
Prospects of Halophytes in Understanding and Managing Abiotic Stress Tolerance

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Abstract

Halophytes are a diverse group of plants with tolerance to high salinity. While most of our crops are glycophytes lacking the genetic makeup for salt tolerance, halophytes are endowed with ability to seize NaCl into their cell vacuoles as an osmoticum. The sensitivity of crops to environmental extremities has become a major limitation to worldwide food production. Study of halophytes can be rewarding as the mechanisms by which halophytes survive and maintain productivity on saline water can be understood to define and manage adaptations in glycophytes. The adaptation mechanisms include ion compartmentalization, osmotic adjustment, succulence, ion transport and uptake, antioxidant systems, maintenance of redox and energetic status, and salt inclusion/excretion. Real benefits can be accrued if sustained efforts are in place to investigate the species-specific regulation during abiotic stresses and extend genetic resource and manipulate stress tolerance mechanisms. Halophytes are also an important plant species with potential for the purposes of desalination and restoration of saline soils, withstand high soil salinity and saline water irrigation, phytoremediation and wetland restoration. It will be invaluable to develop these strategies to ensure sustainability, and future efforts to improve crop performance on marginal and irrigated land.

Keywords

Halophytes • Abiotic stress • Compatible solutes • Antioxidants
• Phytoremediation

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1 Introduction

Environment basically consists of balanced interaction between biotic and abiotic factors, and often abrupt perturbations in abiotic factors surrounding the biotic organisms lead to change the homeostasis, consequently creating a stressful condition for the survival of living organisms. Environmental stresses represent the most limiting factors for agricultural productivity. The abiotic stresses such as shade or high light levels, subzero, low or high temperatures, drought, flooding, high salinity, inorganic nutrient imbalance, infection, predation, and natural or man-made toxic compounds and oxidative stress (Bohnert and Sheveleva 1998) cause losses worth hundreds of million dollars each year due to reduction in crop productivity and crop failure (Zhu 2001; Flowers 2004). In view of their sessile nature, plants should have developed some adaptation strategies to manage the changing environmental conditions particularly with the available resources. Therefore, foremost adaptation carried out by terrestrial plants to its surrounding is adjustment in their water potential as low as that of soil in which they are able to grow. In the course of evolution, some plants have evolved and adapted to freshwater habitat for acquiring nutrients from the low concentrations of minerals present in fresh water such as glycophytes, whereas the plants which retained their habitat in nutrient-rich marine environment were found more successful to combat the adverse abiotic stresses and are referred as “halophytes” (Flowers et al. 2010). These plants can be grown using land and water unsuitable for conventional crops and can provide food, fuel, fodder, fiber, resins, essential oils, and pharmaceutical feedstocks (Table 2.1).

2 Halophytes

Soil salinity and irrigated agriculture have co-existed since ancient times, and ever since the problem of salinity in agriculture has become a challenge. Soils are generally classified as saline when the electrical conductivity of the saturated

paste extract (ECe) is 4 dS m^{-1} or more (which is equivalent to 40 mM NaCl) and generate an osmotic pressure of approximately -0.2 MPa . Based on this, plants differ greatly in their growth response to saline conditions and therefore classified as “glycophytes” or “halophytes” referring to their capacity to grow on highly saline environments (Munns and Tester 2008). Halophytes are remarkable plants which have the ability to complete their life cycle in a substrate rich in NaCl that normally found toxic to other species and destroy almost 99% of their population (Flowers and Colmer 2008). These are highly evolved and specialized organisms with well-adapted morphological, anatomical, and physiological characteristics allowing them to proliferate in the soils possessing high salt concentrations (Flowers et al. 1977; Flowers and Colmer 2008). Moreover, some halophytes consistently require a particular concentration of NaCl in the growth medium are referred as “obligate halophytes” or “true mangroves” and, apart from their growth in highly saline environment, some halophytes have capacity to grow on the soil devoid of salt are called as “facultative halophytes” or “mangrove associates.” This presence or absence of substrate in the form of salt offers advantages for the halophytes in the competition with salt-sensitive plants (glycophytes) for the management of abiotic stress tolerance and utilization of these species for the improvement of crop yield.

In this regard, it is essential to understand the adverse effects of abiotic stresses and tolerance mechanisms developed by the halophytes and exploit such knowledge for the improvement of crop plants which can meet the demand of food, feed, fodder, and industrial raw material. The standard approach to this problem would be to increase the tolerance capacity of conventional crop plants, which otherwise are high yielders. An alternative strategy is to make use of halophytes that already have the required level of stress tolerance and are still productive at high external adverse conditions. Salinity is one of the major abiotic constraints, affecting almost every aspect of plant's physiology at both whole plant and cellular level through osmotic stress in an earlier phase and ionic stress at a later stage of

Table 2.1 List of halophytes used for saline agriculture in Pakistan and other countries (modified from Khan and Qaiser 2006)

Uses	Plant species
Food	<i>A. hortensis</i> , <i>Aizoon canariense</i> , <i>Apium graveolens</i> , <i>Arundo donax</i> , <i>Atriplex halimus</i> , <i>Avicennia marina</i> , <i>Cocos nucifera</i> , <i>Cynamorium coccinium</i> , <i>Echinochloa crusgalli</i> , <i>Glinus lotoides</i> , <i>Glossonema varians</i> , <i>H. stocksii</i> , <i>Haloxylon griffithii</i> ssp <i>griffithii</i> , <i>N. schoberi</i> , <i>Neurada procumbens</i> , <i>Nitraria retusa</i> , <i>Ochradenus baccatus</i> , <i>Oxystelma esculentum</i> , <i>P. sylvestris</i> , <i>Pedaliium murex</i> , <i>Pentatropis nivalis</i> , <i>Pheonix dactylifera</i> , <i>Pisonia grandis</i> , <i>Polypogon monspeliensis</i> , <i>Portulaca oleracea</i> , <i>Rumex vesicarius</i> , <i>S. brachiata</i> , <i>S. persica</i> , <i>Salicornia bigellovi</i> , <i>Salvadora oleoides</i> , <i>Sesuvium portulacastrum</i> , <i>Solanum incanum</i> , <i>Suaeda fruticosa</i> , <i>Triglochin maritime</i> , <i>Zizyphus nummularia</i> , <i>Zygophyllum simplex</i>
Fodder	<i>A. griffithii</i> , <i>A. halimus</i> , <i>A. leucoclada</i> , <i>A. tatarica</i> , <i>Aegiceras corniculatus</i> , <i>Alhaji maurorum</i> , <i>Anagallis arvensis</i> , <i>Artemisia scoparia</i> , <i>Arthrocnemum indicum</i> , <i>Atriplex canescens</i> , <i>Avicennia marina</i> , <i>B. glaucus</i> , <i>Beta vulgaris</i> ssp <i>maritima</i> , <i>Bienertia cycloptera</i> , <i>Bolboschoenus affinis</i> , <i>Caesalpineia bonduc</i> , <i>Camphorosma monspeliectum</i> , <i>Carex divisa</i> , <i>Chloris virgata</i> , <i>Cressa cretica</i> , <i>Dalbergia sissoo</i> , <i>Glinus lotoides</i> , <i>Halocnemum strobilaceum</i> , <i>Haloxylon stocksii</i> , <i>Lobularia maritime</i> , <i>Lolium multiflorum</i> , <i>Neurada procumbens</i> , <i>Orthochloa compressa</i> , <i>P. farcta</i> , <i>P. juliflora</i> , <i>Populus euphratica</i> , <i>Prosopis cineraria</i> , <i>Raphanus raphanistrum</i> , <i>Rhizophora mucronata</i> , <i>Salsola tragus</i> , <i>Seidlitzia florida</i> , <i>Seriphidium quettense</i> , <i>Suaeda fruticosa</i> , <i>T. repens</i> , <i>T. triquetra</i> , <i>Trianthema portulacastrum</i> , <i>Trifolium fragiferum</i> , <i>Vicia sativa</i> , <i>Zaleya pentandara</i> , <i>Zygophyllum simplex</i>
Forage	<i>A. littoralis</i> , <i>A. macrostachys</i> , <i>Aeluropus lagopoide</i> , <i>Agrostis stolonifera</i> , <i>Aristida adscendens</i> , <i>Aristida mutabilis</i> , <i>Atriplex dimorphostegia</i> , <i>C. ciliaris</i> , <i>C. pennesittiformis</i> , <i>Cenchrus biflorus</i> , <i>Chloris gayana</i> , <i>Cynodon dactylon</i> , <i>D. aristatum</i> , <i>D. scindicum</i> , <i>Dactyloctenium aegyptium</i> , <i>Desmostachya bipinnata</i> , <i>Dichantheum annulatum</i> , <i>Diplachne fusca</i> , <i>E. crusgalli</i> , <i>E. japonica</i> , <i>E. superba</i> , <i>Echinochloa colona</i> , <i>Eleusine indica</i> , <i>Eragrostis curvula</i> , <i>Festuca rubra</i> , <i>Halocharis hispida</i> , <i>Halopyrum mucronatum</i> , <i>Haloxylon persicum</i> , <i>Lasiurus scindicus</i> , <i>Nitraria retusa</i> , <i>Oligomeris linifolia</i> , <i>P. minor</i> , <i>P. pratensis</i> , <i>Paspalum paspoides</i> , <i>Phalaris arundinacea</i> , <i>Poa bulbosa</i> , <i>S. helvolus</i> , <i>S. ioclados</i> , <i>S. kentrophyllus</i> , <i>S. tourneuxii</i> , <i>S. tremulus</i> , <i>S. virginicus</i> , <i>Sacchraum bengalense</i> , <i>Salvadora persica</i> , <i>Sporobolus coromandelianus</i> , <i>Urochondra setulosa</i>
Ornamental	<i>Achillea millefolium</i> , <i>Alhaji maurorum</i> , <i>Ammi visnaga</i> , <i>Artemisia scoparia</i> , <i>Avicennia marina</i> , <i>Caesalpineia bonduc</i> , <i>Calotropis procera</i> , <i>Camphorosma monspeliectum</i> , <i>Cassia italic</i> , <i>Centella asiatica</i> , <i>Ceriops tagal</i> , <i>Chenopodium ambrosioides</i> , <i>Corchorus depressus</i> , <i>Cressa cretica</i> , <i>Cynamorium coccinium</i> , <i>Erythrina herbacea</i> , <i>Evolvulus alsinoides</i> , <i>Glinus lotoides</i> , <i>Halogeton glomeratus</i> , <i>Imperata cylindrical</i> , <i>Inula britannica</i> , <i>Ipomoea alba</i> , <i>L. gilsei</i> , <i>L. sinuatum</i> , <i>L. stocksii</i> , <i>Leptadenia pyrotechnica</i> , <i>Limonium axillare</i> , <i>Melhania denhamii</i> , <i>Microcephala lamellate</i> , <i>Neurada procumbens</i> , <i>olanum surrattense</i> , <i>Oligomeris linifolia</i> , <i>Oxystelma esculentum</i> , <i>P. oleracea</i> , <i>Pedaliium murex</i> , <i>Pentatropis nivalis</i> , <i>Populus euphratica</i> , <i>Portulaca quadrifida</i> , <i>Psylliostachys spicata</i> , <i>Rumex vesicarius</i> , <i>S. quettense</i> , <i>Seriphidium brevifolium</i> , <i>Solanum incanum</i> , <i>Sonneratia caseolaris</i> , <i>Thespesia populneoides</i> , <i>Trianthema portulacastrum</i> , <i>Tribulus terrestris</i> , <i>Urginea indica</i> , <i>Verbena officinalis</i> , <i>Withania somnifera</i> , <i>Z. simplex</i> , <i>Zaleya pentandara</i> , <i>Zygophyllum propinquum</i>
Chemicals	<i>Aeluropus lagopoides</i> , <i>Ardisia solanacea</i> , <i>Calotropis procera</i> , <i>Cenchrus ciliaris</i> , <i>Clerodendrum inerme</i> , <i>Dalbergia sissoo</i> , <i>Euphorbia thymifolia</i> , <i>Ficus microcarpa</i> , <i>Halocnemum strobilaceum</i> , <i>Ipomoea pes-caprae</i> , <i>K. iranica</i> , <i>Knorringia sibirica</i> subsp. <i>Kochia indica</i> , <i>Mesembryanthemum crystallinum</i> , <i>N. schoberi</i> , <i>Nitraria retusa</i> , <i>Phyla nodiflora</i> , <i>Polypogon monspeliensis</i> , <i>Raphanus raphanistrum</i> , <i>S. taccada</i> , <i>Scaevola plumier</i> , <i>Sessuvium sessuvioides</i> , <i>T. passerinoides</i> , <i>T. ramosissima</i> , <i>T. szovitsiana</i> , <i>T. tetragyna</i> , <i>Tamarix mascatensis</i> , <i>Thomsonii</i> , <i>Trianthema portulacastrum</i>

