain the decrease in the total growth in several species with increasing salinity (de Villiers 1993). Abd Elhalim et al. (2016) reported that the woody tissues of the old root of halophytes are placed and surrounded by lignified cells for support and to protect water columns from

embolism and balance the high osmotic pressure that the halophytes facing in their rhizosphere (Grigore and Toma 2007). Similarly, Jacobsen et al. (2005) indicate that presence of much lignified cells in the old root is crucial for providing rigidity and also contributes to cavitation resistance. Another root adaptive response is provided by the fact that an increase in the root cortical cells and epidermal thickness was found in crynhalophyte shrubs *Nitraria retusa* and *Atriplex halimus* under saline conditions (Boughalleb et al. 2009), suggestive of participation in ion diffusion reduction into the roots. Furthermore, the phellem which is the outer part of the root could slow down the water absorption, and hence the salts pass with difficulty in the root, but when they penetrate within the root, they spread in it and become diluted and cause less damage to the plants (Grigore and Toma 2007). Such leaf, stem, and root modifications in response to salt stress are primarily adaptive in order to enable the halophytes to withstand the stress conditions, and some of these changes appear to be species specific.

### 7.4.3 Water Relations and Mineral Nutrition

Saline habitats have been conducted on natural systems inhabited by plants that can withstand low soil water potential, adapt to the adverse effects of  $\text{Na}^+$  ions, and thus tolerate their high concentration (Munns 2002; Richards et al. 2005; Bazihizina et al. 2012). Salt-stressed plants have been found to upregulate their xylem sap  $\text{Na}^+$  concentration to maximize hydraulic ability (Munns 1985; López-Portillo et al. 2005, 2014), although no references demonstrated the negative effect of salinity on xylem hydraulics in leaves. However, it is supposed that the effect of salt level of xylem sap on hydraulic efficiency is through its impact on membrane permeability (Zwieniecki et al. 2001; Nardini et al. 2011; van Doorn et al. 2011; Santiago et al. 2013). Another important parameter in water relations of halophytes is predawn disequilibrium (PDD) in water balance between water potential of the soil ( $\Psi_w$ ) and plant. Predawn plant  $\Psi_w$  is used to indicate the abundance of soil moisture to plants and hence is utilized to express an array of ecophysiological measurements like ultimate stomatal conductance and transpiration (Reich and Hinckley 1989; Ameâglio and Archer 1996; Mediavilla and Escudero 2003), plant growth (Mitchell et al. 1993), and differences in root proliferation, adaptation to stress, and habitat sharing between different species (Davis and Mooney 1986; Donovan and Ehleringer 1994; Peuke et al. 2002; Filella and Penuelas 2003). For many halophytes, even at night time and well-watered soils, water loss from the root and shoot is reduced, and PDD can still be of importance (0.2–1.6 MPa) (Donovan et al. 2001, 2003). These authors proposed an explanation that may participate to the significant PDD in halophytes as due to the high solute content in the leaf apoplast. It is noteworthy that water relation studies point to the notion that in absence of low apoplastic  $\Psi_s$ , predawn turgor pressure may reach a level that otherwise induces cell damage (Ritchie and Hinckley 1975; Passioura 1991; Boyer 1995). It is therefore suggested that low predawn apoplastic  $\Psi_s$  could be an effective strategy to modulate  $\Psi_s$  in plants that

have high solute levels or when they are grown in soils with fluctuating water availability (James et al. 2005). Furthermore, inconsistencies present in PDD among halophytes: although Slatyer (1967) indicates that predawn plant  $\Psi_w$  will balance with soil  $\Psi_w$ , a lot of evidence propose that predawn plant  $\Psi_w$  can be markedly lower (i.e., more negative) than  $\Psi_w$  of the rooting zone in various plant species (Ourcival and Berger 1995; Donovan et al. 2001, 2003; Bucci et al. 2004; James et al. 2005). Explanations for absence of plant and soil  $\Psi_w$  equilibration at night have been indicated. They include low hydraulic conductance, night loss of water by the canopy or root system, high capacitance, and diversity in the soil moisture (Blake and Ferrell 1977; Richards and Caldwell 1987; Ourcival and Berger 1995; Sellin 1999). Further, Donovan et al. (2001, 2003) proposed a mechanism that may play role in the large PDD in halophytes which is high level of osmotica in the leaf apoplast, which is documented by the fact that high solute level in the leaf apoplast has been shown during daily transpiration in both glycophytes and halophytes (Meinzer and Moore 1988; Canny 1993). It is obvious that further research is needed to better understand the strategies driving PDD and unmask the adaptive significance and ecophysiological importance of PDD.

