Mirza Hasanuzzaman · Kamrun Nahar
Münir Öztürk *Editors*

Ecophysiology, Abiotic Stress Responses and Utilization of Halophytes

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Foreword

Professor Chedly Abdelly

Land salinization is a major limiting factor for conventional crop production and plant diversity in natural biotopes. Climate change, affecting several regions in the world and marked mainly by the rarefaction of precipitation and the increase in temperatures, exacerbates this situation. The nonrational use of chemical fertilizers and unconventional organic fertilizers as well as pesticides has amplified soil and water salinization and caused soil contamination by heavy metals and several other pollutants. Thus, the global annual losses in agricultural production from salt-affected land are worryingly spreading and worsening. This situation is of major concern considering (i) the current global climate change tendency, and (ii) that agricultural production should increase by 50 to 70% by 2050 to match the projected population growth to 9.3 billion. Increasing yields in saline cultivated lands, creating new productive ecosystems in marginal areas, and implementing appropriate cultural practices based on using unconventional water resources to irrigate crops are the only alternatives to achieve this goal. The majority of conventional crops known for their sensitivity to salinity and all the associated stresses it generates cannot represent the main and relevant actors in these approaches. Then, what are the plant species that can combine high salt tolerance with the ability to improve the physicochemical and biological properties of salinized agricultural lands and to valorize marginal highly saline soils and unconventional water resources through a biomass production useful for human food, for animal feed, and/or for various industrial purposes? These are halophyte species. Halophytes, plants that survive to reproduce in environments where the salt concentration is around 200 mm NaCl or more, constitute about 1% of the world's flora. They have acquired through natural selection pressure the traits required to deal with extreme environmental constraints. This explains the growing interest paid on these plants. Thus, several research institutes in the world currently focus on halophyte species. In the same context, scientific production in terms of articles in specialized journals, books, as well as invention patents valorizing the data acquired on halophytes shows currently a substantial development in terms of quantity and quality.

The book entitled *Ecophysiology, Abiotic Stress Responses and Utilization of Halophytes* edited by Prof. Mirza Hasanuzzaman, Dr. Kamrun Nahar, and Prof. Münir Öztürk, eminent international experts in plant ecophysiology, fits perfectly into the approach dealing with the characterization and valorization of halophytes. The contributions presented in this book are written by internationally reputed scientists who report relevant and adroitly positioned data in relation to recent studies on halophytes. They once again confirm the numerous (fundamental, ecological, and economic) interests of halophytes and provide to potential users of these plants new and relevant pathways to valorize highly saline lands and unconventional water resources.

At the fundamental level, the data documented show the pertinence of using a multidisciplinary approach, bringing together ecophysiological, biochemical, and molecular tools to accurately characterize halophyte responses to environmental stresses, whether separated or combined at different developmental stages of their life cycle. Importantly, contributors show that there are specific mechanisms evolved by halophytes to cope with abiotic constraints and further strengthen the pertinence of using halophytes as the most appropriate "models" to investigate salt tolerance mechanisms in plants. At a more applied level, there are nice and concrete reports on the strong potential of halophytes to desalinate and improve the biological properties of salinized soils. Besides, cultivating halophytes seems to be the only biological approach to decontaminate heavy metal-affected marginal soils. It is known that phytodesalination and phytoremediation are prerequisites in the perspective of rehabilitating marginal lands and their transformation as new productive ecosystems. This book also further highlights the interests of halophytes as precious sources of bioactive substances which have a tremendous potential of utilizations in the agro-food, pharmaceutical, and cosmetic industries. Interestingly, there are also nice reports about the technical and economical feasibility of either cultivating halophytes using seawater or their utilization in integrated farming systems and for biomass production.

To summarize, as plants native to ecosystems with harsh environmental conditions, halophytes are unique and intriguing species. Investigating salt tolerance mechanisms in these plants is of incontestable academic interest, for instance, to generate markers that could be used for breeding programs. But also this generates information with the practical outcome either for agriculture and industrial users or environmentalists and ecologists. As an ecophysiologist who spent more than 35 years working on this topic, I am convinced that the readers of this book will find precious and original data and reviews which will substantially improve their knowledge about salt tolerance traits identified in halophytes and their multiple interests.

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Preface

Halophytes are the plant species that can tolerate high salinity, and their lives are benefitted by salinity up to certain extent and can be adapted in a wide variety of saline habitats such as coastal regions, salt marshes, and inland deserts. There are approximately 1450 halophytic plant species documented (eHALOPH Database), while we consider a total number of plant species which is approximately 350,000 (The Plant List Database), the percentage of halophytes in total plant species is only 0.4%. Since saline habitats and evolutionary history of halophytes are diverse, they have many different adaptation mechanisms, and most of them have more than one adaptation mechanism to able to survive in saline places. Halophytes not only can tolerate salinity but also other stressors like drought, extreme temperature, waterlogging, and toxic metals/metalloids. Halophytes are many times exposed to heavy metal toxicity particularly in the mangroves ecosystem. They act as a major sink of a number of pollutants as they are connected to nearby drainage and rivers.

It is estimated that the world population would be 9.3 billion by 2050, and providing foods for the increasing population will be one of the greatest challenges for agricultural scientists because the arable lands are being decreased at the same time. It is reported that about 7% of the total earth land and 20% of the total arable *area* are *affected* by high *salt* contents. Increasing salinity is one of the negative impacts of climate change, and globally 7% of the total land and 20% of the total arable area are salty. Since halophytes possess special morphological, anatomical, and physiological features, those make them adaptive in saline habitat, learning from the halophytes is one of the viable approaches for understanding salt tolerance mechanisms. The adaptive features of halophytes may be strong genetic traits to be transferred to cultivated plant species toward the improvement and development of salt tolerant cultivars. Apart from the special adaptive features, halophytes have diverse uses such as food, fodder, fuel, and medicines. Therefore, the use of halophytes may be an effective way to enhance food security in the era of climate change. Numerous research works have been carried on different aspects of halophytes in regard to its ecophysiology, special adaptive features, tolerance mechanisms, specialized uses, and so on which made them fascinating plants. This book presents a collection of 19 chapters written by 65 experts in the field of plant ecophysiology, environmental sciences, biotechnology, botany, and agriculture.

We, the editors, would like to give special thanks to the authors for their outstanding and timely work in producing such fine chapters. We are highly thankful to Ms. Khursheda Parvin for her valuable help in formatting and incorporating editorial changes in the manuscripts. We are highly thankful to Dr. Fumiko Yamaguchi, Senior Editor (Editor, Ecology and Animal Science), Springer, Japan, for her prompt responses during the acquisition. We are also thankful to Sivachandran Ravanan, Production Editor of this book, and all other editorial staffs for the precious help in formatting and incorporating editorial changes in the manuscripts. The editors and contributing authors hope that this book will include a practical update on our knowledge for ecophysiological features of halophytes and mechanisms of abiotic stress tolerance. Moreover, the potential uses of halophytes are also discussed. Graduate students (MS and PhD), university faculty members, and researchers working in the field of plant physiology, ecology, soil science, botany, and agriculture will be highly benefited from this book.

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Dr. Münir Öztürk (Ph.D.) completed his M.Sc. degree at Jammu & Kashmir University, Kashmir, and his Ph.D. & D.Sc. at Ege University Izmir, Turkey. Over the last 50 years, he has served in different positions at Ege University. Dr. Öztürk was elected as the "Vice President of the Islamic World Academy of Sciences" in 2017, and has received fellowships from the Alexander von Humboldt Society, Japanese Society for Promotion of Science, and National Science Foundation (USA). He is the Founding Director of the Centre for Environmental Studies at Ege University and has worked as a Consultant Fellow, Faculty of Forestry, Universiti Putra Malaysia, Malaysia and as Distinguished Visiting Scientist, ICCBS, Karachi University, Pakistan. His main fields of scientific interest are Plant Eco-Physiology; Medicinal and Aromatic Plants, Conservation of Plant Diversity; Biosaline Agriculture and Crops; Pollution and Biomonitoring. He has published 40 books, 50 book chapters, and more than 200 papers in prominent journals.

The original version of this book was revised: Affiliation for the author Dr. Pooja was corrected. The correction to this chapter is available at https://doi.org/10.1007/978-981-13-3762-8_20

Chapter 1
Halophyte Responses and Tolerance to Abiotic Stresses

Ganesh Chandrakant Nikalje, Kushi Yadav, and Suprasanna Penna

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Abstract Different anthropogenic activities result in the contamination and degradation of the agricultural ecosystem. Improper disposal of industrial waste, use of excess chemical fertilizers, and mining are major sources of soil contamination. These adverse conditions exert a negative effect on crop growth and yield, while a group of plants, known as halophytes, exhibit greater tolerance. These plants are native to such adverse environments and can withstand different abiotic stresses such as salinity, drought, toxic metal stress, and hypoxia. Halophytes grow luxuriantly in saline soils, which make them suitable for saline agriculture. In addition, they are a

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good source of salt-responsive genes and value-added products. Many halophytes show common biochemical and physiochemical responses to salt stress, whereas under multiple stresses, different mechanisms operate. The accumulation of osmolytes such as proline, selectivity in K:N, the exclusion of sodium and vacuolar compartmentalization, the induction of antioxidant molecules (enzymatic and non-enzymatic) are the most common features of halophytic adaptation to stress. The comparative study of halophytes and glycophytes revealed that the former are well equipped with cross-tolerance mechanism and are well prepared before stress imposition. It is also reported that pretreatment/priming with salinity or other stresses in early developmental stage of halophytes improves their salt tolerance at later stage. This observation suggests that halophytes might have stress memory, which helps them to respond better to stress conditions. In this article, we present a current perspective of the general tolerance mechanism and the responses of halophytes to different abiotic stresses such as salt, drought, toxic metal, and combination of these. Understanding the mechanism of such abiotic stresses alone and in combination will help to identify potential halophytes for re-vegetation or possible breeding for redevelopment of salt-affected agricultural lands.