plant growth (Munns and Tester 2008) and leads to a series of morphological, physiological, biochemical, and molecular changes. In the past 2–3 decades, considerable progress has been made in the evaluation of halophytes to understand their survival mechanisms to be used as crop plants. In the present article, we document different aspects of halophytes, with an emphasis on mechanism of tolerance to salinity, drought and heavy metal tolerance, and their exploitation to manage the problems associated with the abiotic stresses as well as for environmental protection.

Halophytes respond to salt stress at cellular, tissue, and the whole plant level (Epstein 1980). In response to salt stress, the general physiology of halophytes has been reviewed occasionally (Flowers et al. 1977; Epstein 1980; Flowers 1985, 2004) and since then other reviews have examined their eco-physiology (Ball 1988; Rozema 1991; Breckel 2002), photosynthesis (Lovelock and Ball 2002), response to oxidative stress (Jitesh et al. 2006), and flooding tolerance (Colmer and Flowers 2008). Therefore, studies on the halophytes can be instructive from three prospects: first, the mechanism by which halophytes survive and maintain productivity under abiotic constraints can be used to define a minimal set of adaptations required in tolerant germplasm. This knowledge can help to focus the efforts of plant breeders and molecular biologists working with conventional crop plants (Glenn and Brown 1999). Second, halophytes grown in an agronomic setting can be used to evaluate the overall feasibility of high-salinity agriculture, which depends on more than finding a source of tolerant germplasm (Glenn et al. 1997). Third, halophytes may become a potential source of new crops.

3 Halophytes Diversity

Halophytes show immense diversity in habitat and behavior to tolerate the abiotic stress conditions with uneven distribution across the taxa of flowering plants (Flowers et al. 2010). This group of plants has been classified based on their tolerance capacity to salinity stress. Aronson (1989) listed approximately 1,550 species as salt-tolerant

based on their capacity to tolerate the salt concentration more than 80 mM NaCl (equivalent to EC 7.8 dS m⁻¹), whereas, plants limiting the growth beyond this concentration were categorized as glycophytes or salt-sensitive. Using similar features, Menzel and Lieth (2003) recorded total 2,600 species as salt-tolerant. However, considering the salt tolerance limit proposed by Aronson (1989) and Menzel and Lieth (2003) which is found to be significantly lower than the salt concentration of seawater (~480 mM Na⁺ and 580 mM Cl⁻), Flowers and Colmer (2008) defined the halophytes as plants that have evolved and tolerate to complete their life cycle in at least ~200 mM NaCl. Applying the new definition to Aronson's database, Flowers et al. (2010) further classified a total of 350 species as halophytes with major species distributed in 20 orders including 256 families. It has also been suggested that salt tolerance was widely distributed among flowering plant families and had a polyphyletic origin. The authors also stated that distribution and development of evolutionary link of halophytes may account to not more than ~0.25% of the known species of angiosperms.

4 Adaptations to Abiotic Stresses

Halophytes have evolved a number of adaptive traits which allow them to germinate, grow, and achieve their complete life cycle of development under such harsh conditions (Flowers et al. 1977). A variety of studies performed on glycophytes and halophytes subjected to abiotic stresses has demonstrated that impairment in growth under stress condition results from various responses induced through both osmotic effects related to disturbance in plant–water relationships and ionic effects associated with mineral toxicity and deficiency (Lauchli and Epstein 1990). Associated with these primary stresses, higher plants also suffer from secondary stresses provoked by cellular damages especially those induced by oxidative stresses due to imbalance between production and destruction of reduced reactive oxygen species (Zhu 2001).

In order to achieve the tolerance status, three interconnected aspects of plant activity are significant: damage must be prevented, homeostatic condition must be re-established, and growth must resume. At present, there are different mechanisms of abiotic stress tolerance in halophytes that have been proposed which include ion compartmentalization, osmotic adjustment through osmolytes accumulation, succulence, selective transport and uptake of ions, enzymatic and nonenzymatic antioxidant response, maintenance of redox and energetic status, salt inclusion/excretion and genetic control (Flowers and Colmer 2008). Understanding the mechanism of tolerance in halophytes at morphological, anatomical, physiological, biochemical, and molecular levels is crucial to improve the tolerance of the crop plants and their adoption under abiotic stress conditions to exploit such problem soils. A generalized scheme for the plant's response to abiotic stresses and mechanism of stress tolerance is presented (Fig. 2.1).

4.1 Ion Compartmentation

The sensitivity of cytosolic enzymes to salt is similar in both glycophytes and halophytes, indicating that the maintenance of high cytosolic K^+ / Na^+ ratio is a key requirement for plant growth under salt conditions (Glenn and Brown 1999). While dealing with Na^+ , the cell must also acquire nutrient K^+ . The Na^+ ion is the foremost inorganic ion and a cheap source of osmoticum in the halophytes to maintain the osmotic balance under abiotic stresses. Under typical physiological conditions, plant cells require high K^+ (100–200 mM) and lower Na^+ (less than 1 mM) and accordingly the high cytosolic K^+ / Na^+ ratio to maintain the osmotic balance (Tester and Davenport 2003) for proper functioning of the cell. Na^+ competes with K^+ for intracellular influx since both these are transported by common channels present on the membranes and, thus, subsequently increase K^+ efflux from intracellular stores as against the higher Na^+ stress built

up outside the cell. To maintain a high K^+ / Na^+ ratio in the cytosol, plant cell employs primary active transport, mediated by channels and co-transporters for Na^+ extrusion and/or the intracellular compartmentalization of Na^+ into the vacuole (Blumwald 2000). When halophytes are exposed to saline condition, a large increase in extracellular Na^+ level establishes the Na^+ electrochemical potential gradient more than the actual negative electrical membrane potential difference at the plasma membrane (–140 mV) which favor the passive transport of sodium ions from the outer environment inside the cell. Recently, uniporter or ion channel type transporters have been identified for the entry of Na^+ into the cell; these are high-affinity potassium transporter (HKT), low-affinity cation transporter (LCT1), nonselective cation channels (NSCC) like cyclic nucleotide-gated channels (CNGCs) and glutamate-activated channels (GLRs) (Apse and Blumwald 2007). HKTs have been shown to function as Na^+ / K^+ symporter and as Na^+ selective uniporters (Horie and Schroeder 2004). In the process of elevated levels of Na^+ outside the cell, the electrochemical gradient makes the sodium uptake passive; however, the efflux of Na^+ outside cell is an active process and requires energy in the form of ATP. In this process, the Na^+ / H^+ antiporter (NHX) present on the plasma membrane facilitates the Na^+ efflux. This electroneutral exchange of sodium for protons to facilitate efflux is the only mode of transport that has been measured for efflux under physiological conditions (Apse and Blumwald 2007). Besides the efflux of Na^+ , some halophytes have developed mechanism to sequester the Na^+ into the vacuoles as an efficient mechanism to avoid the toxic effects of Na^+ in the cytosol. The transport of Na^+ into the vacuoles is mediated by cation/ H^+ antiporters that are driven by the electrochemical gradient of protons generated by the vacuolar H^+ translocating enzymes such as H^+ -ATPase and H^+ -PPiase (Gaxiola et al. 2007). These transporters play an important role in the sequestration of Na^+ ions into the vacuole or exclusion outside the cell of the halophytes.