It is established that both cations ( $\text{Ca}^{2+}$ ,  $\text{Na}^+$ ,  $\text{Mg}^{2+}$ ) and anions ( $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ,  $\text{HCO}_3^-$ ,  $\text{CO}_3$ ) are available in saline soil but vary in concentration, and usually the proportion of sodium ion cannot exceed the available cations. Meanwhile, if the concentration of  $\text{Mg}^{2+}$  increased in the soil, it may be toxic because the elevated concentration will be accompanied by decreased absorption of  $\text{Ca}^{2+}$  and  $\text{K}^+$  (Gil et al. 2014). Such effect could be decreased through the presence of high concentration of  $\text{Ca}^{2+}$ . However, Anosheh et al. (2016) suggested that the relation between calcium accumulation in plants and salinity level is inversely proportion. For mineral relations, many studies measured ion and osmolyte contents in different halophytes growing in the same conditions and thus make it possible to compare between the responses of different species at the same habitat (Albert and Popp 1977; Gorham et al. 1980; Briens and Larher 1982; Popp and Polania 1989; Tipirdamaz et al. 2006). In monocot halophytes, mechanism of salt tolerance depends on  $\text{Na}^+$  and  $\text{Cl}^-$  exclusion from the plant green parts and at the same time maintains cellular  $\text{K}^+/\text{Na}^+$  ratios relative to dicot halophytes (Flowers and Colmer 2008). In such case, compatible solutes are accumulated in the cytosol for osmotic balance (Albert and Popp 1977; Gorham et al. 1980; Briens and Larher 1982; Rozema 1991; Gil et al. 2014). On the contrary, the dicot halophytes are mainly accumulating  $\text{Na}^+$  and  $\text{Cl}^-$  ions in the plant aerial parts and hence decreasing  $\text{K}^+/\text{Na}^+$  ratios (Acosta-Motos et al. 2017). However, in dicots it is also crucial to minimize  $\text{Na}^+$  content in the cytosol and cellular organelles (Flowers and Colmer 2008). Therefore, the salt tolerance mechanism is apparently based on sequestration of toxic ions into the vacuole to avoid toxicity of the cytoplasm. Adjustment of osmotic balance between the cytoplasm and vacuole depends on gradual gathering of innocent osmotic molecules in the cytoplasm to prevent dehydration of the cytoplasm (Gorham et al. 1980; Briens and Larher 1982; Tipirdamaz et al. 2006; Gil et al. 2014).

High concentrations of cytosolic  $\text{K}^+$  are needed to adjust the plant metabolism (Leigh and Wyn Jones 1984) because  $\text{K}^+$  has an essential role in plant growth,

reproduction, photosynthesis, stress resistance, stomatal movement, osmoregulation, enzyme activation, nitrogen uptake, and protein synthesis (Prajapati and Modi 2012). It is also reported that chloroplasts and mitochondria contain high potassium concentrations (Flowers and Colmer 2008). Despite the key roles of  $K^+$ , halophytic species such as *Atriplex mannifera* (Temel and Surmen 2018), *Suaeda maritima* (Clipson 1987), *Salicornia europaea* (Ushakova et al. 2005), *Rhizophora mangle*, and *Laguncularia racemosa* (Medina et al. 1995) showed  $K^+$  content decline in response to salt stress. In addition to  $K^+$ , calcium plays a crucial role in retaining plasma membrane integrity (Mansour 1995) and thus regulates selective transport of  $K^+$  under high salt, which enable a plant to be more salt tolerant (Epstein 1998). Despite exogenous supplying of  $Ca^{2+}$ , salt stress declined its content in *Aegiceras corniculatum* (Shindle and Bhosale 1985), *Rhizophora mucronata*, *Avicennia officinalis* (Bhosale and Malik 1991), *Allenrolfea occidentalis* (Bilquees et al. 2000), and *Atriplex griffithii* (Khan and Ungar 2000), but no change has been found in  $Ca^{2+}$  content in *Suaeda nudiflora* (Joshi and Iyengar 1987). It is obvious that ion homeostasis is a crucial trait for stress resistance under high salinity, and some studies however showed that it is species specific.