Keywords Halophytes · Abiotic stress · Multiple stress · Salinity · Drought · Toxic metals

1.1 Introduction

Of the world's total land area, 6% is plagued by excess salinity, mainly in arid and semi-arid areas (Flowers et al. 2010). In agriculture, regional salinity problems are increasing owing to low precipitation, high evaporation, naturally saline soil, poor waste management, and saline water irrigation (Hamed et al. 2013). Usually, plants' response to salinity stress alone differs from their natural biotope behavior in comparison with combined stress (Mittler 2006). It was suggested that plants enhance the negative effect of a first stress in the presence of a second stress (Mittler 2006). Hence, increasing plants' tolerance toward stresses requires multiple stress research (Mittler and Blumwald 2010). The salinity tolerance of halophytes predominantly depends upon uptake control and compartmentalization of Na^+, K^+, and Cl^- (Flowers and Colmer 2008; Shabala and Mackay 2011). Halophytes survive not only in a saline habitat, but also in drought, heat, and an alkaline habitat (Hamed et al. 2013). Along with these stresses, halophytes are also exposed to various biotic stress such as pathogen attack and abiotic stress, for example, toxic pollutants including pesticides, noxious gases (SO_2, NOx, O_3), soil acidification, excessive use of fertilizers, heavy metal and intensified UV-B irradiation (Flowers and Colmer 2008). When combined abiotic stress affects halophytes, they usually show tolerance against combined stress (Hamed et al. 2013). Combined stress tolerance is a complex phenomenon to explain because of multitude of events that take place at various stages of plant development.

Salt-tolerant plants with a phenomenal ability of completing their life cycle under saline conditions are known as halophytes (Flowers and Colmer 2008; Grigore et al. 2014). Development of morphological, anatomical, and physiological characteristics during evolution has enabled halophytes capable of growing under high salt conditions (Flowers and Colmer 2008; Grigore et al. 2014). Because of the wide range of stress tolerance environments, halophytes cannot be classified easily, but a few definitions of halophytes are available (Huchzermeyer and Flowers 2013). They are defined as plants capable of accomplishing their life cycle in a living environment with a salt concentration greater than 0.5% NaCl (Xu et al. 2016). Another definition is that they are exposed to salt stress and able to survive for at least a life cycle in an environment that is lethal to a large population of plants (Xu et al. 2016). Halophytes classified on the basis of salt requirement are obligate halophytes, facultative halophytes, and habitat-indifferent halophytes (Braun-Blanquet et al. 1933; Cushman 2001). Obligatory halophytes require salt for their growth, but facultative halophytes can grow in salt-devoid soil in a similar manner to habitat-indifferent halophytes, but differ because they like to grow in salt-devoid soil, but they are also able to survive under saline conditions (Braun-Blanquet et al. 1933). Another classification divides halophytes into reversible extremophytes, irreversible extremophytes, and mesophytes (Grigore et al. 2014). Extremo-halophytes are able to grow massively in a saline environment (Grigore et al. 2014). They are further subclassified on the basis of their habitat, which could be reversible or irreversible (Mishra and Tanna 2017). Modern omics techniques have enabled the understanding of salt tolerance mechanisms in these plants (Xu et al. 2016). With more insights into salt tolerance mechanisms, it has become apparent that there is more to tolerance mechanisms than mere salt tolerance (Xu et al. 2016). In this chapter, we present an account of stress tolerance behavior of halophytes under different abiotic stress conditions and in a combined stress regime. The main attention is given to abiotic stress factors, such as drought, salinity, flood, heavy metal and nutrient deficiency, which are usually lethal to plants other than halophytes.

1.1.1 Flooding

There are potential conditions of submergence of plants in flood water (Armstrong 1980). Complete submergence of plants results in to reduced O_2 supply to plants because diffusion of gases in water is 10,000 times slower in comparison with air (Armstrong 1980). Under dark conditions, O_2 is deficient, which can inhibit tissue respiration, which finally becomes anoxic (Gibbs and Greenway 2003). Internal O_2 level everyday based on CO_2, O_2, and incident light at the site of submergence (Pedersen et al. 2004; Winkel et al. 2013). The amount of CO_2 uptake by shoots for photosynthesis is also reduced because of submergence, mainly under circumstances where there is high resistance across the leaf cuticle (Mommer et al. 2005). In succulent halophytes, internal O_2 production is mainly based on O_2 production during daytime photosynthesis and anoxic when it is dark at night (Pedersen et al. 2006;

Colmer et al. 2013). In association with other problems of exchange of gases under submergence, halophytes also have to maintain an osmotic potential difference between tissues and floodwater, which could lead to swelling of tissues (Flowers and Colmer 2008). In that situation, to constrain such excessive swelling, a strong epidermis may be required, which greatly reduces the rate of gaseous exchange, already diminished because of the gas diffusion pathway and the relatively low surface area to volume (SA/V) ratio of succulent stems (Konnerup et al. 2015). Salicornioideae stem succulents habitually occupy saline, often flooded, habitats around world (Wilson et al. 1993; Shepherd and Wilson 2007). Perennial halophytes, stem succulent species largely endemic to Australia, contain the genus *Tecticornia* (Wilson et al. 1993; Shepherd and Wilson 2007). At ephemeral inland salt lakes, where the environment is distinguished by high soil salinity and episodic flooding punctuated by durations of drought, many *Tecticornia* species are known to grow (Wilson et al. 1993; Shepherd and Wilson 2007). Species zonation was found on the margins of ephemeral salt lakes in Australia in *Tecticornia* communities (English and Colmer 2011, 2013). Usually, *Tecticornia* field distribution has a different tolerance of flood, salinity, and drought, but an elevation in particular plant establishment may depend on the ability of submergence stress tolerance at low marsh conditions (Konnerup et al. 2015).

The SA/V ratio differs among species of succulent halophytes. Plants with thicker stems are more tolerant than others, explained by the internal O_2 dynamics of plants under submergence stress (Colmer et al. 2013). The major barrier is the supply of oxygen to stem tissue under darkness and submergence in the epidermis with the *T. medusa* stem being hypoxic throughout (Konnerup et al. 2013). Oxygen production in photosynthesis builds up owing to the low permeability of the epidermis; for example, *T. medusa* has a less permeable epidermis, but gas films on *T. auriculata* contribute to obtaining a better gas exchange initially after submergence stress, compared with *T. medusa*, in which gas films are absent (Pedersen et al. 2006). Therefore, low epidermis permeability and a low S/A ratio result in different oxygen patterns when there is a manipulation in the presence of light and submergence (Pedersen et al. 2006). Built-up respiratory carbon dioxide does not occur to the same extent in adequate species as they have thin leaves and a more penetrable epidermis without cuticles, which allows them to exchange gases with the surrounding water (Armstrong 1980; Colmer 2003). In waterlogged or submerged plants, the aeration of roots by O_2 diffusion is uncommon (Pedersen et al. 2006). Stem-succulent halophyte species experience problems during the night under submergence stress owing to O_2 depletion (Flowers and Colmer 2008). The O_2 depletion occurs because of the great fluctuation, as during the day time stem-succulent halophytes are voluminous and have low epidermal permeability (Konnerup et al. 2015). The survival of stem-succulent halophytes under submergence stress is associated with carbohydrate conversion, resistant osmotic stress, and the organized production of new tissue after the flood is over (Bailey-Serres and Voesenek 2008). To assist the survival of the plant, either in an environment susceptible to prolonged deep floods or during a short transient flood, the plant resumes better growth after the flood water has receded, which is considered a quiescence response (Bailey-Serres and Voesenek 2008).

1.1.2 Heavy Metals

In the earth's crust, heavy metals are present as a natural component (Lutts and Lefèvre 2015). However, anthropogenic activities have led to the acceleration of heavy metal accumulation in the environment (Han et al. 2013). Various industrial and agricultural activities, for example, mining, smelting, burning of fossil fuel, and the excessive use of fertilizers, pesticides, fungi, and sewage sludge in agricultural practices are responsible for rapidly increasing heavy metal pollutants such as Cu, Cd, Pb, and Zn (Ernst and Nelissen 2000; D'Amore et al. 2005). These pollutants not only pose a serious threat to the environment, but also affect the health of living beings and disrupt the food chain (Sirguey and Ouvrard 2013). In the rhizosphere, through microbial activity, many organic pollutants can be converted into harmless compounds, but heavy metals cannot degrade and hence remain in the soil for long periods of time (Batty and Dolan 2013). These toxic compounds affect various plant species by inhibiting their growth, influencing the water status, photosynthesis, and inducing over-synthesis of reactive oxygen species (ROS), which is responsible for various physiological disorders that finally leads to plant death (Vázquez et al. 1994). There are some exceptional plant species known as hyper-accumulators. These hyper-accumulators display a higher shoot concentration of heavy metals than roots and these have the ability to absorb and also to translocate heavy metal (Vázquez et al. 1994; Yang et al. 2004).