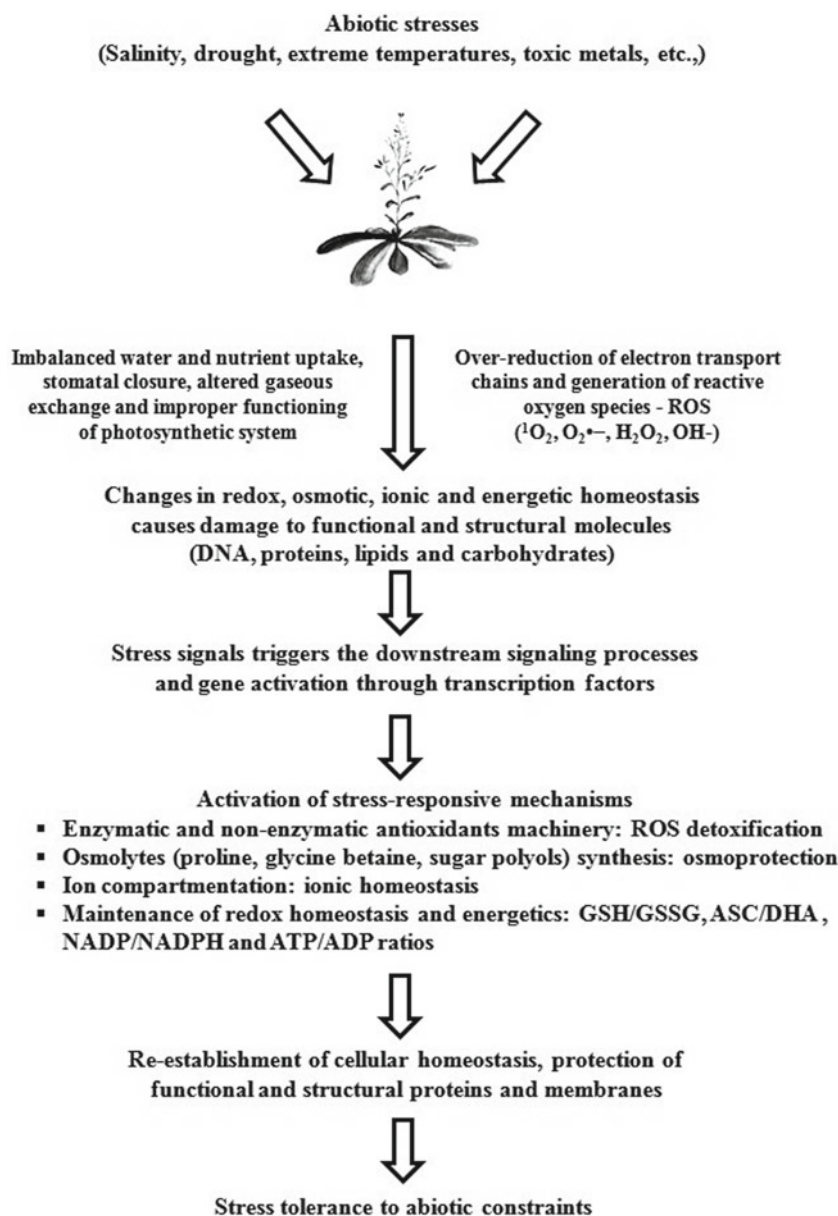


Fig. 2.1 Generalized scheme for plant responses to abiotic stresses and mechanism of stress tolerance. Plants exposed to various abiotic stresses (salinity, drought, extreme temperatures, toxic metals, etc.) initiate the cascade of changes in plants' functioning such as imbalanced water and nutrient uptake, stomatal closure, altered gaseous exchange, improper functioning of photosynthetic systems due to over-reduction of electron transport chains in chloroplast and mitochondria causing generation of reactive oxygen species (ROS). The integrative effect of these factors leads to induce the oxidative damage to functional and structural molecules (DNA, proteins, lipids, and carbohydrates) making the changes in the redox, osmotic,

ionic, and energetic homeostasis of the plant. These stress signals triggers the downstream signaling processes and gene activation through transcription factors. Activation mechanisms involve enzymatic and nonenzymatic antioxidants for detoxification of ROS, osmolytes (proline, glycine betaine, sugar polyols) synthesis for osmotic balance and protection to structural molecules, ion compartmentation for ionic homeostasis and maintenance of redox and energetics through the higher ratios of GSH/GSSG, ASC/DHA, NADP/NADPH, and ATP/ADP. The coordinated action leads to re-establish the cellular homeostasis, protection of functional and structural proteins and membranes, and ultimately the tolerance to abiotic stresses

4.2 Succulence

Succulence is commonly called as halosucculence and found to occur within a range of salt concentrations optimal for growth. The sequestration of saline ions into the vacuoles leads to the plant to increase the succulence, one of the common characteristics of the halophytes (Flowers et al. 1977). Succulence minimizes the toxic effects of excessive ion accumulation and has been reported to be associated with accretion of osmotically active solutes for the maintenance of cell turgor pressure. The succulent halophytes unlike glycophytes tend to accumulate sodium in the vacuole to higher levels than in the cytoplasm and as the volume of the vacuole is much greater than that of the cytoplasm in fully expanded cells, the total sodium content of the root will approximate to the sodium content of the vacuole (Yeo and Flowers 1986). Succulent halophytes generally have thick leaves and stems, mainly associated with an increase in the size of their mesophyll cells along with smaller intracellular spaces. It has also been shown that succulent leaves have more and large-sized mitochondria because the succulent halophytes require excess energy for salt compartmentalization and excretion. Whether succulence is a response to salinity or adaptation to salinity is debatable. But as halophytes tend to become succulent in response to salinity (due to physiologically less available water which affects the changes in the integral part of the plant development), the succulence might be the adaptation to salinity stress (Waisel 1972). This adaptive nature of succulence made the halophytes more successful in the course of evolution exposing to various environmental constraints. Most of the halophytes such as *Sesuvium portulacastrum*, *Suaeda* sps., *Lobularia maritime*, *Mesembryanthemum crystallinum*, *Halosarcia pergranulata* subsp. *Pergranulata*, etc. were found more amenable to accumulate the excess Na^+ in their leaves and stems and increase the succulence under optimum NaCl concentrations in the range of 100–400 mM which leads to sequester these saline ions into the vacuole and become more successful for their growth in saline environment (Qi et al. 2009; Lokhande et al.

2010a). Thus it appears that increased succulence could be due to a “diluting” effect on the ion content of cells which might otherwise rise to toxic levels, and sodium acts as a specific stimulant of growth which can be considered as tending to reduce the turgor pressure component of the water potential of the cell (Jennings 1968).

The succulent halophytes are able to balance the growth and ion accumulation through its sequestration into the vacuole; however, some of the halophytes were adapted to saline environment through secretion of salts from salt glands, cuticles or in guttation fluid, re-transported back to the roots and soil via the phloem or become concentrated in salt hairs. Salt glands act as transient cells because they are devoid of vacuole and have a large number of mitochondria and other organelles. The halophytes which secrete the saline ions include *Limonium latifolium*, *Spartina* sps., *Sporobolus spicatus*, *Atriplex* sps., etc. (Ramadan 2000). However, not all halophytes have salt glands; neither do they all discard salt saturated tissue, demonstrating that individual halophytes utilize different salt tolerance traits under different stress periods.

4.3 Osmotic Adjustment

Osmotic adjustment in response to abiotic stresses is an adaptive mechanism in the halophytes in order to maintain their water balance (Flowers and Colmer 2008). Besides the accumulation of inorganic ions and its sequestration in the vacuole, the osmotic balance between vacuole and cytoplasm is also maintained through the synthesis of organic solutes to retain the stability of the proteins in cells in response to drop in the water potential of the environment (Glenn and Brown 1999). Plant cells synthesize a variety of organic solutes such as proline, sucrose, polyols, trehalose and quaternary ammonium compounds (QACs) such as glycine betaine, alaninebetaine, prolinebetaine, choline-*O*-sulfate, hydroxyprolinebetaine, and pipecolatebetaine (Rhodes and Hanson 1993). These are low molecular weight, highly soluble compounds and are nontoxic even at high cellular concentrations (Ashraf and Foolad 2007) without

disturbing intracellular biochemistry and cellular functions (Cushman 2001), protects subcellular structures, mitigate oxidative damage caused by free radicals (Attipali et al. 2004), maintains the enzyme activities under salt stress and protection of cellular components from dehydration injury (Ashraf and Foolad 2007). The osmolytes accumulation is frequently reported in glycophytes and halophytes being continuously exposed to abiotic stresses; however, synthesis of these osmolytes is an energy-dependent process which consumes large number of ATP molecules (Raven 1985), thus affecting the growth. Osmolytes synthesis and their overproduction in transgenic plants has been achieved in transgenic crop plants, however little success has been achieved on the desired protective levels of these osmolytes in plants. In contrast, some plants showed increased tolerance to abiotic stresses after exogenous application of these organic solutes (Ashraf and Foolad 2007). Although increased accumulation of these osmolytes by the plants exposed to abiotic stresses has been reported, not all plant species synthesize the all kinds of osmolytes at a time; some plant species synthesize and accumulate very low quantity of these compounds while some plant species not do so (Ashraf and Foolad 2007).