## 7.5 Using Halophytes as Bioremediators

Sustainment of crop productivity needs good strategies to cultivate the unused and marginal lands. One of the most important struggles is the desalination and saline soil recovery. Over the past two decades, improvement of the conditions of both saline and sodic soils was performed through using chemical amendments. Because of over-demands of these amendments by developed countries, the costs are continuing to increase (Qadir et al. 2007). The disadvantage of using chemical amendments for the treatment of saline soils necessitates using phytoremediation techniques which has been proven to be an effective improvement strategy (Qadir et al. 1996). Phytoremediation using halophytic species is a promising approach to reduce salt contents in the saline soils. Phytoremediation is a strategy in which living plants are utilized to cleanse contaminated soil, air, and water from dangerous contaminants that otherwise damage plant life (Salt et al. 1998). For instance, Akhter et al. (2003) indicate that salt-tolerant species are an effective means to address both climate and amendment costs. The authors demonstrate the phytoremediation ability of *Leptochloa fusca* (kallar grass, salt-tolerant species) as this species has the potentiality to leach salts from surface (0–20 cm) to lower depths (>100 cm) resulting in decrement of soil salinity, sodicity, and pH. The soil pH was declined by both release of  $CO_2$  and solubilization of  $CaCO_3$  by kallar grass roots. Additionally, it is important to note that in the first 3 years, kallar grass showed an improvement in soil chemical environment, and further grass growth up to 5 years restored and maintained soil fertility, highlighting the contention that growing salt-tolerant plants can avoid depletion of saline barren lands. Recently, using phytoremediation as a low-cost, solar energy-driven cleanup approach to manage the salinity problem has been



introduced (Kumar 2017). In support, several reports indicate that reclamation of salt-affected soils was operated by cultivated halophytic species (Chaudhri et al. 1964; Ravindran et al. 2007). In addition, the possibility of using halophytic species as oil seed crops and as forage has also been reported (Glenn et al. 1999). Evidence confirming the beneficial usage of halophytic species as bioremediators comes from the following findings. In Pakistan, Chaudhri et al. (1964) working on *Suaeda fruticosa* showed the ability of this species to accumulate sodium and other salts in their leaves. Also, Ravindran et al. (2007) found that both *Suaeda maritima* and *Sesuvium portulacastrum* have the ability to accumulate salts in their tissue and reduce salts from saline soil. Both halophytes have the ability to eliminate 504 and 474 kg of NaCl, respectively, from 1 ha of the saline soil in a 4-month period. Moreover, due to using the phytoremediation technique to remove salts from saline soils, the farmers' economy will not only increase from salt-affected land treatment, but also they get industrial raw material, food, fodder, and fuel wood. The advantages of utilizing the phytoremediation approach may include the following: (1) we will not need to pay for chemical amendments, (2) we will not only improve the land with halophytes, but also we will get money as a result, (3) amelioration of physical properties of soil (stability, macropores) as well as rapid increasing number of roots, (4) availability of nutrient in soil after phytoremediation, (5) improvement of soil profile, and (6) environmental issues as far as carbon sequestration is concerned in the post-amelioration lands (Hasanuzzaman et al. 2014).

Further evidence for using halophytes as phytoremediators is given in this section. For example, Boyko (1966) demonstrated that both saline soil and water could be desalinated using halophytes. Also, Zahran and Abdel Wahid (1982) used *Juncus rigidus* and *Juncus acutus* to reclaim badly drained soils in Egypt. The authors report that the EC of soil had a 50% saturation decrease in a single growth period. Further, Helalia et al. (1992) showed that saline-sodic soil could be remediated using *Echinochloa stagnina* through reducing sodium level at the soil surface layer. Another study indicated approximately 20 tons of dry weight per hectare have 3–4 tons of salt produced by *Suaeda salsa* (Ke-Fu 1991). Interestingly, *Portulaca oleracea* had salt uptake of 497 kg ha<sup>-1</sup> accompanied with 3948 kg ha<sup>-1</sup> biomass production (Hamidov et al. 2007). Rabhi et al. (2010) consistently report that *Arthrocnemum indicum*, *Suaeda fruticosa*, and *Sesuvium portulacastrum* seedlings grown in salty soil greatly decreased the soil salinity and EC via up taking Na<sup>+</sup> ions. The authors also observed that *Sesuvium portulacastrum* accumulate almost 30% of Na<sup>+</sup> content in the shoots over 170 days. Similarly, when three salt accumulator halophytes, namely, *Tamarix aphylla*, *Atriplex nummularia*, and *Atriplex halimus*, were used to remediate saline-sodic soil in Jordan Valley, a remarkable decrease in soil salinity was recorded (Al Nasir et al. 2010). Based on the above evidence, it is obvious that salinity problem could be resolved by environmentally safe and clean technique such as introducing salt-accumulating plants in order to regulate salinity and conserve farmland sustainability.