Overproduction of ROS leads to oxidative stress (Demidchik et al. 2010). This oxidative stress is the major cause of oxidative damage to proteins, nucleic acids, and lipid peroxidation, which may also lead to programmed cell death (PCD) (Demidchik et al. 2010; Nikalje et al. 2017a, b, c; Demidchik 2015). Transition metals in response to oxidative stress generate hydroxyl radicals (Zepeda-Jazo et al. 2011; Rodrigo-Moreno et al. 2013), which activate plasma membrane Ca^{2+} and K^+ channels, and lead to Ca^{2+} influx and K^+ efflux (Demidchik 2015). Halophytes need proper regulation of Na and K concentrations inside their cells, exhibiting a defense response to hydroxyl radicals (Flowers and Muscolo 2015). In *Zygophyllum fabago*, the significance of K relocation in cells of photosynthetically active tissues in response to heavy metal toxicities were studied (Lefèvre et al. 2014). The accumulation of reduced form of transition metals such as Cu, Mn, and Fe is favored by anoxic conditions in some cases (Rodrigo-Moreno et al. 2013). In apoplast and cytosol through the Fenton reaction, transient metals in the presence of H_2O_2 catalyze the production of hydroxyl radicals (Rodrigo-Moreno et al. 2013). Essential components of the plant antioxidant defense systems are Cu and Fe, which are part of superoxide dismutase (SOD) (Bose et al. 2014). When Cu and Fe become over-absorbed, they may result in metabolic disturbance such as loss of chloroplast integrity, remodeled plastid membrane, and also inhibits photosynthetic electron transport (Bose et al. 2014). Further ROS overproduction is generated owing to the disruption of electron transport (Bose et al. 2014). Cu and Zn toxicities are important factors that result in secondary oxidative stress, but Cu and Zn are not involved directly in ROS synthesis (Lutts and Lefèvre 2015). Glutathione, ascorbate, and α-tocopherol are some of the antioxidants present in plants (Bose et al. 2014; Ozgur et al. 2013). Among antioxidant enzymes, Catalase and peroxidase remove H_2O_2 and, SODs catalyze the disproportion of superoxide radicals to O_2 and H_2O_2 (Bose et al. 2014; Ozgur et al. 2013). The greater constitutive antioxidant defense activities of halophytes play an important role in heavy metal toxicity, salinity and other stress (Wang et al. 2014).

In response to heavy metal and metalloids such as Cd, Ni and As, *Salicornia brachiata* is able to up-regulate catalase (CAT) and SOD activities (Lefèvre et al. 2010). The expression of the *CAT1*, *GST*, and *PrxQ* genes responsible for enzymes activity is increased by cadmium (Cong et al. 2013). In shoots of *Suaeda salsa* in response to Zn, Pb or a combination of both metals, only CAT gene expression level increased significantly in contrast to activities of antioxidant enzymes SOD, glutathione peroxidase (GPxS), and catalase increased in response to Zn and Zn+Pb (Bose et al. 2014; Jithesh et al. 2006). SOD activities play a significant role in the protection of halophytes from extreme environmental changes (Bose et al. 2014; Jithesh et al. 2006).

Glutathione by phytochelatin synthase enzymatically synthesizes phytochelatin and low-molecular-weight polypeptide with general structure (γGlu-Cys)n Gly ‘n’ varying from 2 to 11 (Lutts and Lefèvre 2015). These polypeptides help to reduce damage under heavy metal stress conditions (Lutts and Lefèvre 2015). In *Avicennia germinans*, on exposure to a polluted environment, shows a high level of tolerance due to the overexpression of the *AvPCS* in response to high concentration of Cu^{2+} and Cd^{2+} within few hours (Tennstedt et al. 2008). This over-expression triggers a tolerance mechanism during long-term exposure, and remains transient (Baena-González et al. 2007). Proteins are found in almost all plants, animals, and microbes, that bind to metal and microtubules rich in cysteine (Cobbett 2003). According to the location and distribution of cysteine residue, plant microtubules are divided into four types (Cobbett 2003). Microtubules bind metals efficiently, which leads to metal tolerance. In *Bruguiera gymnorrhiza*, Zn, Cu, and Pb up-regulate genes encoding type 2 microtubules (*MT2*) (Lutts and Lefèvre 2015). Such results were also obtained in *Avicennia marina* and transgenic *E. coli* LB4 (Huang and Wang 2009). Expression of gene coding *MT2* has a differing impact according to the various elements (Huang and Wang 2010). As in *Prosopis juliflora*, Cu and Cd stress cannot change the expression of *PjMT2*, but Zn up-regulates the expression of *PjMT2* (Usha et al. 2009). Similarly, in *Salicornia brachiata*, expression of *SbMT2* is unaffected by Pb and is up-regulated in the presence of Zn and Cu (Chaturvedi et al. 2012).

Halophytes lead to osmotic stress owing to the high NaCl concentration in soil, but to maintain internal osmotic pressure and water uptake, various organic compounds accumulate and maintain the water gradient (Flowers and Colmer 2008). These compounds protect cellular structures and enzymes (Lutts and Lefèvre 2015). Halophytes are able to synthesize protective compounds rapidly in response to ion toxicity, which describes the ability of halophytes to tolerate heavy metal stress

(Rastgoo and Alemzadeh 2011). An accumulation of proline in cytosol is frequently associated with vacuolar Na^+ sequestration (Lutts and Lefèvre 2015). This not only results in osmotic function protecting the protein quaternary structure and stabilizing the cell membrane through direct interaction with phospholipid (Rastgoo and Alemzadeh 2011). In *Aeluropus littoralis*, proline content increased heavy metals such as Cd, Co, Pb, and Ag (Lutts and Lefèvre 2015). In a facultative halophyte, *Mesembryanthemum crystallinum*, Cd exposure caused accumulation of proline and total soluble sugars (Lefèvre et al. 2009). In a similar manner, some amino acids such as histidine, glutamine, alanine or asparagine form complexes in response to metal stress (Sharma and Dietz 2006). In *Suaeda salsa*, in response to Cd and Zn, branch chain amino acids such as leucine, isoleucine, valine, glutamine, glutamate, tyrosine, threonine, arginine, phenylalanine, and tryptophan content increased (Lefèvre et al. 2009). For methionine and GSH/PC synthesis, cysteine is required and acts as a central metabolite in antioxidant defense and metal sequestration (Liu et al. 2011). However, whether these accumulations are related to metal tolerance or protein degradation is unclear (Wu et al. 2013). In different halophyte plant species, heavy metal stress and NaCl in combination may trigger the accumulation and synthesis of quaternary ammonium compounds, such as glycine betaine, resulting in the maintenance of membrane integrity, protecting other cellular structures, stabilizing macromolecule structures, and protecting chloroplasts and Photosystem II (Wu et al. 2013). In leaves of *Atriplex halimus*, over-synthesis of glycine betaine in response to Cd was observed (Bose et al. 2014; Ozgur et al. 2013; Lefèvre et al. 2009). *Sesuvium portulacastrum*, a metallo-protectant halophyte, also accumulates trans-4-hydroxyproline betaine and 3,5,4-trihydroxy-6,7 dimethoxyflavone 3-glucoside (Adrian-Romero et al. 1998; Nikalje et al. 2018). This mechanism differs according to variation in species, such as in *S. salsa*, glycine betaine can decrease on exposure to Cd, while choline increases (Liu et al. 2013). Synthesis of Polyamines (PAs) and small aliphatic amines during plant development is considered to have myriad biological functions in response to ion toxicities. They also act as protective molecules to repair and protect stress-induced injuries by forming a direct interaction with numerous cell structures and biochemical responses in *Atriplex halimus* (Lefèvre et al. 2014; Lutts et al. 2012).

1.1.3 Salinity

Almost 72% of the Earth's surface is covered with saline water dominated by Na^+ and Cl^- (Flowers and Colmer 2015). In ocean water, usually 19 g of Cl^- and 11 g Na^+Kg^{-1} with substantial concentration of Mg^{2+}, SO_2^-, K^+ and Ca^{2+} are found (Flowers and Muscolo 2015). But the essential nutrients $H_2PO_4^-/HPO_4^{2-}$ and NO_3^- required for plant growth are in very low supply (Flowers and Colmer 2015). Even in such diverse conditions, there are a few exceptional plants such as halophytes that can still survive (Flowers et al. 2010). Hence, halophytes are considered the flora of saline environments (Saslis-Lagoudakis et al. 2015). The salt tolerance capacity of halophytes develops early in some lineages and in many other origins (Saslis-Lagoudakis et al. 2015). Salt tolerance is observed in a few current species, which indicates that the trait has been gained and lost, or various salt tolerant species are becoming extinct throughout evolution (Saslis-Lagoudakis et al. 2015). Phylogenetic analysis can tell us about the macroevolution of salt tolerance, for example, C_4 photosynthesis metabolism has evolved and increased multiple stress tolerance in plants (Saslis-Lagoudakis et al. 2015). The halophyte species are still evolving and relatively new, but have some common features among them (Flowers and Muscolo 2015). This describes recent advancement in halophytes evolution and systematics (Flowers and Muscolo 2015). Their management of salt tolerance is mainly based on the relationship between salt and water. Halophytes are able to reduce the ion concentration of the solution in the xylem owing to which the quantity of salt delivered to the leaves is assimilated by growth and ion excretion through salt glands (Munns and Tester 2008). The ion regulation through the xylem is usually found in all plants to tolerate salinity stress, but halophytes are capable of Na^+ and Cl^- exclusion at high salt concentrations (Bennett et al. 2009). Ion retrieval is the removal of Na^+ from xylem sap as it rises to the leaves and leads to a genotypic difference in the "apparent exclusion" of Na^+ from entering leaves (Munns and Tester 2008). Mangroves growing in tidal wetland show a range of 90 to 99.6% of external Na^+ as a degree of "exclusion" (Reef and Lovelock 2015). Such a high range of exclusion in mangroves is achieved by anatomical adaptation that decreases and prevents apoplastic movement of solution from outside the root to the xylem, guards the cell membrane, and their transporters may be determined ions that pass into the xylem. Halophytes can tolerate multiple stresses (Flowers and Colmer 2015).