4.3.1 Proline

Similar to glycophytes, proline accumulation is a common adaptive response to various abiotic stresses. Several studies using transgenic plants or mutants demonstrated that proline metabolism has a complex effect on development and stress responses, and that proline accumulation is important for the tolerance to certain adverse environmental conditions (Hong et al. 2000; Miller et al. 2010). In plants, proline is mainly synthesized from glutamate using two important enzymes such as pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR). Proline is synthesized in cytoplasm; however in mitochondria, the catabolism occurs via sequential action of proline dehydrogenase (PDH) producing pyrroline-5-carboxylate (P5C) and its conversion to glutamate using P5C dehydrogenase (P5CDH) (Szabados and Savoure 2009). Halophytes have shown vast diversity for

the accumulation of proline in response to abiotic stresses, wherein plants from the Aizoaceae family accumulate large quantities of proline showing its role in osmoprotection (Delauney and Verma 1993). Proline concentrated in the cytosol, chloroplast and vacuoles and compatible with enzyme activity in the cytoplasm showed its significant contribution to osmotic adjustment. Besides being an osmoprotectant, proline also has a role in detoxification of reactive oxygen species and act as an antioxidant, stabilization of proteins and protein complexes and as a signaling/regulatory molecule (Szabados and Savoure 2009). It also function as a protein-compatible hydrotrope (Srinivas and Balasubramanian 1995), alleviating cytoplasmic acidosis, and maintaining appropriate NADP⁺/NADPH ratios compatible with metabolism (Hare and Cress 1997). Also, rapid breakdown of proline upon relief of stress provides sufficient reducing agents that support mitochondrial oxidative phosphorylation and generation of ATP for recovery from stress and repairing of stress-induced damages (Hare and Cress 1997). In halophytic plant species in response to abiotic stresses, proline accumulation in the cytosol has been shown to contribute substantially to cytoplasmic osmotic adjustment. For example, in cells of *Distichlis spicata* treated with 200 mM NaCl, the cytosolic proline concentration was estimated to be more than 230 mM (Ketchum et al. 1991). In *Sesuvium portulacastrum*, Lokhande et al. (2010a, b, 2011a) found an extensive increase in proline content when the callus and axillary shoot cultures exposed to salt and drought stress alone or under iso-osmotic stress conditions of NaCl and PEG. Higher proline accumulation has also been shown in *S. portulacastrum* plants exposed to various abiotic constraints that include salinity, drought, and heavy metals (Messedi et al. 2004; Slama et al. 2008; Ghnaya et al. 2007; Moseki and Buru 2010; Lokhande et al. 2011b). Such an osmotic adjustment through proline accumulation is also evident in other species like *Plantago crassiflora*, *Salicornia europaea*, *Atriplex halimus*, *A. halimus* subsp. *schweinfurthii*, *Avicennia marina*, *Hordeum maritimum*, *Ipomoea pes-caprae*, *Paspalum vaginatum*, *Phragmites australis*, and *Suaeda* sps.

(Vicente et al. 2004; Reda et al. 2004; Nedjimi and Daoud 2009; Pagter et al. 2009; Lefevre et al. 2009; Sucre and Suarez 2010). Among different halophytic plants, *S. portulacastrum* has been reported as a high proline accumulator, with levels reaching 300 $\mu\text{mol g}^{-1}$ leaf dry matter (Slama et al. 2008). Such a pronounced accumulation of proline and its physiological role in osmotic adjustment may have made the halophytes more successful to grow under adverse environmental stresses.

4.3.2 Glycine Betaine

Among the variety of quaternary ammonium compounds, glycine betaine (GB) is one of the most abundantly occurring and synthesized at higher concentrations in the plants exposing to dehydration stress due to adverse environmental calamities. GB is located in chloroplast where it plays an important role in osmotic adjustment and protection of thylakoid membrane, by maintaining the photosynthetic machinery in active state (Robinson and Jones 1986). GB is synthesized mainly from choline, which is converted to betaine aldehyde and then to GB through sequential enzymatic action of choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH), respectively. Although other pathways such as direct *N*-methylation of glycine are also known, the pathway from choline to GB has been identified in all GB-accumulating plant species (Ashraf and Foolad 2007). It is widely believed that synthesis and accumulation of GB protects cytoplasm from ion toxicity, dehydration and temperature stress and helps normal functioning of the metabolic machineries in the cell during stressed conditions by stabilizing macromolecule structures, protecting chloroplast and photosynthesis system II (PSII) by stabilizing the association of the extrinsic PSII complex proteins and indirectly interacting with phosphatidylcholine moieties of membranes to alter their thermodynamic properties (Subbarao et al. 2001). It has been shown that tolerant species are more amenable to accumulate higher GB in comparison to sensitive species as a response to abiotic stress imposition. Based on the GB and proline accumulation potential,

Tipirdamaz et al. (2006) categorized the halophytes from inland and salt marsh habitats of Turkey. The studies have shown that the species that behaved as GB accumulators appeared poor proline accumulators and vice versa. The GB accumulation reported in the halophytes is generally in the range of 1.5–400 $\mu\text{mol g}^{-1}$ DW and some of the highest GB accumulating halophytes are members of the Chenopodiaceae (*Halocnemum strobilaceum*, *Petrosimonia brachiata*, *Suaeda confuse*), Compositae (*Artemisia santonicum*), and Frankeniaceae (*Frankenia hirsuta*). Increased accumulation of GB has also been demonstrated in other halophytes such as *Beta vulgaris* (Subbarao et al. 2001), *Spartina anglica* (Mulholland and Otte 2002), *Atriplex halimus* (Martinez et al. 2005), *A. Nummularia* (Silveira et al. 2009), and *S. portulacastrum* (Lokhande et al. 2010a, b). Increased GB accumulation has also been correlated with increased betaine aldehyde dehydrogenase gene expression (BADHmRNA) in *Salicornia europaea* and *Suaeda maritima* leaves exposed to salt stress (Moghaieb et al. 2004). Considering the significance of GB in the osmotic balance of the halophytes under stressful environment, different methods can be derived to enhance the concentration of this compound in crop plants to increase their stress tolerance. The approaches can include breeding of sensitive cultivars with their tolerant relatives from halophytes with natural abilities to produce high levels of GB or genetically engineer the sensitive species through transformation of the genes responsible for GB synthesis. Although some progress has been made in introducing the genes for the production of these compounds in naturally accumulating or low-accumulating plant species, levels of these compounds' accumulation in transgenic plant have often been low or insufficient to the plant stress tolerance (Ashraf and Foolad 2007).

4.3.3 Soluble Sugars

In general, modulations in the carbon metabolism and the levels of carbohydrates (sugars) are seen due to changes occurring in the process of photosynthesis and carbon partitioning of the plant at organ level and in whole plants exposing

to abiotic stresses (Gonzalez et al. 2009). Soluble sugars function as metabolic resources and structural constituents of cells, besides acting as signals regulating various processes associated with plant growth and development. Such signaling can modulate stress pathways into a complex network to further orchestrate metabolic plant responses. A variety of sugar compounds such as sucrose, glucose, mannose, maltose, trehalose, and many other sugar alcohols have been studied in response to abiotic stresses (Briens and Larher 1982; Yuanyuan et al. 2009) and the accumulation of soluble sugars has been attributed as an important parameter of osmotic adjustment in the halophytes. Briens and Larher (1982) screened different organs of 16 halophyte species for soluble carbohydrates and other osmolytes and found that all the species accumulated sucrose, fructose and glucose whereas *Plantago maritime*, *Juncus maritimus*, *Phragmites communis* and *Scripus maritimus* showed the highest accumulation of soluble sugars. The presence of higher amounts of soluble sugars has been reported as main contributors to osmotic adjustment in the *Atriplex halimus* plants exposed to PEG and NaCl stresses and it is correlated with the response of NaCl stress on soluble sugar synthesis (Martinez et al. 2005). The accumulation of total soluble sugars has also been correlated with the variations at genotypic level among two genotypes of *Cakile maritime* namely Jebra and Tabarka which showed differences in the total soluble carbohydrate concentrations. While the content of the sugars was unaffected in the leaves of Jerba plants at moderate salinity, the plants of the salt-sensitive Tabarka showed a slight increase in soluble carbohydrate contents during leaf development. The contribution of this compatible solute group to the “osmotic pool” was found higher in the salt-tolerant Jerba than in the salt-sensitive Tabarka seedlings exposed to 400 mM NaCl stress (Megdichi et al. 2007). Further, *Sesuvium portulacastrum* axillary shoots exposed to salinity stress showed optimum growth at 200 mM NaCl in comparison to control and exhibited increased synthesis of total soluble sugars over proline and glycine betaine (Lokhande et al. 2010b). Salinity-induced soluble sugar accumulation has

also been observed in *P. euphratica* (Zhang et al. 2004). Accumulation of soluble sugars has been observed in plants undergoing drought, flooding, and water logging conditions (Chai et al. 2001; Munns 2002; Li and Li 2005). *Chenopodium quinoa* exposed to water deficit and water-logging stresses showed no changes in starch, sucrose, or fructose content but showed increased glucose and total soluble sugar content in stressed plants in comparison to control (Gonzalez et al. 2009). These studies in halophytes demonstrate that soluble sugars play a significant role besides other osmolytes in the osmotic adjustment.

4.4 Antioxidant Systems

The halophytic plants display a cascade of events upon exposure to environmental stresses leading to metabolic disturbance. The cascade of events include physiological water-deficit abscisic acid-regulated stomatal closure in leaves, limited CO₂ availability, over-reduction of electron transport chain in the chloroplast and mitochondria and finally generation of reactive oxygen species (ROS). These ROS are highly toxic and in the absence of protective mechanism in the plant can cause oxidative damage to proteins, DNA, and lipids (Mittler 2002; Miller et al. 2010). Additionally, this may also lead to alteration in the redox state resulting in further damage to the cell (Mittler et al. 2004). To regulate the ROS levels, plant cells are evolved with complex enzymatic and nonenzymatic antioxidant defense mechanisms, which together help to control the cellular redox state under changing environmental conditions. A correlation between enzymatic and nonenzymatic antioxidant capacitance and abiotic stress tolerance has been reported in several plant species such as *Crithmum maritimum*, *C. maritime*, *Plantago* genus, *Sesuvium portulacastrum*, *Mesembryanthemum crystallinum* (Ben Amor et al. 2005; Jitesh et al. 2006; Sekmen, Turkan and Takio 2007; Ashraf 2009; Lokhande et al. 2010a, b, 2011a-c). Superoxide dismutase (SOD) constitutes the first line of defense converting O₂^{•−} to H₂O₂, which is further reduced to

Table 2.2 Examples of halophytic plant species studied for the antioxidant responses in response to abiotic stresses