Several researchers similarly indicate that hyperaccumulating plants tend to accumulate enormous salt quantities from saline soils in their aboveground biomass (Purakayastha et al. 2017; Suska-Malawska et al. 2019). These authors indicate that

one of the environmental and economic solutions in phytoremediation is the use of salt-accumulating halophytes which own a multifunction role in the remediation of saline soils, animal fodder, and organic composts. The ability of halophytic species to remove salts is therefore very crucial particularly when no enough precipitation in arid and semi-arid regions to leach the high salt concentration in the root area. It is noteworthy that cleaning up contaminated soils and underground water at large scale utilizing phytoremediation approaches needs plants with greater rate of salt uptake, tolerance to more than one environmental threat, as well as large biomass. De Souza et al. (2012) studied growth patterns and anatomical changes in *Atriplex nummularia* Lindl and found that this species is a promising halophyte that assists under different conditions such as water deficit, sodic, or saline soil, and hence this halophyte has an important role in managing soil and water quality in semiarid regions. Despite the large evidence presented in this regard, the effectiveness of phytoremediation has some restrictions that should be solved to have a common usage. First, it takes several growing seasons to decrease the level of soil contamination, and therefore it can be time-consuming. Second, it works only in certain soil depths that are associated to rooting zone. Third, remediation of high salinity soil is not easy task since salinity greatly inhibits the germination and growth of several plant species, and therefore selecting suitable plant species for remediation is very crucial. Forth, the plant species must also have a deep and robust root growth as well as enough aerial biomass production for exploring and accumulating more salts (Pajević et al. 2009). Accordingly, it is recommended that halophytes with higher biomass of shoots and root roots should be mainly chosen for remediation. Highly salt-tolerant, food, and fodder plant species are very useful in this connection. Despite the obvious discussed evidence, it seems that using halophytes for soil reclamation needs more research for good utilization of these precious species.

## 7.6 Mechanisms of Salt Tolerance

High levels of  $\text{Na}^+$  in the cells cause salt toxicity which impacts enzymes and impairs cellular metabolism (Hasegawa et al. 2000). High salinity also disturbs  $\text{K}^+$  absorption and content, despite the fact that  $\text{K}^+/\text{Na}^+$  ratio has been reported as a key determinant of plant salt tolerance (Hasegawa et al. 2000). Maintenance of cytosolic  $\text{Na}^+$  and  $\text{Cl}^-$  ions in a low concentration with adequate  $\text{K}^+$  is a key tolerance feature in halophytes, and thus ion homeostasis is an urgent mechanism. Halophytes complete their life cycle at external salts more than 200 mM and accumulate more than 500 mM in their shoot (Flowers et al. 2015; Zhang et al. 2015; Santos et al. 2016). Understanding the mechanism of  $\text{Na}^+$  transport in halophytes and how they deal with high  $\text{Na}^+$  content at cellular and molecular levels is thus needed. It is reported that halophytes have distinct integration of different adaptive mechanisms mainly physiological rather than morphological or anatomical (Shabala 2011). Halophytes tolerate high concentration of salt via strategies working at cellular level which results in evolved defense mechanisms (Flowers and Colmer 2008).

These mechanisms include osmotic adjustment (tissue tolerance), ion homeostasis involving PM and vacuolar membrane transport systems, antioxidant defense systems either enzymatic or nonenzymatic, and alterations of the membrane components (Mansour and Salama 2019). Ion homeostasis mainly includes ion compartmentation in includer halophytes and ion exclusion in excluder halophytes (Hasanuzzaman et al. 2014). Understanding these strategies greatly facilitates developing tolerant plant species/cultivars to saline conditions, which allows utilization of salt and marginal lands (Hasanuzzaman et al. 2014).