In a solute compartmentalization model of salt tolerance, it was suggested that osmotic adjustment occurs firstly with the ions (Na^+ and Cl^- mostly) in their environment, but under high concentrations of toxic salts the potential disturbance of metabolism results in ions becoming concentrated in vacuoles, relative to cytosol (Konnerup et al. 2015). Whether concentrations of Na^+ and Cl^- are toxic when halophytes are exposed to supra-optimal saline condition is not clear. To decrease growth and eventual death, other factors contribute, such as low cytoplasmic K^+, cellular dehydration, mineral deficiency, reduced stomatal conductance, which limits the net photosynthesis rate, hormonal imbalance, elevated ROS production, and energetic requirement for either ion transport or the synthesis of compatible solutes (Slama et al. 2015). Diverse compatible solutes (amino acid, quaternary ammonium compound, tertiary sulfonium compound, sugars, and sugar alcohols) also explain the role of osmolytes in the cellular compartmentalization model (Flowers et al. 2015). These osmolytes/organic solutes explain the main halophytes families found, their synthesis pathways, and the importance of osmotic adjustment (Flowers and Colmer 2015). Osmolytes act as chemical chaperones and scavengers of hydroxyl radicals and also describe osmotic regulation and transport, which can participate in salt tolerance by enhancing the use of transgenics or by exogenous application to increase these compounds in plant tissue (Flowers and Colmer 2015). Halophytes reduce stomatal opening by generating ROS, which ultimately maintains water transport to diminish the net salt uptake in shoots (Uzilday et al. 2015). Hence, the water–water cycle enzyme may prevent excessive ROS accumulation in chloroplasts to protect photosynthesis machinery (Hou and Bartels 2015). The main factor behind salt tolerance is the ability of halophytes to regulate Na^+ and Cl^- uptake while maintaining cytoplasmic K^+ and Mg^+ concentrations required for essential enzyme activation (Bose et al. 2015).

1.1.4 Combined Stress [Salt + Drought]

Plant transpiration, or soil evaporation in plants, is increasing because of a rise in the surface temperature resulting from global climate change (Brown and Pezeshki 2007). Halophytes show positive effect of salinity under drought or water scarcity, such as *Sesuvium portulacastrum, Zygophyllum xanthoxylum, Atriplex halimus, Ipomoea pes-capra*, and *Bruguiera cylindrica* (Slama et al. 2007, 2008; Ma et al. 2012; Atreya et al. 2009). Under the combined stress of salinity and water scarcity, the higher leaf Na^+ concentration, increased stomatal conductance (g_s), and net photosynthesis rate (P_n) leads to the inference that Na^+ can enhance photosynthesis and also perform osmotic adjustment for the improvement of water status (Slama et al. 2007; Martínez et al. 2005). Various species show differential involvement of Na^+ in total osmotic adjustment, such as under the combined stress condition of salt and drought (Slama et al. 2007). *Atriplex halimus* shows a negligible contribution of Na^+ in total osmotic adjustment (Zribi et al. 2012). Different species have different approaches to dealing with Na^+. For example, in *Atriplex halimus*, absorbed Na^+ accumulates in trichomes or large bladder cells, but in *Sesuvium portulacastrum*, Na^+ is sequestered in the vacuoles of parenchyma cells (Slama et al. 2007, 2008). In *Sesuvium portulacastrum*, Na^+ acts as an osmoticum, because under combined drought and salinity, the stress level of proline accumulation is higher than with salinity alone and with drought alone (Hamed et al. 2013) suggesting that there might be a correlation between proline and water potential, i.e., the level of proline increases when the water potential is low (Slama et al. 2007). Under combined stress, proline improves plant tolerance through mechanisms that provide the multiple functions of proline (ROS), scavenging, protein stabilization, and the regulation of cellular redox potential (Szabados and Savouré 2010; Glenn et al. 2012). Another mechanism for increasing tolerance toward combined stress is reduced stomatal conductance, leading to increased water use efficiency (WUE), which results in a slow growth rate, but accelerated carbon fixed per unit of water transpired (Glenn and Brown 1998). This mechanism has been reported in *Atriplex canescens, Atriplex lentiformis*, and *Atriplex halimus* (Zhu and Meinzer 1999; Nemat Alla et al. 2011).

1.1.5 Combined Stress [Salinity + Flood]

Large saline areas are unusually wet land habitats such as coastal zones and salt marshes (Flowers and Colmer 2008). To survive in these habitats, plants have to tolerate both tidal flooding and high salinity, because, owing to these stress conditions, root respiration becomes restricted (Baena-González et al. 2007), which leads to decrease in the activity of H^+-ATPase and inhibits Na^+ and K^+ intake (Barrett-Lennard 2003; Shabala et al. 2014). Exclusion of toxic compounds, such as CO_2, ethylene, hydrogen sulfide and carboxylic acid can accumulate in plant tissue in response to reduced O_2 and reduces the uptake of essential nutrients, such as NH_4^+ and Ca^{2+} (Greenway et al. 2006; Bradley and Morris 1990; Rengel 1992). Despite combined flood and salt stress, there are some halophytes, e.g., *Spartina*, that show high productivity. *Spartina* can increase net primary productivity up to 40 tons dry weight (DW) ha^{-1} $year^{-1}$ (Mishra and Tanna 2017). Barrett-Lannard listed data on waterlogging and salinity interactions for two species, i.e., *Atriplex amnicola* and *Casuarina* sp. (Barrett-Lennard 2003). Further data on a large number of halophytes (15 species) was added by Colmer and Flowers (Flowers and Colmer 2008). Several species show reduced growth when both waterlogging and salinity were imposed (Hamed et al. 2013). A well-known indicator of a wet land ecosystem is *Phragmites australis* (common reed) because it shows an efficient Na^+ exclusion mechanism from leaves and a high K^+:Na^+ selective ratio under hypoxic conditions over salinity (Gorai et al. 2010). There are some other similar species, e.g., *Melilotus siculus* and *Puccinellia* shoots. Hence, a high value of intrinsic membrane potential is associated with a high H^+ pumping rate, which describes more about K^+ retention in their roots under combined stress conditions (Jenkins et al. 2010). The importance of K^+ retention by roots and shoots for tolerance to combined salinity and hypoxia is explained by comparative studies between halophytes in contrast to water logging (Jenkins et al. 2010). Flower and co-workers used *Suaeda maritima* as a model halophyte for salinity and flood tolerance studies (Flowers 2004). The plant *S. maritima* showed reduced growth, but it is tolerant and survives under saline flooding conditions (Hamed et al. 2013). Research also revealed that *S. maritima* showed increased antioxidant capacity under both natural and controlled saline flood conditions, which was also compared with well-drained conditions (Hamed et al. 2013). Further insights described the contribution of lactate production by roots to tolerate flooding when *S. maritima* was compared with nonhalophyte species such as *Arabidopsis*, tomato, soybean, and tobacco. The former halophyte showed high production of lactate in roots (Teakle et al. 2013). In *S. maritima*, a large amount of lactate is stored in the root vacuoles (concentration of ~120 mM) along with sodium (concentration of more than 200 mM), leading to sodium lactate solution, which prevents vacuole acidification (Teakle et al. 2013). Unlike *S. maritima*, in some other halophyte species, such as *Limonium*, formation of lactate is continuous, but lactate concentration is much lower because most of the lactate is secreted into medium found by Rivoal and Hanson (Flowers and Colmer 2015). To prevent lowering of cytoplasmic pH, it was important for lactate to transport out of cytoplasm (Bazihizina et al. 2012). Some plants show reduced growth; others were unaffected, but rarely stimulated. Owing to various tolerance traits, such as salt exclusion, K^+:Na^+ selectivity and antioxidant capacity are amplified in most of the reported species, whereas pH activity and lactose production are important in *S. maritima* roots (Hamed et al. 2013).

1.1.6 Combined Stress [Salt + Metal]

A site for the accumulation of industrial and urban effluents contaminated by heavy metals is natural saline soil (Ghnaya et al. 2005; Zaier et al. 2010). Owing to repeated irrigation with sewage sludge or poor quality water, the use of pesticides and phosphorous fertilizers in agricultural soil leads to metal contamination (Hamed et al. 2013). Some halophytic species are accumulators and some are hyper-accumulators of certain metals such as *Sesuvium portulacastrum*, which can tolerate and accumulate high levels of cadmium and lead in aerial parts (Ghnaya et al. 2005; Zaier et al. 2010). In a similar manner, *Mesembryanthemum crystallinum* is a copper hyper-accumulator because it accumulates 3500 μg g^{-1} DW of copper in its tissues. *Sesuvium portulacastrum* produces a higher biomass than *Mesembryanthemum*; hence, *Mesembryanthemum* is a poor candidate for phytoremediation of contaminated soil (Thomas et al. 1998). *Atriplex halimus* has high biomass, but accumulates low concentrations of lead and cadmium; however, it is a viable candidate for use in phytoextraction in arid and saline soils (Manousaki and Kalogerakis 2009). One more suggested suitable species for phytoremediation because of its high translocation rates of cadmium and lead toward above ground tissue is *Halimione portulacoides* (Lutts et al. 2004). *Salicornia maritima* can accumulate reasonable levels of copper and zinc and tolerates moist or dry saline soil, but it is not a metal hyper-accumulator (Reboreda and Caçador 2007). The high metal tolerance of halophytes is associated with salt tolerance traits that include an antioxidant system, and osmoprotectant synthesis, such as proline, which scavenges free radicals and leaf surface excretion by using specialized salt glands (Milić et al. 2012). The major advantage of halophytes is that they can grow and accumulate metal in saline soil (Jithesh et al. 2006; Thomas et al. 1998). In the presence of optimal salinity, when exposed to cadmium stress *Sesuvium portulacastrum* showed improvement in growth and decreased the cadmium accumulation in roots and shoots (Manousaki and Kalogerakis 2011). In contrast, the quantity of cadmium extraction from plants is higher under combined (salinity and heavy metal stress) than under cadmium alone (Manousaki and Kalogerakis 2011; Ghnaya et al. 2007). It was suggested that Na^+ might indirectly contribute to the tolerance of *Sesuvium portulacastrum* from combined stress by osmotic adjustment (Ghnaya et al. 2007). It was found that the most toxic form of cadmium (Cd^{2+}) was removed in favor of another form bound to chloride anion and phytochelatins on NaCl treatment (Ghnaya et al. 2005). A comparison of leaves of Cd+NaCl-treated plants and NaCl-treated alone showed high proline and polyamine concentrations in leaves under Cd+NaCl conditions, which could have helped *Atriplex halimus* to tolerate cadmium inside leaf tissue (Hamed et al. 2013). Salinity reduces the harmful effect of cadmium in halophytes such as *Kosteletzkya virginica* by reduced oxidative stress and altering the hormonal status through reduced ethylene and abscisic acid accumulation (Han et al. 2013).