Plant species	Enzyme/protein/gene studied	References
<i>Avicennia marina</i>	SOD, CAT, POX, APX, MDHAR	Cherian et al. (1999), Jitesh et al. (2006), Kavitha et al. (2008), and Kavitha et al. (2010)
<i>Bruguiera parviflora</i> , <i>B. gymnorrhiza</i>	SOD, CAT, APX	Takemura et al. (2000) and Parida et al. (2004)
<i>Beta vulgaris</i> , <i>B. maritima</i>	SOD, CAT, APX, GR	Bor et al. (2003)
<i>Crithmum maritimum</i>	SOD, CAT, POX	Ben Amor et al. (2005)
<i>Hordeum vulgare</i>	SOD, POX, CAT, GR	Patra and Panda (1998)
<i>H. maritimum</i>	SOD, CAT, GPX, APX, MDHAR, DHAR, GR	Hafsi et al. (2010)
<i>M. crystallinum</i>	SOD, ferritin, CAT, Mn, Fe, Cu/Zn SOD	Slesak et al. (2002, 2008), Slesak and Misalski (2003), Hurst et al. (2004), and Parmonova et al. (2004)
<i>Nitraria tangutorum</i>	SOD, CAT, APX	Yang et al. (2010)
<i>Phragmites australis</i>	SOD, CAT, APX, POX, DHAR, GST	Carias et al. (2008)
<i>Phaseolus vulgaris</i>	SOD, APX, CAT, GPX	Jebara et al. (2005)
<i>Sesuvium portulacastrum</i>	SOD, CAT, APX, GR	Lokhande et al. 2010a, b, 2011a-c)
<i>Suaeda nudiflora</i> , <i>S. salsa</i>	SOD, CAT, POX	Cherian and Reddy (2003), Wang et al. (2004a), and Fang et al. (2005)
<i>T. halophila</i>	SOD, APX, POX	Taji et al. (2004), Wang et al. (2004a, b), and M'rah et al. (2006)

water and oxygen by ascorbate peroxidase (APX) and catalase (CAT). Monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), and glutathione peroxidase (GPX) are an important enzymes involved in regeneration of ascorbate and GSH for the proper functioning of ASC-GSH cycle (Noctor and Foyer 1998; Mittler 2002; Miller et al. 2010).

Halophytes have evolved various mechanisms of adaptations of which increased antioxidant enzyme activities was found one of an important mechanism of stress tolerance. Halophytes have capacity to maintain high metabolic activity even at inhibitory concentrations of intracellular Na^+ due to enhanced antioxidant mechanism (Jitesh et al. 2006). Most of the early studies in halophytes were on photosynthesis and respiration and related to ion compartmentation, osmotic adjustment (Flowers et al. 1977; Fukushima et al. 1997). However, recently, more emphasis has been given on abiotic stresses in relation to antioxidant enzymes in halophytes (Takemura et al. 2000; Cherian and Reddy 2003; Parida et al.

2004; Slesak et al. 2002, 2008; Slesak and Misalski 2003; Jitesh et al. 2006; Lokhande et al. 2010a–b, 2011a, c). The response of antioxidant enzyme systems in the halophytes exposed to abiotic stresses has been reviewed by Jitesh et al. (2006) and is summarized in Table 2.2. Most of the halophytes have shown increased efficiency of antioxidant enzyme machinery thus removing the ROS levels to a greater extent and maintain the plants survival under stressful conditions.

4.5 Redox and Energetics

The cellular redox state is made tangible in terms of the redox state of the individual redox-active molecules in a cell. For each redox-active molecule, its redox state can be defined as the proportion of reduced molecules relative to the total pool size, or alternatively as the ratio between reduced and oxidized molecules within a pool (Potters et al. 2010). A large number of redox-active compounds such as ascorbate (ASC), glutathione

(GSH), pyridine nucleotides (NADH and NADPH), carotenoids, tocopherols, distinct redox-active phenolics, polyamines and proteins carrying redox-active S-groups are contained in plant cells (Smirnoff 2005; Queval and Noctor 2007). The enzymatic and nonenzymatic antioxidants involved in ROS scavenging significantly contribute to the redox state maintenance of the cellular environment through continuous channeling of these redox-active components which facilitate the proper functioning of the cell under stressful conditions. In general, the maintenance of redox state is correlated with the energy metabolism of the plant cell in terms of ATP/ADP ratio. Under stressful conditions, the ROS produced due to oxidative stress requires more energy in the form of ATP to maintain the cellular homeostasis such as ion compartmentation, osmolytes synthesis, etc. The ATP requirement for these processes is different, such as 3.5, 41 and 50 ATP molecules are required for the synthesis or accumulation of one molecule of Na⁺, proline, and glycine betaine, respectively (Raven 1985). Thus, the energetic status of the plant is also dependent on the type of molecule synthesized or accumulated by the plant. It is possible that halophytes evolved to survive under abiotic stress conditions through proper maintenance of a higher redox and energetic status which could have conferred a plasticity to grow under stress. Not much information is available on the redox signaling and energetics in case of the halophytes. Recently, Lokhande et al. (2010c) for the first time demonstrated that maintenance of redox and energy state plays a major role in mediating salinity tolerance and in achieving a balance between tolerance and growth in *Sesuvium portulacastrum*. The plants under optimum levels of NaCl (250 mM) showed retention in the growth whereas significantly toxic levels of NaCl (1,000 mM) disturbed the homeostasis of the plant due to abrupt changes in the ratios of redox-active compounds (ASC/DHA, GSH/GSSG, NADP/NADPH) and energy molecules (ATP/ADP) (Fig. 2.2a–f). Further to stick this work, more efforts could be initiated to unravel the redox and energetic of the halophytes to gain the knowledge of redox control. The concept of a cellular redox

state, as proposed by Foyer and Noctor (2005), is very useful in terms of elucidating the importance of redox reactions in gene expression, metabolism control, signal transduction, and cellular defense. The concept must now be developed to identify and quantify those redox-active compounds that are the specific regulators of cellular responses (Potters et al. 2010).

4.6 Genomic Approaches

Plant adaptation to environmental stresses is controlled by a cascade of molecular networks. In this regard, the application of genomic technologies has made more impact on understanding the plant responses to the abiotic stresses (Cushman 2003). The technology has made remarkable success in understanding the abiotic stress tolerance at genome level with potential to modify plants' tolerance for increasing yield under stressful conditions (Bohnert et al. 2006). In contrast to traditional breeding and marker-assisted selection programs, the direct introduction of a small number of genes by genetic engineering has also become tangible and attractive as a rapid approach to improve the plants' stress tolerance (Cushman and Bohnert 2000; Popova et al. 2008) to re-establish homeostasis and to protect and repair damaged proteins and membranes (Wang et al. 2003).

In the course of studies on mechanism of abiotic stress tolerance, *Arabidopsis thaliana* has emerged as an excellent model system (Zhu 2001) because most of the crop plants are glycophytes. However, study of some novel mechanisms unique to halophytes or stress-tolerant plants may be difficult with *Arabidopsis* and this has been made possible by the available genome information on *Mesembryanthemum crystallinum*, which, when compared with the *Arabidopsis* genome, seems to contain a number of transcripts that have no counterparts (Wang et al. 2004b). Thereafter, several halophytes such as *M. crystallinum*, *Suaeda* species, *Atriplex* species have been employed to dissect out the molecular basis of stress tolerance mechanism of the halophytes. Recently, *Thellungiella halophila* (salt cress), a member of the Brassicaceae, has emerged as a

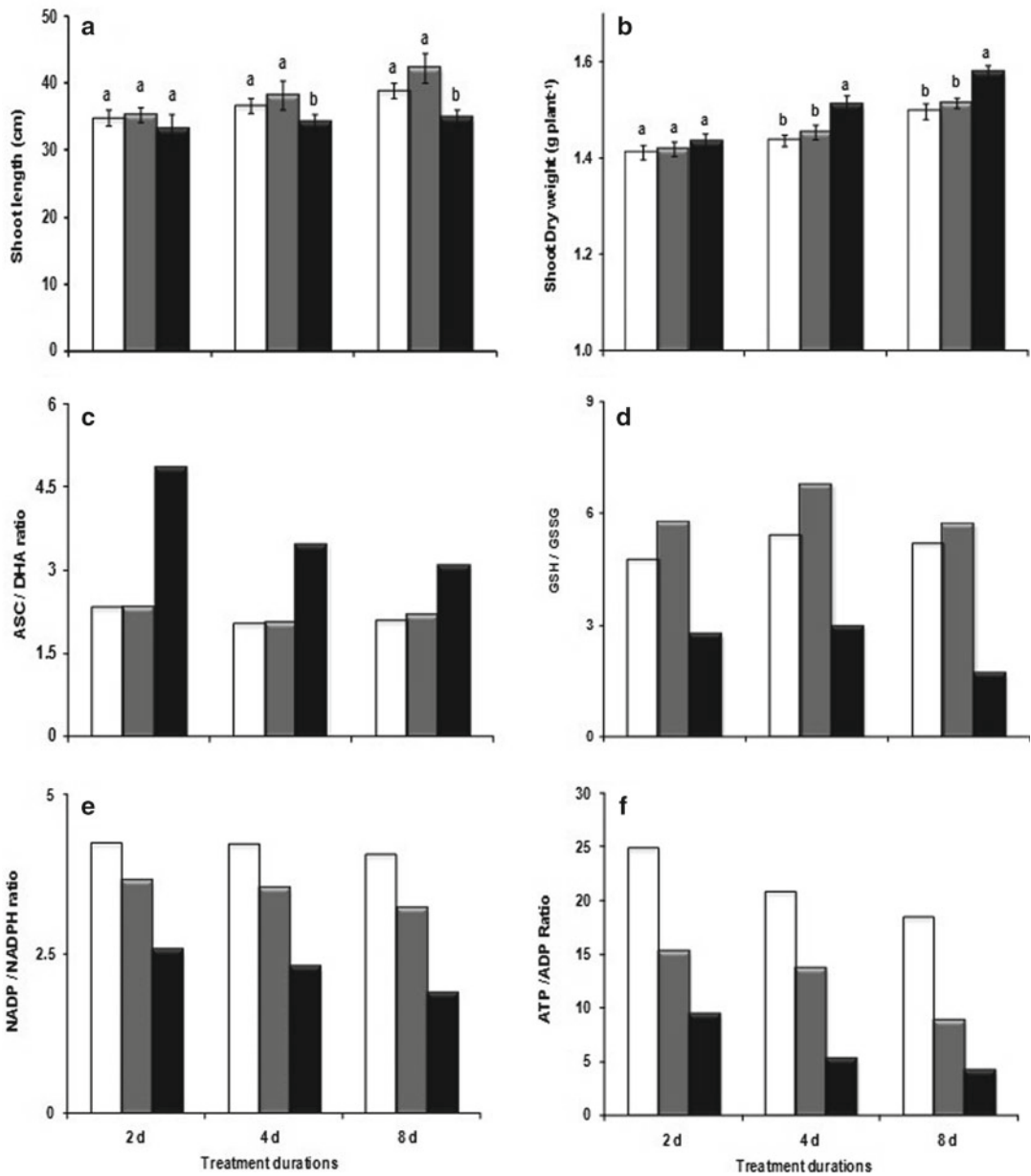


Fig. 2.2 The salinity stress responses (growth, redox, and energy status) of *Sesuvium portulacastrum* exposed to optimum (250 mM) and supra-optimal (1,000 mM) concentrations of NaCl