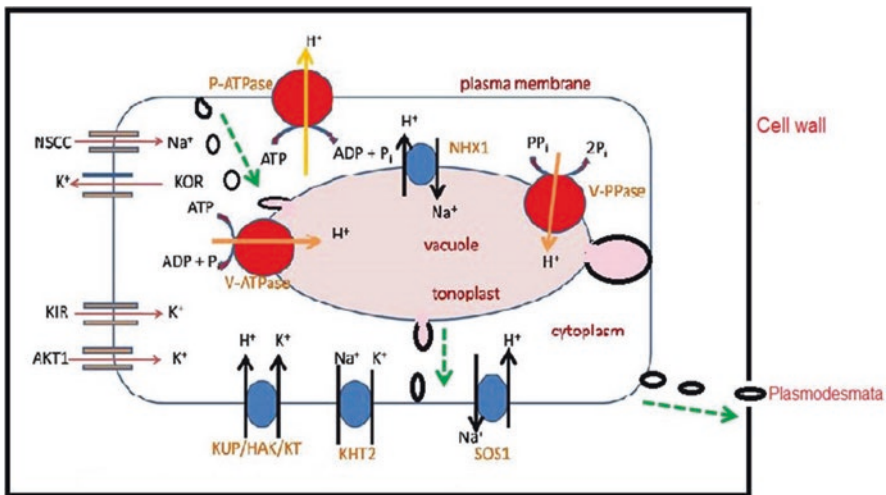
### ***7.6.1 Tissue Tolerance***

Tissue tolerance is the plant capability to maintain tissue activity through accumulating high  $\text{Na}^+$  in older leaves, rather than in younger leaves, where leaf senescence appears first. In addition, salinity induces osmotic action which affects plant growth due to lowered water potential in the surrounding medium. In order to keep continuous water absorption, the cellular water potential needs to be reduced, relative to that of the soil solution, in order to provide water potential gradient between the soil and plant. This water potential gradient drives water entrance to the plant that helps in maintaining the cell turgor and elongation, which eventually promotes growth. Halophytes decline their cellular water potential through absorption and storage of toxic ions ( $\text{Na}^+$  and  $\text{Cl}^-$ ) in the vacuole to avoid cytoplasmic toxicity; compartmentation of ions in the vacuole is regarded as one mechanism of tissue tolerance (Munns and Tester 2008). The solute potential of the cytosol is adjusted and balanced to that of the vacuole by elevation of  $\text{K}^+$  and compatible osmolytes or innocent solutes in the cytoplasm (Mansour and Salama 2019). It is well established that halophytes synthesized and accumulate compatible osmolytes, such as proline, glycine betaine, polyphenols, and soluble sugars, under saline conditions (Bartels and Dinakar 2013); this accumulation of organic solutes is also one facet of tissue tolerance. Accumulation of inorganic ions and organic innocent solutes in response to high salinity counterbalances the osmotic action of salinity as such mechanism keeps water absorption going on. In addition to their involvement in osmotic adjustment, these compatible solutes also participate in the protection of cellular macromolecules, ROS scavenging, nitrogen and carbon storage, and chaperones (Munns and Tester 2008; Mansour et al. 2015; Mansour and Salama 2019).

### ***7.6.2 Salt Includers and Excluders***

Transport of ions in halophytes can clarify the way by which plants avert the injurious impacts of salt on cellular metabolism. It is worth mentioning that halophytes can tolerate high levels of salts in their cytoplasm. The mechanisms or strategies by

which plants get rid of toxic ions are crucial for better plant performance under high salinity. Halophytes that accumulate large amounts of  $\text{Na}^+$  ions (i.e., includers) pump  $\text{Na}^+$  into the vacuoles by specific transporters (detailed below) in order to avert accumulation of ions in the cytoplasm which is illustrated to be a cellular adaptation response leading to tissue tolerance in halophytes (Munns and Tester 2008). It is important to note that the vacuoles of the halophytes are proposed to remodel the composition of their membrane lipids to avoid  $\text{Na}^+$  flow back into the cytoplasm (Bartels and Dinakar 2013). Another strategy to keep a reasonable cytosolic concentration of  $\text{Na}^+$  is found in recretrohalophytes; this type of halophytes excludes  $\text{Na}^+$  out through special structures (Yuan et al. 2016). Also, some other types of halophytes prevent intracellular  $\text{Na}^+$  ion accumulation (i.e., excluders) through maintaining  $\text{Na}^+$  in their roots and prevent its transport to the aerial green shoot or retrieve it from the shoot to the roots through xylem (Bartels and Dinakar 2013). Flowers et al. (2010) confirm the regulation of ion transport from root to shoot as a vital strategy for halophytes to cope with adverse effects of salinity. In a recent review by Flowers et al. (2019), the transport of toxic ions via transport protein (channels and transporters) and vesicles (exo- and endocytosis) is shown in Fig. 7.5 and discussed below.