1.1.7 Combined Stress [Salt + Nutrient Deficiency]

Usually, Na^+ and Cl^- are dominant in saline soil. Seawater has a dominant ion concentration around 500 mM and sodic soil with pH >8.5 has CO_3^{2-} and HCO_3^- as dominant anions (Reboreda and Caçador 2007; Debez Huchzermeyer et al. 2011). Seawater contains 11 mineral nutrients needed by plants in sufficient concentrations for the growth of crops, but deficient in N and PO_4 (Hamed et al. 2013; Debez et al. 2011). Halophytes grow on seawater with supplied N and PO_4^{2-} and show similar biomass production to that of plants grown on full-nutrient solution such as *Suaeda fruticosa* and *Spartina alterniflora* (Zribi et al. 2012). Hence, in the next section the combined stress of N or PO_4^{2-} deficiency with salinity is discussed.

1.1.8 Combined Stress [Salinity + Nitrogen Deficiency]

Nitrogen (N) is an essential plant growth element. Higher plants absorb N in two major forms, i.e., NO_3^- (nitrate) and NH_4^+ (Bennett et al. 2009). However, in halophytes, the form of N used under high salt conditions varies among species and with both NH_4^+ and NO_3^- (Lu et al. 2005). *Suaeda maritima* shows high nitrate reductase activity in low-marsh (waterlogged) in comparison with high-marsh plants (drained) (Britto and Kronzucker 2002; Lewis et al. 1989; Leidi et al. 1991). As plants response to NH_4^+ has not been studied, the concept is unclear (Mahmood and Kaiser 2003). It was found that the contribution of nitrate in osmotic adjustment is greater than chloride in *Suaeda physophora* in an intertidal zone, even though the soil has a low nitrate concentration and high salinity (Wetson and Flowers 2010). Under low N and high NaCl conditions, some halophytes, such as *Salicornia bigelovii*, *Phragmites australis*, *Glyceria maxima*, and *Spartina alterniflora*, show that ammonium is beneficial for their growth (Song et al. 2006). *Suaeda salsa* accumulates high NO_3 even in soils with low NO_3 content and regulated Cl at low level at intertidal zone. In addition, the PSII machinery remains intact under high salinity, which is an important characteristic of this plant (Song et al. 2009). When NH_4^+ was dominant, K^+ regulated growth in *Salicornia bigelovii*. Owing to comparative inhibition, Na^+ absorption was suppressed by increased NH_4^+ and consequently K^+ was selectively absorbed (Kudo and Fujiyama 2010; Munzarova et al. 2006; Hessini et al. 2009). In the case of *Leptochloa fusca*, a comparison of NH_4^+ and NO_3^- nutrients revealed that there was considerable root growth reduction and a strong modified concentration of divalent cation in shoots that did not affect its salt tolerance (Hessini et al. 2013). Some halophytes avoid inhibition comparing Cl^- and NO_3 by an improved mechanism of utilizing NH_4^+ and overcoming NH_4^+ toxicity (Amtmann 2009). Some halophytes under saline conditions, show beneficial effects of NH_4^+ by utilizing salt-affected soil because they have salt and NH_4^+ tolerance and use NH_4^+ instead of NO_3^- as essential N source (Hamed et al. 2013).

1.1.9 Combined Stress [Salt + Phosphorous Deficiency]

Usually in alkaline, calcareous soil, an aquatic ecosystem has a high pH and the concentration of P is very low (Mahmood and Kaiser 2003). Plants require a substantial amount of P for living cells, but inorganic phosphate acts as an obstacle, owing to the indirect uptake of P from the environment (Hamed et al. 2013). Pi is usually immobile and not uniformly distributed, and is therefore not readily available to roots (Hamed et al. 2013). In seawater, there is little light and the ammonium level is elevated with a low P concentration and increased vulnerability of the seagrass *Zostera noltii* (Touchette and Burkholder 2000). To facilitate the acquisition of external Pi, consumption of Pi is restricted, and to maintain cellular Pi homeostasis, there is an adjustment in internal recycling carried out by the adaptive processes of plants (Raghothama and Karthikeyan 2005). Under inadequate Pi conditions, Pi homeostasis was maintained by the accelerated acquisition of external Pi and conversion and the remobilization of internal Pi (Raghothama and Karthikeyan 2005). The alteration of metabolic pathways and reallocation and recycling of internal Pi among different organs or cellular compartments led to the conversion and remobilization of internal Pi (Brun et al. 2008). A combination of salinity and P nutrient on halophytes show very complex and contradictory outcomes (Hamed et al. 2013). The interaction between salinity and P nutrient is majorly dependent upon plant species, developmental stage of plant, composition, salinity level, and concentration of P in substrate (Hamed et al. 2013). In *Hordeum maritimum*, P deficiency and salinity stress are applied separately, which leads to restricted whole plant growth and nutrient uptake with a clear effect of P-deficient stress rather than salinity (Zribi et al. 2012). Plants show a significant increase in root growth and root:shoot DW ratio rather than correspondence of the total well-known root adaptation response to mineral deficiency under P-deficient stress (Hamed et al. 2013). When NaCl is added to *Hordeum maritimum*, P-deficient plants show remarkable improvement in photosynthesis activity, capacity for osmotic adjustment, selective absorption of K^+ over Na^+, and antioxidant defense (Hamed et al. 2013).

1.2 Cross Tolerance

In response to single or multiple stresses, plants generally activate a common type of response, which is known as cross-tolerance (Hamed et al. 2013). Halophytes have evolved cross-tolerance mechanisms to manage stressful conditions and develop stress anticipation (Dhar et al. 2013). The signaling cascade of cross-tolerance is independent on the number of pathways activated. At the final stage, more than two pathways may result in the same response, where they may have interacted with each other or operated independently (Knight and Knight 2001). *Thellungiella* is tolerant to both oxidative and salt stress, which indicates possible cross-talk between these two stressors (Taji et al. 2004). Stress sensors such as calcium, calcineurin B-like interacting protein kinases, Ca^{2+}-dependent protein kinases, mitogen-activated protein kinase cascade, and transcription factors are the main components of cross-talk (Chinnusamy et al. 2004). Several halophytes show cross-tolerance against combined stressors (Hamed et al. 2013). The evolved signaling system involves antioxidants, hormones, and oxidant molecules; they show improved tolerance to many stressful conditions (Munne-Bosch et al. 2013).

1.3 Stress Memory

There is a difference among three kinds of stress responses given by plants, such as a negative response, which results in stress damage, a neutral response exhibiting assimilation, and an improved response, which exhibits additional sensory memory (Walter et al. 2013). After exposure to stress, the plant maintains a stress memory “imprint” that improves the plants’ response (Bruce et al. 2007). The accumulation of transcription factor or signaling protein, epigenetic change involving chemical change in DNA (DNA methylation and acetylation), histone modification, or the accumulation of small RNA are considered possible mechanisms of the stress imprint (Hamed et al. 2013). The mechanism has not yet been revealed, but research into this aspect is underway. Long stress memory in plants pre-exposed to salinity, drought or cadmium results in decreased oxidative stress in the halophyte *Cakile maritima* when subsequently exposed to salinity (Hamed et al. 2013). There are plants that continue for several weeks after relief of the first stress that allow plants pre-exposed to stress to either protect or scavenge ROS more efficiently than plants that have not been pre-exposed (Ellouzi et al. 2011). In stress memory, hormones such as salicylic acid, abscisic acid, and jasmonic acid also play important roles. In *C. maritima*, exposure to high salt concentration and increased level of jasmonic acid result in a strong response in correlation with low H_2O_2 and malondialdehyde level (Jaskiewicz et al. 2011). Stress pre-treatment alleviates salt-induced oxidative stress and reduces the jasmonic acid level in leaves (Ryals et al. 1996). Upon cellular oxidation, the metabolic priming effect of drought and cadmium is similar to salt stress pre-exposure, signifying an effective cross-tolerance response in the above-mentioned species (Ryals et al. 1996). The ability of an organism to use its present environment to trigger gene expression and lead to physiological change to adapt further to the environment is referred to as anticipation (Hamed et al. 2013). The concept of anticipation and memory has significance in the response of plants to pathogenic infection. Plants acquire systemic immunity to further infection after local infection by a pathogen (Hamed et al. 2013). This systemic immunity requires salicylic acid accumulation in tissue distal from the infectious site and is called systemic acquired resistance (D'Amore et al. 2005). Some exogenous applications of salicylic acid trigger abiotic and biotic stress resistance mechanisms with some salicylic acid analogs such as benzo (1, 2, 3) thiodiazole 7-carbothionic acid S-methyl ester (Conrath 2009).