model for understanding adaptation of the halophytes to abiotic stress tolerance due to its homology with the glycophyte model, *A. thaliana* (Wang et al. 2004b; Amtmann 2009). This halophyte has the ability to grow in high salt concentrations which otherwise become inhibitory for the growth of its salt-sensitive relative *A. thaliana*

and other crop plants (Zhu 2001; Nah et al. 2009). The salient features of *T. halophila* such as small diploid genome (240 Mb and $2n=14$), short and self-fertile life cycle and ease of floral dipping method of transformation have enabled it as a successful candidate for molecular detailing of its response to abiotic stress tolerance and relative

comparison with *A. thaliana*. The comparative genomics of *T. halophila* and *A. thaliana* revealed extensive and novel information on presence of differential genes responsible for abiotic stress tolerance in *T. halophila* in comparison to *A. thaliana* (Nah et al. 2009). Taji et al. (2004) studied the differences in the regulation of salt tolerance between salt cress and *Arabidopsis* by analyzing the gene expression profiles using a full-length *Arabidopsis* cDNA microarray. Only a few genes were induced by 250 mM NaCl in salt cress stress compared to *Arabidopsis*. Even in the absence of stress, a large number of known abiotic- and biotic-stress inducible genes, including Fe-SOD, P5CS, PDF1.2, AtNCED, P-protein, b-glucosidase, and SOS1, were expressed at high levels. The study also found salt cress to be more tolerant to oxidative stress than *Arabidopsis*. The salt tolerance mechanisms between salt-sensitive glycophytes and salt-tolerant halophytes could result from alterations in the regulation of the same basic set of genes involved in salt tolerance among these plants. Kant et al. (2006) used gene-specific primers of *Arabidopsis* that showed similar real-time PCR amplification efficiencies with both *A. thaliana* and *T. halophila* cDNA and concluded that the expression of specific salt tolerance orthologues differs between unstressed and stressed plants of both species.

The development of expressed sequence tags (ESTs) and cDNA libraries using various genomic approaches such as suppressive subtractive hybridization (SSH), differential display reverse transcription-polymerase chain reaction (DDRT-PCR), representational difference analysis (RDA), serial analysis of gene expression (SAGE), and cDNA microarray (Breyne and Zabeau 2001) provided an enormous databases for understanding the genetic network involved in abiotic stress tolerance mechanism of halophytes (Wang et al. 2004b; Kore-eda et al. 2004; Popova et al. 2008). Using this approach, various genes responsible for stress tolerance have been isolated from halophytes and cloned or overexpressed in the bacterial systems as well as sensitive cultivars of glycophytes to enhance the stress tolerance capacity and improve crop yield (Table 2.3).

Transcript-profiling experiments in *Arabidopsis* in response to drought, cold, or salinity

stresses using the *Arabidopsis* GeneChip array or full-length cDNA microarrays have shown that extensive changes occur in the transcriptome of *Arabidopsis* (Fowler et al. 1999; Kreps et al. 2002; Seki et al. 2002). It is known that approximately 30% of the transcriptome on the *Arabidopsis* GeneChip 8 K oligoarray changed in stress treatments (Kreps et al. 2002). The expressed sequence tag analyses of *Thellungiella* clones revealed 90–95% identities between *Thellungiella* and *Arabidopsis* cDNA sequences (Wang et al. 2004a, b; Wong et al. 2006). In a comparison of three stresses (cold, low water availability, and saline conditions) as well as recovery from water deficits in *Thellungiella*, Wang et al. (2006) employed an expression profiling strategy to identify stress responses. There was not much degree of overlap among genes responsive to drought, cold, or salinity suggesting relatively few common end responses triggered by these stresses existed in this halophyte. While *Thellungiella* had shown activation of the expression of some well-known stress-responsive genes, it was found to downregulate a large number of biotic stress-related genes under drought and salinity treatments. The study has made a significant step in showing the emergence of *Thellungiella* as a model species for the molecular elucidation of abiotic stress tolerance, and that *Thellungiella* responds precisely to environmental stresses, thereby conserving energy and resources and maximizing its survival potential.

SOS1 (*Salt Overly Sensitive 1*) is known to play key role in the ion homeostasis mechanism movement (Shi et al. 2000). Although *SOS1* has been intensely studied in *Arabidopsis*, its involvement in the salt tolerance of halophytes is not much known. Oh et al. (2009) investigated the role(s) by which *ThSOS1*, the *SOS1* homolog in *Thellungiella*, was involved in modulating the halophytic character using ectopic expression of the gene in yeast and in *Arabidopsis* and *Thellungiella* *SOS1*-RNA interference (RNAi) lines. The knockdown of *SOS1* expression totally altered *Thellungiella* into a salt-sensitive plant like *Arabidopsis*. The authors found that the activity of *ThSOS1* could limit Na⁺ accumulation and the distribution of Na⁺ ions.

Table 2.3 Source of genes from halophytes for the improvement of abiotic stress tolerance

Source organism	Genes	Trait improved	Target organism	References
<i>Atriplex gmelini</i>	Vacuolar Na ⁺ /K ⁺ antiporters <i>AgNHX1</i>	Eightfold higher activity of the vacuolar-type Na ⁺ /H ⁺ antiporter	<i>Oryza sativa</i>	Ohta et al. (2002)
<i>Medicago sativa</i>	Vacuolar Na ⁺ /K ⁺ antiporters <i>MsNHX1</i>	Increased osmotic adjustment and MDA content	<i>A. thaliana</i>	Bao-Yan et al. (2002)
<i>Aeluropus litoralis</i>	Vacuolar Na ⁺ /K ⁺ antiporters <i>AtNHX1</i>	Compartmentalize more Na ⁺ in roots and keep a relative high K ⁺ /Na ⁺ ratio in the leaves	<i>N. tabacum</i>	Zhang et al. (2008)
<i>Atriplex centralasiatica</i>	Betaine aldehyde dehydrogenase <i>AcBADH</i>	Improved synthesis of glycine betaine	<i>N. tabacum</i>	Yin et al. (2002)
<i>Suaeda liaotungensis</i> , <i>Beta vulgaris</i> , <i>Atriplex hortensis</i> , <i>A. nummularia</i>	Choline monooxygenase <i>CMO</i>	Three- to sixfold increased activity of CMO increases glycine betaine synthesis	<i>N. tabacum</i>	Russell et al. (1998), Shen et al. (2001), Tabuchi et al. (2005), and Li et al. (2003, 2007)
<i>Avicennia marina</i>	Monodehydroascorbate reductase (MDHAR)	Ascorbate regeneration and ROS scavenging	<i>N. tabacum</i>	Kavitha et al. (2010)
<i>Sesuvium portulacastrum</i>	Fructose-1,6-bisphosphate aldolase <i>SpFBA</i>	Strongly expressed in roots than in leaves and stems under abiotic stresses	<i>Escherichia coli</i>	Fan et al. (2009)
<i>Mesembryanthemum crystallinum</i>	IMT1, myo-Inositol O-methyl-transferase	Inositol methylation	<i>E. coli</i>	Rammesmayr et al. (1995)
<i>Thellungiella halophila</i>	FLC gene	Controls vernalization response pathway	<i>T. halophila</i>	Fang et al. (2006)
<i>Suaeda salsa</i>	Peroxioredoxin Q gene <i>SsPrx Q</i>	Thioredoxin-dependent peroxidase activity	<i>E. coli</i>	Guo et al. (2004)

5 Role of Halophytes in Abiotic Stress Management

5.1 Desalination and Stabilization of Saline Soils

The problem of salinity is widespread covering at least 75 countries (Goudie 1990). Various physical, chemical, and biological approaches have been developed for the reclamation of such saline soils (Shahid 2002). Biological methods include organic manure, crop rotation, salt-tolerant crops (Shahid 2002), as well as vegetative bioreclamation (Qadir and Oster 2004). The reclamation of saline soil using such biological means is also referred as desalinization (Zhao 1991), biodesalinization, and desalination of salt-affected soils by halophytes (Rabhi et al. 2009). The potential of plants to accumulate enormous salt quantities depends often on the capacity of their above-ground biomass (hyper-accumulating plants) (Rabhi et al. 2010). This ability could be significant particularly in the arid and semi-arid regions where insufficient precipitations and inappropriate irrigation systems are unable to reduce the salt burden in the rhizosphere of plants and suitable physicochemical methods are too expensive (Shahid 2002). The plant-based method of saline soil stabilization is of importance especially in several developing countries where chemical amendments are getting more and more expensive. In this regard, the use of Na^+ and Cl^- hyper-accumulating plants for soil desalination is often suggested as a strategy (Ravindran et al. 2007). A large number of species has been utilized for soil desalination based on their suitability and capacity to accumulate the salt. Halophytes are one of the important categories of plant species extensively used for this purpose with rice as the only one glycophytic exception (Iwasaki 1987). In order to be useful for desalination purpose, the plant species to be used should have high salt resistance, high biomass production, considerable shoot sodium content, and high degree of economic utilization (such as fodder, fuel, fiber, essential oil, and oil seeds) (Rabhi et al. 2010). Shoot-succulent halophytes such as *Sesuvium*

portulacastrum and *Suaeda* sps. meet these criteria since they are able to accumulate enormous Na^+ quantities within their above-ground organs. They can become useful candidates for the desalination of salt-affected soils under nonleaching conditions. Zhao (1991) calculated that *Suaeda salsa* produced about 20 ton DW ha^{-1} and withdraw 3–4 ton NaCl. Ravindran et al. (2007) estimated that *Suaeda*, *Sesuvium*, *Excoecaria*, *Clerodendron*, *Ipomoea*, and *Heliotropium* species could remove 504, 474, 396, 360, 325, and 301 kg NaCl, respectively, from 1 ha land in 4 months.