**Fig. 7.5** The plasma and vacuolar membrane transport proteins as well as  $\text{Na}^+$  vesicular transport participating in ion homeostasis and salt tolerance. (Adapted from Mansour and Salama (2019) and Flowers et al. (2019) with modifications)

### 7.6.3 *PM and Vacuolar Transport Proteins*

As no Na<sup>+</sup> pumps have been characterized in plant, uptake of the toxic ions takes place passively via using secondary active transport (Pedersen and Palmgren 2017). PM transport systems operate to either include or exclude Na<sup>+</sup> ions into the cytoplasm, whereas tonoplast transport systems sequester Na<sup>+</sup> in the vacuoles. For secondary transport systems (ion channels and transporters) to work, plasma and vacuolar membrane proton pump activity is required to establish and maintains the electrochemical potential gradient (the proton gradient and membrane potential) across the membrane (Mansour 2014). Membrane channels and transporters involved in the secondary active transport can couple this electrochemical potential gradient to movement of ions against their concentration gradients (Flowers et al. 2010; Mansour 2014). A detailed review by Mansour (2014) presents evidence for the involvement of high-affinity K<sup>+</sup> transporter, AKT1-type channel, and Na<sup>+</sup>/H<sup>+</sup> antiporter in the regulation of Na<sup>+</sup> uptake and exclusion under salt stress. Increased activity and expression of PM H<sup>+</sup>-ATPase in different halophytes and tolerant glycophytes under high salinity points to the important of this pump in salt tolerance (Bose et al. 2014). In addition, the crucial role of vacuolar ATPase and pyrophosphatase in plant resistance to salt stress is reported by Mansour and Salama (2019). In support to the involvement of plasma and vacuolar transport systems in salt resistance is the finding that expression and activity of plasma membrane and vacuolar membrane H<sup>+</sup>-ATPase significantly increased in *Suaeda salsa* in response to NaCl treatment (Chen et al. 2010; Yang et al. 2010).

Halophytes control the cytosolic concentration of Na<sup>+</sup> within 100–200 mM via Na<sup>+</sup>/H<sup>+</sup> antiporters or ion channels of PM and vacuole to keep the crucial high ratio of K<sup>+</sup>/Na<sup>+</sup> in the cytosol (Flowers et al. 2019). Transporting Na<sup>+</sup>, Cl<sup>-</sup>, and K<sup>+</sup> into the halophyte cells is proposed to involve 18 or more transporters (Flowers and Colmer 2008). These transporters include low-affinity cation transporter 1 (LCT1), AKT-type ion channels, K<sup>+</sup> transporters from the KUP/HAK/KT family, members of the HKT1 and HKT2 classes of transporters, as well as nonselective cation channels that possibly participate in Na<sup>+</sup> transport across the PM (Wang et al. 2007; Almeida et al. 2013; Wu 2018). So far, the only characterized antiporter that dumps Na<sup>+</sup> from the cytosol to outside the cells is SOS1, and it is located at the PM (Wu 2018). Inhibition of SOS1 activity increased salt sensitivity in the halophytic *Arabidopsis*; the finding confirms the important role of the SOS1 Na<sup>+</sup>/H<sup>+</sup> antiporter in plant salt tolerance. In addition, during Na<sup>+</sup> compartmentalization, vacuolar Na<sup>+</sup>/H<sup>+</sup> exchangers (NHX) play also crucial roles in Na<sup>+</sup> and K<sup>+</sup> transport and homeostasis: vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter overexpression has been illustrated to enhance tolerance to high salinity in various plant species (Silva and Gerós 2009). It is noteworthy that although membrane ATPase and ion transporters have been reported to have a prime role in salt tolerance of halophytes, the specific mechanism whereby Na<sup>+</sup> and Cl<sup>-</sup> enter and leave the cells needs further elucidation (Meng et al. 2018).

#### 7.6.4 Vesicular Transport

Vesicular transport of ions is widespread among eukaryotes with the mechanism of exo- and endocytosis being conserved (Cucu et al. 2017). Recently, Flowers et al. (2019) reviewed the mechanism of ion transport via vesicles which participate in exporting ions into salt glands. In endocytosis, vesicles formed by the Golgi apparatus are combined with the PM, surround the ion, and export it to salt glands. Vesicle-mediated transport systems may also be produced from the vacuole to the PM in order to carry solutes from the vacuole through tonoplast vesicles into apoplast. Exocytosis acts to the recovery of membrane material from the PM. Ion transport through vesicle is different from that by transporters or ion channels (Flowers et al. 2019) where vesicular ion transport depends on ion concentration near forming vesicle and electrical charge of vesicular membrane, whereas transport via intrinsic proteins is determined by its structure. Vesicular traffic of  $\text{Na}^+$  and  $\text{Cl}^-$  is considered as a part of salt resistance in halophytes (Flowers et al. 2019). Further investigations at the molecular, cellular, and whole plant are needed to prove the role and the way of vesicular transport in halophytes.