1.4 Conclusions and Future Prospective

Halophytes have the capability to survive under harsh conditions because of their developed adaption mechanisms, not only toward salinity, but also to other abiotic stresses (Table 1.1, Fig. 1.1). These tolerance mechanisms help plants to tolerate a wide range of abiotic stresses. Tolerance mechanism involved in abiotic stress include ion toxicity, water stress, oxidative burst, osmotic adjustment, and homeostasis. Interaction between salinity and other abiotic stresses leads to physiological and biochemical amplification of certain traits, which are usually associated with salinity, such as proline accumulation and antioxidant capability. Halophytes are considered as a source of new traits and genes for tolerance to multiple stressors because of their ability to tolerate various forms of abiotic stresses. There is already a growing concern about the scarcity of water and increased demand for food. Therefore, there is a need to utilize saline soil for the production of food crops, and secondary metabolites which can be made are possible by analysis of the response of halophytes to combined stress. This could provide several relevant tools for environmental and agricultural practices. For the development of economic and environmental sustainability, such approaches are required that are purely based on appropriate farming practices and the identification of multiple stress-tolerant species.

Table 1.1 List of halophytes subjected to a combination of abiotic stresses and showing high tolerance to other abiotic stresses

Combination of abiotic stress	Tolerant halophyte species	References
Salinity and drought	*Cakile maritime*	Ellouzi et al. (2013)
	Bruguiera cylindrica	Atreya et al. (2009)
	Sesuvium portulacastrum	Slama et al. (2008)
	Atriplex halimus	Slama et al. (2007)
	Atriplex hortensis	Glenn et al. (2012)
	Atriplex canescens	Glenn et al. (2012)
	Atriplex lentiformis	Glenn et al. (2012)
	Zygophyllum xanthophyllum	Ma et al. (2012)
	Ipomoea pes-carpra	Hamed et al. (2013)
Salinity and flood	*Suaeda maritima*	Wetson et al. (2012)
	Phragmites australis	Gorai et al. (2010)
	Puccinellia ciliate	Teakle et al. (2013)
	Thinopynum ponticum	Jenkins et al. (2010)
	Melilotus siculus	Teakle et al. (2013)
	Lotus tenuis	Teakle et al. (2006)
	Tecticornia pergranulata	Colmer and Voesenek (2008)
	Limonium	Hamed et al. (2013)
Salinity and heavy metal	*Sesuvium portulacastrum*	Ghnaya et al. (2005)
	Mesembryanthemum crystallinum	Thomas et al. (1998)
	Atriplex halimus	Manousaki and Kalogerakis (2009)
	Halimione portulacoides	Reboreda and Caçador (2007)
	Salicornia maritima	Redondo-Gómez (2013)
	Spartina densiflora	Kholodova et al. (2005)
	Spartina alterniflora	Golldack et al. (2014)
	Kosteletzkya virginica	Han et al. (2013)
Nutrient deficiency and salinity		
Nitrogen deficiency and salinity	*Suaeda maritime*	Wetson and Flowers (2010)
	Suaeda physophora	Song et al. (2006)
	Salicornia bigelovii	Kudo and Fujiyama (2010)
	Phragmites australis	Munzarova et al. (2006)
	Glyceria maxima	Munzarova et al. (2006)
	Spartina alterniflora	Hessini et al. (2009, 2013)
	Leptochloa	Mahmood and Kaiser (2003)
Phosphorus deficiency and salinity	*Zostera noltlii*	Lin et al. (2009)
	Crithmum maritimum	Nieman and Clark (1976)
	Hordeum maritimum	Zribi et al. (2012)

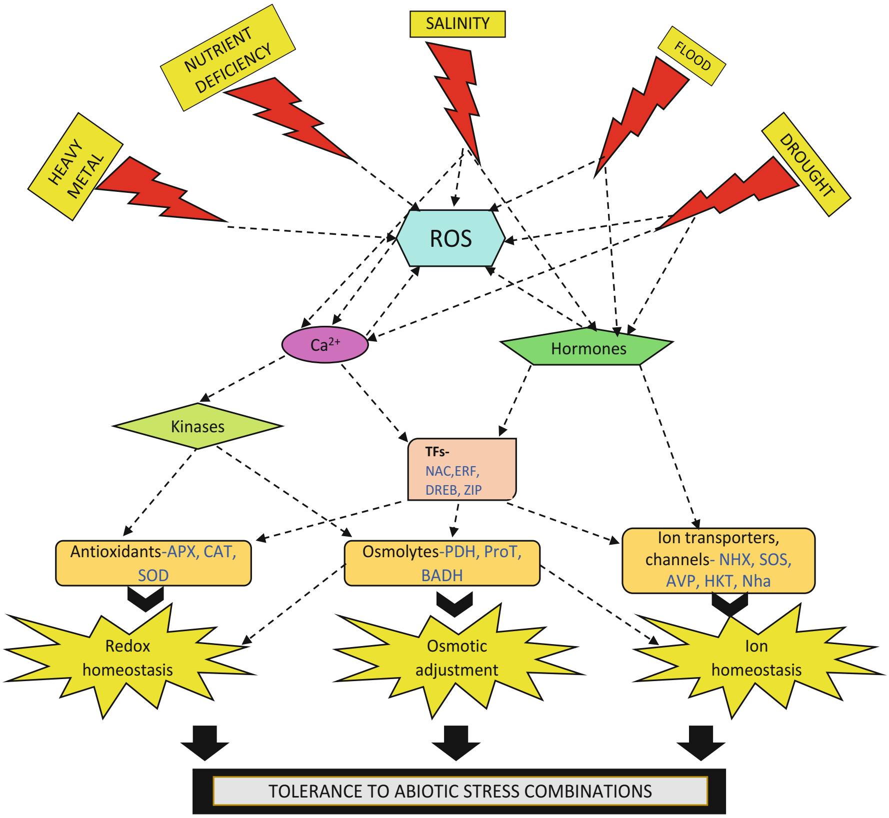

Fig. 1.1 Diagrammatic representation of abiotic stress responses and components involved in the adaptation mechanism of halophytes

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Chapter 2
Behavior of Halophytes and Their Tolerance Mechanism Under Different Abiotic Stresses

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Abstract Chemical toxicity, drought, extreme temperatures, salinity, and oxidative stress, these are the abiotic stresses, and they are menace to field production and the nature of the environment. Toxic environmental conditions cause a major hazard in crops and affect the plant growth. Morphological, physiological, biochemical, and molecular changes adversely cause loss in productivity worldwide. Because of increase in stresses, the devastating global effects are observed in arable land, resulting in 30% land loss, and it may be up to 50% by the year 2050. The first approach is to increase crop production dramatically which depends on improving plant productivity under stress conditions. Halophytes could be a leading choice to meet the respective goal. Inhabiting areas for halophytic plants range from inland desert to wetland areas. To tolerate different types of stresses, halophytes have been considered better as compared to glycophytic plants. These plants have adapted themselves with the simple mechanisms like compartmentalization and accumulation of organic solutes. Under drought stress, these plants express differential response to water deficit. During drought stress, plants evolve a number of strategies including high tolerance, storage of a large amount of water, and compartmentalization of salinity in mesophyll cells.

Keywords Stress · Antioxidant · Salinity · Environment · Senescence

2.1 Introduction

Predominantly environment is companionship between the abiotic and biotic component, and instantaneous change in abiotic components causes a disturbance in biotic component which often creates a tough environment for their survival. So, stress is defined as the state of physiological imbalance resulting from the variation among the situational demand and the ability of individual and motivation to achieve those needs. It can originate from its surrounding environment which is known as abiotic or biotic stress. It is a factor which is external that can possess unfavorable effect on the plants by limiting their growth, development, and even their percentage of chances of survival. This external stress is major constraints for global crop production (Sharma et al. 2016). Plants are more prone to diverse ecological stresses which makes plants distinct from animals. Plants have a significant wide array of defense method to tangle by these stresses. Approximately 3.6 billion of the world's dry land used for agriculture suffers from erosion, salinity, and soil degradation. Harsh climate and soil conditions are the major limitations for worldwide food production because plants are sensitive to these factors (Cakmak 2002).

2.2 Different Types of Abiotic Stress

Abiotic stress is defined as any inert exterior cause mostly environmental surroundings which can decline plant development and they result a huge effect on farming efficiency. According to our knowledge, due to these abiotic stresses, major loss in crop production occurs worldwide. Flowers et al. 2010 studied that the total per year loss in farming production from saline soil is US$12 billion and rising day by day. Abiotic stressors are classified into many different categories, and it comes in many different forms. People can easily identify the most common stressors, but there are subsequently many other fewer identifiable abiotic stress factors which influence environment continuously. Some necessary stressors contain drought, severe temperature, salinity, heavy metals/metalloids, high winds, flood, and other natural disasters like tornadoes and wildfires. Alternatively, lesser-known stressors usually occur on a less significant range. These consist of pH levels, high radiations, compaction, contamination, and rapid dehydration during seed germination.

2.3 Impact of Abiotic Stress on Agriculture

Abiotic stress is unavoidable. It is the leading factor affecting the growth and productivity of many crops worldwide. Collectively the abiotic stressors are found to possess synergistic effect on plant crops. Currently in front of farming, there are many challenges to meet the adequate food supply as a result of the undesired climate changes, affecting crop productivity globally. Adverse climate not only causes changes in agroecological conditions but in some way affects the profits of farmers, thus raising the demand for agricultural production. Abiotic stress is that natural part of the ecosystem that affects plants in different ways. One or more metabolic dysfunction occurs in plants when injured by the stress. If the stress is moderate and short term, the injury may be temporary, and for short time duration when the stress is removed, the plant may recover. If the stress is severe, then it possibly will put a stop to flowering and seed development and induce senescence which causes the death of the plant.