Selection of suited species is the first step for affordable soil desalination at a wider scale in the arid and semi-arid regions (Rabhi et al. 2009). In a case study, a significant decrease in electrical conductivity of the soil having a 50% saturation percentage was recorded from 33 to 20 dS m^{-1} in the presence of single growth cycle of *J. rigidus* in Egypt (Zahran and Wahid 1982). *Suaeda salsa* showed its potential to reduce the soil Na^+ content at depth 0–10 cm by 2.4 with a density of 15 plants m^{-2} and by 3.8 with a density of 30 plants m^{-2} (Zhao 1991). It has also been demonstrated that the growth of annual glycophytes (*Medicago* spp.) was much better on the soil previously desalinated with perennial halophytes in saline ecosystems (Abdelly et al. 1995). It was concluded that perennial halophytes desalinize and fertilize the rhizosphere, offering a favorable microhabitat for a better growth of annual glycophytes. Ravindran et al. (2007) evaluated the capacity of six halophytic species (*Suaeda maritima*, *Sesuvium portulacastrum*, *Clerodendron inerme*, *Ipomoea pes-caprae*, *Heliotropium curassavicum* and one tree species *Excoecaria agallocha*) to desalinize the upper 40 cm of soil under field conditions in India. This study demonstrated that after 120 days of cultivation of the halophytes, *Suaeda maritima* and *Sesuvium portulacastrum* showed a decrease in electrical conductivity of saline soil from 4.9 to 1.4 and 2.5 dS m^{-1} , respectively. The potential of native halophytes *Arthrocnemum indicum* and *Suaeda fruticosa* to desalinize saline soils was compared with that of an introduced halophyte, *S. portulacastrum*. In this study, Rabhi et al. (2009) confirmed *S. portulacastrum* as the most suitable

plant with higher accumulation of Na^+ in its shoot parts for desalination purpose in arid and semi-arid regions where precipitation is too low to leach salts from rhizosphere. Similarly, successful germination and growth of *Hordeum vulgare* (barley) was observed on the soil desalinated with salt accumulator halophyte *S. portulacastrum* (Rabhi et al. 2010). Taken together, the reports suggest that salt accumulator halophytes can be exploited as a potential source for desalination of agricultural land in the arid and semi-arid regions as well as for the stabilization of saline lands along the coastal regions of the world.

5.2 Phytoremediation

Contamination of agricultural soil by heavy metals (such as Cu, Cd, Zn, Mn, Fe, Pb, Hg, As, Cr, Se, Ur, etc.) has become a serious environmental concern due to their potential impact on the ecosystems. Such toxic elements are considered as soil and water pollutants due to their widespread occurrence, and their acute and chronic toxic effect on plants grown in such soils as well as on humans living in their surrounding (Yadav 2010). Plants, as sessile organisms have developed diverse detoxification mechanisms against absorbing a diversity of natural and man-made toxic compounds. Pollutant-degrading enzymes in plants are a natural defense system against a variety of allelochemicals released by competing organisms, including microbes, insects and other plants. Therefore, plants act as natural, solar-powered pump-and-treat systems for cleaning up contaminated environments, leading to the concept of phytoremediation (Aken 2008). A variety of plant systems have been studied for phytoremediation practices of contaminated soil; however, each species has limitations to accumulate the toxic metals and detoxify to nontoxic compounds through the enzymatic actions. In the course of evolution from marine to freshwater habitat, halophytes are found most successful group of plants which have shown adaptations to a variety of abiotic stresses, tolerance to heavy metal stress is one of these. In recent years, more emphasis has been placed to remove the toxic

metals from contaminated soil and water bodies and reclamation of such lands for sustainable agriculture. In this regard, extensive research is undertaken to exploit the use of metal hyper-accumulating plants and search for a suitable plants that can significantly accumulate heavy metals and metalloids (Zabłudowska et al. 2009). However, phytoremediation constitutes a group of strategies meant not only to reduce the metal load at the contaminated site but also to stabilize the site. These strategies are referred as “phyto-extraction” or “phytostabilization” and the selection of a plant may depend on the level of contamination at the site of concern. Both strategies can be integrated into operation at highly contaminated mine sites with a plant that may not be a hyper-accumulator but can tolerate even very high concentrations of toxic metals (Lokhande et al. 2011b). Various halophytes have evolved distinct morphological specializations for dealing with abiotic stressed environments such as presence of “aerial stilts” in the members of families Rhizophoraceae and “pneumatophores” in the members of Avicennaceae and Sonneratiaceae which enable gaseous exchange and oxygenation for respiration in an anoxic environment (Hutchings and Saenger 1987); however, the members of Myrsinaceae, possess no aerial roots. Table 2.4 presents phytoremediation potential of some halophytes.

Numerous laboratory-based trials suggested that the concentrations of metals required to show significant negative effects on halophytes may be significantly higher when compared to their aquatic and terrestrial floral counterparts (MacFarlane et al. 2007). For example, there were no adverse effects on the growth of *Rhizophora mucronata* and *Avicennia alba* seedlings treated with Zn ($10\text{--}500\text{ }\mu\text{g ml}^{-1}$) and Pb ($50\text{--}250\text{ }\mu\text{g ml}^{-1}$). In *Kandelia candel* seedlings, only at the highest applied metal concentrations (400 mg kg^{-1} Cu and Zn) inhibition of leaf and root development was observed (Chiu et al. 1995). Similarly, Pb ($0\text{--}800\text{ }\mu\text{g g}^{-1}$) had little negative effect on *Avicennia marina* seedlings (MacFarlane and Burchett 2002). Studies have demonstrated the accumulation of metals (Cu, Zn, Pb, Fe, Mn, and Cd) predominantly in root

Table 2.4 Examples of halophytic plant species used for the purpose of phytoremediation

Plant species	Phytostabilization/phytoextraction/ phytoexcretion of heavy metals	References
<i>Sesuvium portulacastrum</i>	Cd, Pb and As	Ghnaya et al. (2007), Nouairi et al. (2006), Zaier et al. (2010a, b), and Lokhande et al. (2011b)
<i>Mesembryanthemum crystallinum</i>	Cd	Ghnaya et al. (2007) and Nouairi et al. (2006)
<i>Halimione portulacoides</i> , <i>Spartina maritima</i>	Cd, Cu, Pb, and Zn	Reboreda and Caçador (2007, 2008)
<i>Arthrocnemum macrostachyum</i> , <i>Spartina argentinensis</i>	Cd and Cr	Redondo-Gómez et al. (2010a, b)
<i>Triglochin maritima</i> , <i>Juncus maritimus</i> , <i>Sarcocornia perennis</i> , <i>Halimione portulacoides</i>	Hg	Castro et al. (2009)
<i>Atriplex halimus</i> subsp. <i>Schweinfurthii</i>	Cd	Nedjimi and Daoud (2009) and Lefevre et al. (2009)
<i>A. halimus</i>	Pb and Cd	Manousaki and Kalogerakis (2009)
<i>Spartina densiflora</i> , <i>S. maritima</i>	As, Cu, Fe, Mn, Pb, and Zn	Cambrolle et al. (2008)
<i>Aster tripolium</i>	Cu and Pb	Fitzgerald et al. (2003)
<i>Sarcocornia perennis</i>	Fe, Mn, and Hg	Lilebo et al. (2010)
<i>Halimione portulacoides</i>	Zn, Pb, Co, Cd, Ni, and Cu	Sousa et al. (2008) and Almeida et al. (2009)
<i>Tamarix smyrnensis</i>	Pb and Cd	Kadukova and Kalogerakis (2007), Kadukova et al. (2008), and Manousaki et al. 2008
<i>Juncus maritimus</i>	Al, Cd, Cr, Cu, Fe, Mn, Ni, Pb, and Zn	Almeida et al. (2006)
<i>Sporobolus virginicus</i> , <i>Spartina patens</i> , and <i>Atriplex nammularia</i>	Zn, Cu, and Ni	Eid and Eisa (2010)
<i>Salicornia europaea</i>	Cd	Ozawa et al. (2009)

tissue, rather than in foliage, in numerous mangrove species grown in the field conditions, such as *Avicennia* sps., *Rhizophora* sps. and *Kandelia* sps. (Peters et al. 1997). It has also been observed that for some mangroves, concentrations of translocated metals are low, with bio-concentration factors (BCF; ratio of leaf metal to corresponding sediment metal concentration) ranging from <0.01 in *Rhizophora mangle* to 0.06 for other species such as *A. marina* (Lacerda 1997). However, other studies suggest that mangroves may accumulate and translocate some metals with leaf BCFs greater than 1, for example, 1.5–2.4 for *A. marina* (Sadiq and Zaidi 1994), 1.7 for *Aegiceras corniculatum* and 1.2 for *Kandelia candel* (Chen et al. 2003) and behaved

as hyper-accumulating species. Lokhande et al. (2011b) recently demonstrated the arsenic (As) accumulation potential of *Sesuvium* exposed to As(V) (100–1,000 μM) for 30 days, wherein the growth of the plant was not affected even after prolonged exposure to arsenic stress with the significant As accumulation (155 $\mu\text{g g}^{-1}$ dry weight) and a bioaccumulation factor of more than ten at each concentration. On the basis of total As accumulation, bioaccumulation factor and known biomass production capacities, the *Sesuvium* like other As hyper-accumulator plants has been suggested to use as potential candidates for application in arsenic removal and land re-vegetation/reclamation projects in the As-contaminated sites of the world.