Specialized salt glands are well-known tolerance trait in several halophytes to control toxic ion levels under high salt stress (Flowers and Colmer 2015; Yuan et al. 2016; Santos et al. 2016). Recretahalophytes are the groups that have a specific salt excretory structure originating from the epidermis (Yuan et al. 2016). The salt exclusion mechanisms differ among recretahalophytes species according to the structure of salt excluder. In Aizoaceae and Amaranthaceae, toxic ions are deposited in bladder cell vacuole and thus accumulated in the bladders (Agarie et al. 2007; Park et al. 2009). The bladder cells are next ruptured and ions are accumulated on the surface of the epidermis. Such mechanism to compartmentalize salts in the vacuoles of the bladder cells is similar to that utilized by several halophytes and glycophytes where salt is sequestered in the vacuoles of the mesophyll cells of the succulent leaves (Park et al. 2009). Agarie et al. (2007) indicated that toxic ions are sequestered into the epidermal bladder cells of the common ice plant (*Mesembryanthemum crystallinum*) maintaining ion homeostasis suitable for green active tissues and thus contributing to plant tolerance to saline conditions.

Other species of halophytes exclude  $\text{Na}^+$  via bicellular salt gland as chloridoid grasses (Amarasinghe and Watson 1988). However, multicellular glands were also found in *Limonium bicolor* (Feng et al. 2014) and in *Aeluropus litoralis* (Barhoumi et al. 2008). Multicellular glands are composed of basal accumulating cells and secretory cells (Thomson et al. 1988). The collecting cells are supposedly to maintain a downhill gradient to accumulate ions from surrounding mesophyll cells and then transport them to the secretory cells (Faraday and Thomson 1986). Tan et al. (2013) report that for the secretory cells to prevent leakage of ions back to the surrounding cells, they are surrounded by a cuticle except the connection between them and the basal collecting cells. The basal collecting cells may partially be connected with plasmodesmata; thus, salt is most likely transported actively from the collecting cells into the secretory cells and eventually to outside the cell through the



pores in the cuticle (Faraday and Thomson 1986). It is obvious that understanding the mechanism of salt secretion via the salt gland performance can enable us to develop salt-tolerant crops which makes it possible to cultivate non-used saline lands.

### 7.6.5 Antioxidant Defense Systems

High salinity induced the formation of reactive oxygen species (ROS) which are produced from the electron or energy transfer in the mitochondria and chloroplasts and hence cause oxidative stress in plants (Das and Kumar 2016; Meng et al. 2018). The ROS cause oxidation and damage of cellular macromolecules such as protein, membrane lipid, and nucleic acids leading to impairing their functions (Mansour and Ali 2017). To detoxify ROS, plant increases the activity, expression, and biosynthesis of antioxidant systems to protect cells from oxidative damage (Mansour and Salama 2019). It is therefore crucial that the plant cell produces antioxidant defense systems to combat the deleterious impacts of ROS. The antioxidant defense systems include either enzymatic or nonenzymatic species, targeted as tissue tolerance mechanism. In several halophytes, antioxidant enzymes have been identified to play crucial roles in the protection against ROS damage, such as glutathione transferases from *Salicornia brachiata* (Jha et al. 2011), ascorbate peroxidases from *Suaeda salsa* and *Populus tomentosa* (Li et al. 2012; Cao et al. 2017), superoxide dismutases from *Tamarix* (Wang et al. 2010), and monodehydroascorbate reductase from *Avicennia marina* (Kavitha et al. 2010). Consistently, when *Salicornia brachiata* metallothionein gene *sbMT-2* is overexpressed in tobacco, transgenic plants showed enhance salt tolerance with elevated superoxide dismutase expression, peroxidase, and ascorbate peroxidases, confirming antioxidant enzymes' role in ROS detoxification and eventually salt resistance (Chaturvedi et al. 2014). Together with antioxidant enzymes, increased contents of nonenzymatic antioxidants including ascorbic acid, glutathione, polyphenols, tocopherols, and flavonoids have been illustrated in several halophytes under high salinity and have been found to greatly participate in their salt resistance (Ben Amor et al. 2006; Ivan and Oprică 2013). In agreement with that, the importance of nonenzymatic antioxidants in halophyte salt tolerance is emphasized as a powerful system acting against the damaging effects of hydroxyl radicals on cellular macromolecules (Bose et al. 2014).