As a result of abiotic stress like heavy metal stress, salinity stress, water stress, etc., reactive oxygen species (Fig. 2.1) are produced which is an undesirable phenomenon. Reactive oxygen species are highly reactive in nature and cause the

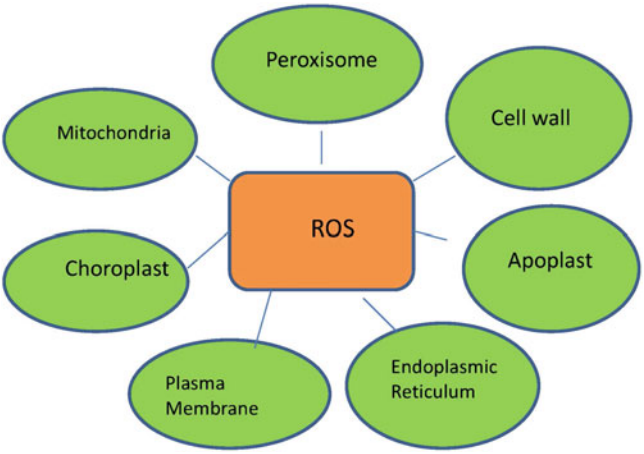

Fig. 2.1 Explaining oxidative stress and antioxidant defense in plant

oxidation of cellular bimolecular compounds like proteins, lipids, enzymes, and DNA. Under various types of stress like chilling, drought, heavy metal, salinity, and UV radiation (Miller et al. 2010), production of reactive oxygen species is a common phenomenon. Sometimes under biotic stress in plants, a sudden increase in reactive oxygen species has also been observed.

Production of ROS has a very important role for the growth of plants when produced in limited amount. But when produced in excess, it leads to oxidation and causes cellular damage and cell death (Fig. 2.1). For the usefulness of ROS, the antioxidant defense system must be active and under control (Noctor and Foyer 1998). Reactive oxygen species causes oxidative stress in the plants which has harmful effect on the plant structures. According to Noctor and Foyer (1998), ROS harmful effects are because of their capability to cause carbohydrate oxidation, DNA damage, lipid peroxidation in cellular membranes, oxidation of proteins, photosynthetic pigment denaturation, and impairment of enzymatic activity. Reduction of oxygen generates short-lived, not readily diffusible free radicals OH^- and O_2^- that are responsible for the oxidation of particular amino acids like tryptophan, histidine, etc. ROS causes weakening of cell membranes by peroxidation of lipids. Hydroxyl radical is responsible for oxidative damage to nucleic acid along with proteins. Higher toxicity of OH^- causes maximum damage near to the site of formation as it has a higher affinity for biomolecules.

2.3.1 *Salinity Stress and Effect*

Physiology of plant is affected due to salinity at the total plant level or at the cellular stage due to the accumulation of osmotic and ionic stress (Joset et al. 1996). Deficiency of water causes the osmotic stress, and there is no direct function of sodium ions (Joset et al. 1996; Hayashi and Murata 1998; Munns 2002). Extreme accumulation of sodium ion and chloride ion causes the ionic inequity in the cell which causes the reduction of uptake of other mineral ions like potassium ion, calcium ion, and manganese ion (Ball et al. 1987; Hasegawa et al. 2000). Toxic amount of the salt accumulated in the leaf apoplast leads to the dehydration, turgor loss, and death of the leaf cell and tissue. Accumulation of high amount of sodium leads to the high sodium and potassium ratio, and high ratio of the sodium inactivates the enzymes and so many metabolic pathways in the plants (Booth and Beardall 1991). Due to salt stress, a variety of physiological processes of the plant life get exaggerated. The processes that get affected are primarily changes in plant growth, increased rate of respiration, ion toxicity, membrane instability resulting from calcium and sodium disarticulation, and membrane permeability (Marschner 1986; Gupta et al. 2002).

2.3.2 *Drought Stress and Effect*

Due to nonavailability of water, drought stress takes place in the plant. This can happen due to low rainfall or nonavailability of water because of no irrigation in the crop. Physiological and biochemical responses in plants occur due to drought stress. These responses are mainly activation of respiration, photosynthesis, repression of cell growth, and stomatal closure. In response to drought stress, transcript profiling experiments have been performed in *Arabidopsis* via full-length cDNA microarray. The result showed that changes occurred in the transcriptosome of *Arabidopsis* (Kreps et al. 2002; Seki et al. 2002). Nearly 30% of transcriptosome on the *Arabidopsis* gene chip 8 K oligoarray changed in stress treatment. (Kreps et al. 2002). Plants have evolved different adaptive mechanisms in response to drought stress at the cellular, physiological, and molecular levels (Marco et al. 2015).

The outcome of a plant to abiotic stress involves the sensitivity of extracellular stress indicator through receptors of the cell. Extracellular stress indicator includes signal transduction and transcriptional regulation of stress-responsive gene expression that affects the resistance of plant to stress (Hong et al. 2012). To prevent the drought stress, plants have to close its stomata, reducing absorption, and decreased sweating resulting into low transpiration rate (Shekari 2000). The physiological study has been performed in two halophytic grass species *Halopyrum mucronatum* and *Cenchrus ciliaris* under drought stress. Under stress, halophytic plant expressed differential response to water deficit. Stomatal conductance and free proline content were higher in *Halopyrum mucronatum* than *Cenchrus ciliaris*.

2.3.3 Heavy Metal Stress and Effect

Mobilizations of heavy metals by man behavior occur through mining of ore, and dispensation in different uses led to the release of these elements into the environment. The major problem of the heavy metals is that they are non-biodegradable, they accumulate in the environment, and they afterward pollute the food succession. This pollution poses a risk to the surroundings.

In soil, heavy metals are present as natural components and increasing as a result of human activities. The soil contamination due to heavy metals becomes the serious and a big problem due to adverse ecological effects on the environment. Activities of enzymes are very much important for plant metabolism, and they get retarded due to heavy metal interference with activities of soil microorganisms. Gyuricza et al. (2010) found the effect of metal phytotoxicity on plants is inhibition of growth, nutritional imbalance, disturbance in the water and ion regime, and impairment in the photosynthetic pigments.

2.4 General Description of Halophytes

Plants appear on the earth to grow in the extreme environmental conditions from the deserts to swamps, from tundra to tropical forests, and even in the oceans also. There are a lot of species of the plants that tolerate drought, floods, cold, and heat. Water is sufficient on the earth, but it is mostly present in the oceans, and land has the very little amount of fresh water (Goldschmidt 1954). Those plants which complete their whole life cycle in a habitat having a high quantity of salt content are known as halophytes or salt plants. So, halophytes are highly evolved plants that are capable to take nutrients from the high salt environment. These plants have the ability to complete their whole life cycle in the substrate rich in saline conditions or sodium chloride (Flowers and Colmer 2008). The leaf of these plants is thick. The size of the mesophyll cells is found increased in stems. About 2% of all the plant species are halophytic. But relating halophytes only in relation to salinity could be reductionist. There are so many definitions of halophytes. Halophytic vegetation is commonly found in close proximity to the seashores where the mesophytes and other freshwater hydrophytes cannot continue to exist smoothly. Although these plants develop in the areas which are well covered with water, they cannot avail of the water because of high concentration of salt. So the halophytes are the plants of physically wet condition but physiologically dry. Saline habitats are classified as (i) aquatic haline, (ii) terrestro haline, and (iii) aero haline.

In plants, there are so many ways to cope with the problems of various stresses either to avoid it, bypass it, or tolerate various kinds of stresses. In India (many places of Rajasthan and other desert areas) soil is salty because of the presence of potassium chloride, calcium sulphate, sodium bicarbonate, sodium chloride etc. Halophytes are adapted to salty soils and crop up naturally in the area ranging from maritime estuaries to leftovers salt lakes in the dry areas. In the flowering plants, vascular halophytes are widely distributed. Facultative halophytes are those which can grow in both saline and nonsaline habitat. But obligate halophytes can survive only in saline conditions.

2.5 Success of Halophytes

The increase of plant production in saline habitat is a major problem. To solve this issue, there are two solutions. The first (intensive) approach is to increase the production of the crop by improving the plant productivity on currently used arable land under stress conditions. Crop breeding denotes a major finding for stress tolerance. But diversity of stress tolerance in the traditional crops seems to be too constricted to attain the goals (Flowers et al. 2008). Stress tolerance genes must be introduced into the traditional crops after identification in the extremophiles. So, the halophytes are the alternative to attain the goals. The deep rooting halophytes which are naturally present in the environment are very much significant because these plants are characterized by an excess of toxic ions often sodium and chloride. The second (extensive) approach to solve this problem is to transfer the center of farming production to marginal land. We can increase agriculture productivity by using alternative crop species like domestication of halophytic plants in the saline areas (Epstein et al. 1980; Flowers and Yeo, 1995; Flowers 2008).

Various physiological and biochemical mechanisms are developed by the plants in order to survive halophytic conditions. Principle mechanisms which occur in halophytic plants are ion homeostasis and compartmentalization, ion transport and uptake, biosynthesis of osmoprotectants, compatible solutes, synthesis of various antioxidant compounds, and activation of antioxidant enzymes. Some halophytes like succulents are adapted to salinity through secretion of salt from cuticle or guttation and from salt glands. Halophytes which secrete saline ions are *Spartina* sps, *Limonium latifolium*, and *Atriplex* sps.