Heavy metal uptake in halophytes is generally regulated at the root endodermis through modifying uptake from predominantly apoplastic to selective symplastic transport. The contribution of each tissue type is dependent on the molecular properties of the plasmalemma (i.e., specific membrane transport proteins) and on the metal in question (MacFarlane and Burchett 2000). Some halophytic genera such as *Aegiceras* and *Avicennia* secrete excessive Na^+ and K^+ through specialized glands or glandular trichomes on abaxial and adaxial leaf surfaces, while such specialized structures are absent in nonsecretors, for example, *Rhizophora* and *Sonneratia* (MacFarlane and Burchett 1999). Indeed mangroves and a number of other estuarine halophytes with glandular tissue are known to excrete heavy metals concomitantly with other solutes (MacFarlane and Burchett 2000). The variation in morphology/function of nutritive root tissue and glandular tissue to deal with the challenges of excess cations in saline environments could become significant for metal accumulation, transport, partitioning, and excretion among halophytic plant species (MacFarlane et al. 2007).

5.3 Wetland Restoration and Re-vegetation

Mangrove forests are ecologically important coastal ecosystem currently covering 146,530 km of the tropical shorelines of the world (FAO 2003). There has been a steady decline from 198,000 km of mangroves in 1980 and 157,630 km in 1990 (FAO 2003) which represents about 2 and 1% losses per year between 1980–1990 and 1990–2000, respectively (Lewis 2005). Mangroves have provided ecological benefits in terms of shorelines stabilization, reduction in wave and wind energy against shorelines thus protecting inland structures, supporting coastal fisheries for fish and shellfish through direct and indirect food support and provisions for habitat, and support of wildlife. However, increasing human activities and adverse environmental conditions have led to destruction of mangrove forests thus limiting the available resources.

Therefore, restoration and re-vegetation of mangrove forest has become important for the development of sustainable agriculture and to avoid the destructive natural calamities. In this context, restoration or rehabilitation of saline lands using potential halophytes will act as an effective strategy. Restoration or rehabilitation is recommended when an ecosystem is altered to such an extent that it can no longer self-correct or self-renew. This could result in total disturbance to ecosystem homeostasis and permanent stopping of the normal processes of secondary succession or natural recovery from damage. Wetlands play an important role in nutrient cycling, sediment accretion, pollution filtration, and erosion control in the world. In addition, they are known for their distinctive flora and rich spectrum of wildlife, especially waterfowl, which makes them more valuable and more prone to human impact than other ecosystems (Mitsch and Gosselink 2007). However, only a small percentage of the original wetlands have remained around the world after over two centuries of intensive development and urbanization. Having lost so many wetlands, it seems that there are many opportunities for wetland restoration along coastal lines, rivers, lakes, etc. The deteriorated saline wetland can be restored using halophytes and salt-tolerant plants. The research on salt-tolerant plants and halophytes has attracted attention of many scientists because these plants could be used for saline agriculture and biomass energy on saline land, and for overcoming the worldwide problem of food shortage and energy crisis. Restoration of areas of damaged or destroyed mangrove forests has been previously discussed by many workers (Brockmeyer et al. 1997; Lewis and Streever 2000; Saenger 2002). Saenger and Siddiqi (1993) described one of the largest mangrove afforestation programs which covered plantings of primarily one species (*Sonneratia apetala*) over 1,600 km² on newly accreting mud flats in Bangladesh.

Research in this field of wetland restoration has demonstrated the potential of salt-tolerant plants and halophytes (Wang et al. 2008a, b; Zhang et al. 2008) for restoration and re-vegetation of barren lands and wetlands along the

coastal regions. Use of halophytes from the ancient period for restoration of wetlands is summarized here. *Scirpus* species have been extensively used in constructed wetlands for wastewater treatment as the species has ability to efficiently remove nutrients and pathogens from effluent (Huang et al. 2000; Coleman et al. 2001). Besides *S. robustus* showed efficiency for removal of selenium (Se) from contaminated water demonstrating potential for Se phytoremediation by wetlands (Pilon-Smits et al. 1999). Tissue culture mode of plant regeneration has been suggested as an efficient tool for producing plants required in wetland creation and restoration (Wang et al. 2003). Seliskar and Gallagher (2000) have further proposed that tissue culture-induced somaclonal variation can be advantageous to produce plants with particular characteristics for use in wetland restoration. Further, Wang et al. (2006) evaluated the wetland restoration potentials of selected tissue culture regenerants of ecologically important salt marsh monocots, *Spartina patens*, *S. alterniflora*, *Juncus gerardi*, *J. roemerianus* and *Scirpus robustus* in a simulated marsh fields.

5.4 Saline Agriculture

The rapidly increasing human population in the arid and semi-arid regions of the world has tremendously increased the pressure on the availability of good quality water and land resources for human usage, industry and agriculture. In addition, improper and poor quality irrigation practices have increased the level of under-ground water and large areas have become water logged which eventually results into higher salinities of the soil (Yensen 2006). Salinity affects the growth of the plant to a sever extent thus reducing the crop productivity in the arable lands. It becomes a serious threat of growing any conventional crops which are otherwise sensitive to high salt concentrations and expect the yield at higher level in such saline lands to fulfill the demand of ever-growing human population for food, fodder, shelter and as a raw material for the industrial purposes. The research work on engineering the salt tolerance of the crop plants has not yet

produced the successful transgenic plants which could tolerate the excess saline stress and yield more productivity in such conditions. Therefore, extensive efforts should have been undertaken to protect the available resources of freshwater and arable lands in the arid and semi-arid regions of the world through the application of halophytes for the variety of uses as a source of nonconventional cash-crops such as food, fodder, forage, medicinal, ornamental, chemical, timber, and other usage of wood and fibers (Khan and Qaiser 2006). Introduction of these potential halophytes has led to cover the barren saline land along the coastal zones of the world and provided economic benefits to the humans.

A variety of halophytic plant species have been categorized into different groups such as euhalophytes, xerohalophytes, and hydrohalophytes on the basis of their growth performance in variable climatic conditions and salt concentrations in the soil which has been utilized as a source of nonconventional cash-crops (Khan and Qaiser 2006; Khan and Ansari 2008). Hollington et al. (2001) described the successful stories of the utilization of halophytic species for the improvement of sustainable agriculture as well as sources of economy. *Atriplex* species showed the highest productivity and increases water uptake whereas tree species of *Acacia* and *Prosopis* have shown its role in re-vegetation and for biological drainage. Further, the use of raised-bed technology and on-farm seed priming have improved the production and efficiency of a range of halophytic plant species in saline conditions. Zhao et al. (2002) have screened the halophytic species distributed along the coast of China and categorized into different groups and suggested their uses in saline agriculture for the economic purposes. The variety of halophytic species so far used as a non-conventional source for various purposes in Pakistan have been reviewed extensively (Khan and Qaiser 2006; Khan and Ansari 2008) and presented in Table 2.1. Similarly, various strategies have been utilized for managing the saline or alkaline soil for sustainable agricultural production in South Africa (Sharma and Minhas 2005). Besides, Masters et al. (2007) also reviewed the utilization of halophytic grasses and shrubs

(such as *Medicago sativa*, *M. polymorpha*, *Trifolium* spp., *Hordeum vulgare*, *Distichlis spicata*, *Suaeda* spp., *Sporobolus* spp., etc.) in biosaline agriculture for the production of forage and livestock which showed their growth potentials in highly saline soil with salt concentrations >25 dS m^{-1} and produce 0.5–5 ton of edible dry matter $year^{-1}$. The potentials of five halophytic plant species namely *Diplachne fusca*, *Spartina patens*, *Sporobolus virginicus* (Smyrna-smooth), *Sporobolus virginicus* (Dixe-coarse), and *Medicago sativa* have been studied as a source of forage plants in Egypt on the soils irrigated with different concentrations of seawater. The studies showed that *S. virginicus* (Dixe) produced the highest biomass upon irrigated with either 25 or 37.5% sea water, followed by *S. patens* and *D. fusca* whereas *S. virginicus* showed the lowest yield. The studies conducted on cultivation of *Salvadora persica* in semi-arid saline and alkali soils showed its efficiency for growth and as a source of industrial oil on both saline and alkali soils for economic and ecological benefits which is otherwise not suitable for conventional arable farming (Reddy et al. 2008). Therefore, considering the approach of biosaline agriculture more efforts should have been undertaken on the cultivation of nonarable lands with nonconventional plant resources such as halophytes to bring the uncultivable land for the use of economic purposes of the human being. This strategy will help to improve the gross economy of the developing countries.

6 Conclusions and Future Perspectives

Worldwide food production is affected to a large extent by environmental extremities and the sensitivity of crops is a major limitation for achieving higher plant productivity. Plants have evolved adoptive mechanisms which can be understood and exploited as an important resource for development of crops tolerant to extremities. Halophytes show a diversity of growth responses to increasing salinity. Halophytes have evolved to the changing environmental conditions through developing

variety of tolerance mechanisms such as halosucculence, ion compartmentation (exclusion/inclusion), osmoregulation, enzymatic and nonenzymatic antioxidants and maintenance of redox and energy status. Research on understanding the abiotic stress tolerance mechanism of halophytes has been on the upfront using wide array of physiological, biochemical, and molecular tools. Some of the halophytes (e.g., *Thellungiella halophila*) that tolerate adverse conditions have become the choice model systems for unraveling the different pathways associated with halophytic behavior. However, research in the context of progress in metabolomics, genomics, and proteomics has to be initiated in diverse halophytic species with the use of advanced techniques to gain detailed knowledge of abiotic stress tolerance.

Halophytes have also been utilized practically for managing the stressful environment and shown to be involved in increasing the economy of developing countries in many parts of the world. Halophytes have shown their role in desalination of saline lands from arid and semi-arid regions as well as the stabilization of saline lands along the coastal sides, phytoremediation of heavy metal contaminated sites and wetland restoration and revegetation through introduction of variety of halophyte species. This has led to developing agriculture on saline lands for supporting the sources of food, forage, fodder, medicine, ornamental and important plant-based chemicals to ever-growing human population. In addition, this may also help in reducing the burden on the crop plants which are facing the productivity problems due to exposure to various abiotic stresses. Considering these applications, constructive strategies have to be developed and implemented for the protection of world's nonrenewable resources, wherein available halophyte diversity can be utilized as an important source. Investigation of the gene regulation and the balance of individual stress tolerance mechanisms will aid in translating the information to other salt-sensitive crops. Such studies will be helpful for ensuring sustainability of future research efforts to improve and manage crop performance on marginal and irrigated land through genetic manipulation.

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