### 7.6.6 Membrane Lipid Modeling

Alteration in the membrane structure and composition is an evolved strategy in salt tolerance mechanism (Mansour and Salama 2019). The structure and composition of PM highly affect the fluidity, permeability, stability of membrane, and membrane transport system activities (Mansour 2013; Mansour et al. 2015; Meng et al. 2018; Mansour and Salama 2019). The pivotal roles of the PM constituents in plant

adaptation to high salinity and the relationship between PM lipid modulations and tolerance to saline conditions are detailed in a recent review by Mansour et al. (2015). The membrane changes in halophytes were always in the positive and sustainable direction to retain membrane integrity and transport system activity, and therefore these changes are correlated with salt tolerance under saline conditions. For example, membrane lipid alterations have shown to relate with type of salt accumulation and resistance in ten wild halophytes (Rozentsvet et al. 2014). In the halophyte *Thellungiella halophila*, Sui and Han (2014) found high phosphatidylglycerol content as well as greater unsaturated fatty acids under high salt stress. The study revealed that these alterations enhanced the resistance of photosystem II to high salinity. In addition, PM different lipid and phospholipid species were altered in *Zygophyllum album* and *Zygophyllum coccineum* as a result of soil pollution with the increase in saturation/unsaturation ratio of both species (Morsy et al. 2010), which also contributed to stress tolerance. In the same trend, PM lipid changes in salt marsh grass (*Spartina patens*) under saline environments were found to be correlated with salt resistance (Wu et al. 2005). In agreement with these findings, introducing the *Suaeda salsa* gene encoding enzyme catalyzed phosphatidylglycerol synthesis in *Arabidopsis* resulted in transgenic plants with enhanced resistance to high salinity (Sui et al. 2017). Additionally, increased unsaturated fatty acid contents in membrane lipids preserve photosystems I and II which improves salt resistance in *Suaeda salsa* and tomato (Sun et al. 2010; Sui et al. 2010). Also, when Leach et al. (1990) studied isolated vacuoles from the halophyte *Suaeda maritime*, it turns out that the vacuolar membrane lipids as well as the degree of fatty acid saturation have a key role in NaCl compartmentation in the vacuole. Similarly, PM high sterol content and high unsaturated fatty acids are related to salt resistance in the halophyte *Cakile maritime* (Chalbi et al. 2015). The importance of modeling of membrane lipids under high salinity comes from the fact that this modeling ensures presence of certain lipid species required for maintenance of membrane integrity as well as for proper functioning of membrane transport proteins involved in ion homeostasis under high salinity (Chalbi et al. 2015; Mansour et al. 2015). Further, the role of membrane lipids as intracellular mediators in signaling pathways in plant environmental responses is documented (Ruelland et al. 2015). Despite the clear association between membrane lipid remodeling and salt resistance, more research is needed at the molecular level to further examine and document the role of certain lipid classes in salt tolerance mechanism.

## 7.7 Future Perspectives

Increasing population will bring certainly increased demands for food all over the world. There is every reason to believe that challenge to produce more and better food at lower cost will be met. Therefore, long-term studies are urgently needed to demonstrate the viability of halophyte crop production and its economic prospects for potential farmers.

Real benefits can be achieved if concerted efforts are made to investigate species-specific regulation during abiotic stress, expand genetic capital, and exploit mechanisms of stress tolerance in crops.

In this regard, several studies have shown that the genes cloned from halophytes promote stress tolerance when expressed in glycophytes.

Future research should also work on identifying additional salt-responsive genes by exploring more suitable halophytes that help us better understand the mechanisms of salt tolerance and apply the findings to the production of high salinity transgenic crops. Moreover, halophytic crops should undergo the same process undergone by conventional agricultural crops such as breeding to improve their agricultural traits, and thus during short time spans, economically profitable and consumer-acceptable products can be attained. For example, halophytic crops have been indicated to possess economic importance, such as vegetable, forage, and oil-seed crops, and also can be used as resource for the future to reduce the water crisis (Koyro et al. 2011).

More use of halophytes is supported by the notion that halophytes are an important plant species with high soil salinity and saline water irrigation, thus having the potential for desalination (phytoremediation) and saline soil restoration. As for long term, a promising issue will be raised and can be a must by then which is the halophyte biofuel production costs will be lower than other alternative energy resources and advancing halophyte cultivation will be an ultimate goal.

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