2.6 Stress Tolerance Mechanisms in Halophytes

2.6.1 Salinity Tolerance Mechanisms

According to Hellebust (1976), halophytes are the plants flourishing under high concentrations of salt in swamps, marshes, estuaries, and bog that condition dump 99% of the other plant species. It is found that seeds of *Kochia scoparia* have the ability to grow in the excess salinity levels and a good model of adjustment of halophytes to high saline soils. Plants grown under saline conditions affected by osmotic stress intercede closure of stomata, reduction in cell growth in tender leaves, and growing areas in root and shoot (Fig. 2.2). If there is sustained growth of flora in an environment of NaCl or combinations of mixed salts, that will be known as salt-tolerant plants. Levitt (1980), has said that plants accumulate salt within their tissues, and there is the absence of negative effects on growth of the plants (Fig. 2.2). Consequently, there occurs accumulation of sodium ion in the photosynthetic system that negatively hampers the photosynthetic machinery like carotenoid and chlorophyll (Hasegawa et al. 2000; Chinnusamy et al. 2005).

Halophytes have adapted themselves essentially by different mechanisms which are minimization of the sodium ion uptake, reduction of the sodium ion influx,

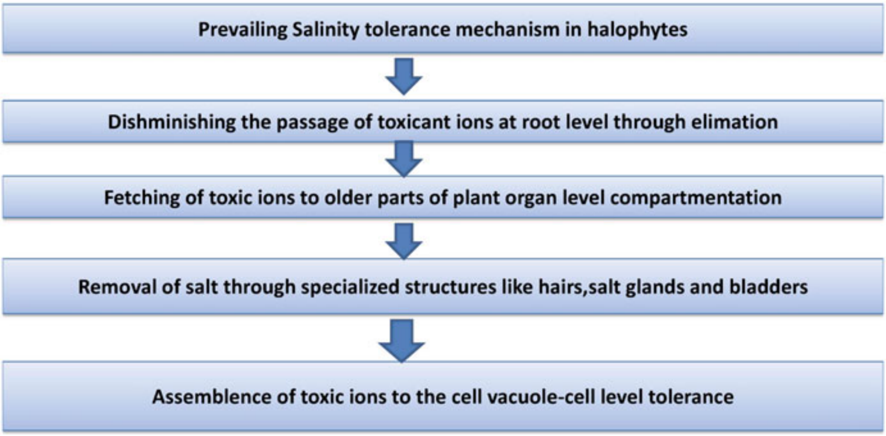

Fig. 2.2 Explaining salinity tolerance mechanism in individual plant at different levels

vascular compartmentalization of sodium ion, and elimination of sodium ion through plasma membrane and sodium ion/hydrogen ion antiporters (Taji et al. 2004). To overcome the abiotic stress, the plant has to maintain ion homeostasis through the osmotic adjustment in the plant's cell compartment (Munns and Tester 2008).

2.6.1.1 Sodium Uptake Sensing and Signaling in Plants

A plant flourishing under salinity has to develop many characters for the perception of signals, processing, and responses to the stimulus. With the advancement in technology, many signaling molecules have been discovered. Some of the tolerance mechanisms involve cascade pathways that are involved in the improvement of salinity stress tolerance. In spite of possible harmful effects of reactive oxygen species, there are some advantages due to accomplished signaling molecule regarding its properties and movability in cell's organelles. With the activation of antioxidant system, plants can overtake abiotic stresses through mitogen like MAPKKK, MEKK1, MPK4, and MPK6 (Xing et al. 2008; Jammes et al. 2009). Reactive oxygen species are complexed with cellular homeostasis and hormones allowing plants to adapt different abiotic stresses (Miller et al. 2010).

2.6.1.2 Role of Ion Homeostasis in Salinity Tolerances

Much higher accumulation of sodium ion into the soil imbalances the nutrients and is responsible for deficiency in plants (Munns 2005; Tuteja 2007; Maris and Blumwald 2007). High level of saline condition is not tolerated by both glycophytes and halophytes at cytoplasmic level. For restricting the entry of sodium ion into the cytoplasm, plants have to adapt themselves by salt exclusion and compartmentalization of sodium ion into the vacuole. Sodium ion entered through nonspecific ion channels which initiates salt stress signals through membrane depolarization (Seki et al. 2002). Due to high-salinity stress, activation of reactive oxygen species and ABA-responsive proteins occurs (Hernandez et al. 2001; Xiong and Zhu 2003). But plants regulate osmotic and ionic homeostasis which helps in protecting the plants from damage caused due to reactive oxygen species. For the maintenance of ideal ratio potassium ion/sodium ion in the plant, plants adapt various strategies like sodium ion efflux from the cell, regulation of potassium ion uptake, and exclusion of sodium ion entry into the cell (Zhu 2002). Root also plays a vital role in efflux of excess of sodium ion. SOS1 plays very important role in efflux of sodium ion from epidermis of root and from root to shoot in case of *Arabidopsis* (Shi et al. 2000).

2.6.1.3 Role of Solute Accumulation and Osmotic Protection

Compatible solutes are the group of organic compounds which are chemically diverse, and they are polar, soluble, and uncharged in nature. These solutes do not obstruct any of the cellular metabolisms even at high concentration. Under stress conditions (in most of the plants), the cellular concentrations of osmotically active compounds increase. Generally compatible solutes are hydrophilic in nature, and they replace the water from the surface of proteins. Mostly amino acids and the derivatives of the amino acids like cyclic polyols and acyclic polyols, fructans, ectoine, quaternary amino acids, sugars, and sulfonium compounds act as compatible solutes (Suprasanna et al. 2005). Compatible solutes accumulate in response to osmotic stress and play an osmoregulatory function, but some solutes such as trehalose do not respond to the osmotic stress. Even at low concentration, compatible solutes are protective in function and act as osmoprotectants (Slama et al. 2015). Mostly in halophytic plants in response to abiotic stress, the accumulation of proline in cytosol plays a substantial role in osmotic regulation. Ketchum et al. (1991) reported that in the cells of *Distichlis spicata* treated with 200 mM sodium chloride, cytosolic proline concentration was 230 mM. *Sesuvium portulacastrum* when exposed to various abiotic stresses like salinity, drought, and heavy metals accumulated higher proline concentration (Messedi 2004; Ghnaya et al. 2007; Slama et al. 2008; Lokhande et al. 2011).

2.6.1.4 Role of Antioxidants in Salinity Tolerances

To counter the deleterious effects of ROS production, plants have developed the dynamic ROS-scavenging mechanisms which consist of enzymatic and nonenzymatic protection pathways. Antioxidant enzymes include ascorbate peroxidase (APX), catalase (CAT), dehydroascorbate reductase, glutathione peroxidase, glutathione reductase (GR), glutathione *S*-transferase (GST), guaiacol peroxidase, monodehydroascorbate reductase, and superoxide dismutase (SOD).

In addition to antioxidant enzymes, the nonenzymatic antioxidants like alkaloids, alpha tocopherol, ascorbic acid (ASC), carotenoids, glutathione (GSH), nonprotein amino acids, and phenolic compounds also take part in scavenging free radicals (Jithesh et al. 2006; Gill and Tuteja 2010). Oxygen radicals are metabolized by superoxide dismutase (SOD) to hydrogen peroxide which defends the plant cell from injury. SOD is an antioxidant enzyme which is essential in the defense mechanism against the free radical toxicity by disputation of superoxide radicals to produce hydrogen peroxide (Fig. 2.3). Catalase scavenges hydrogen peroxide during β-oxidation of fatty acids and is engaged in photorespiratory functions during salt and other abiotic stress. Catalase has highest turnover rates for all enzymes as one molecule of CAT can convert six million molecules of hydrogen peroxide into water and oxygen per minute (Gill and Tuteja 2010). Lokhande found that in halophytes an increase in catalase activity is a measure of antioxidant defense. Water-soluble antioxidant (ascorbic acid) is found in plant tissues usually higher in photosynthetic cells and meristems (Gill and Tuteja 2010). Glutathione reductase (GR) activity was

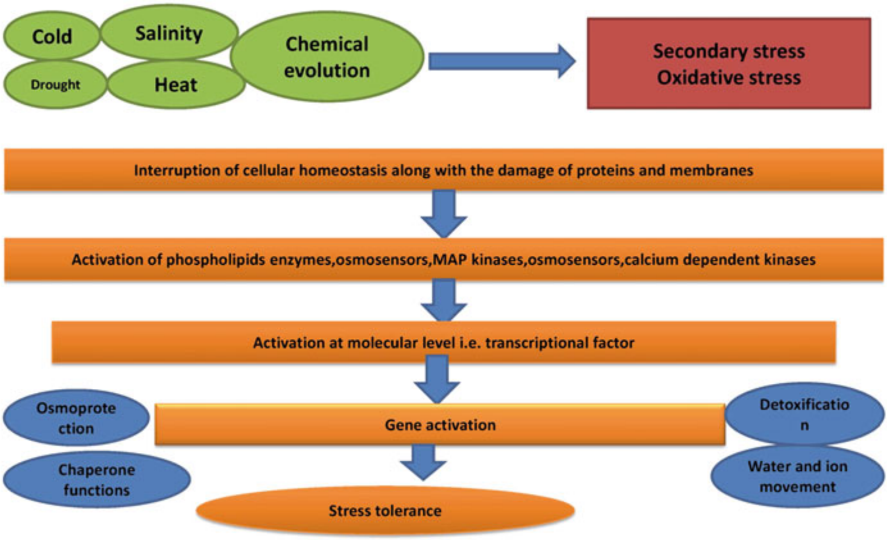

Fig. 2.3 Explaining different abiotic stress producing oxidative and secondary stresses with the activation of gene in the stress tolerance

shown to be high in leaves of salt-stressed plant as compared to control (Azevedo Neto et al. 2006).

2.6.2 *Heavy Metal Tolerance Mechanisms*

Heavy metal is defined as the naturally occurring chemical element with the relatively high atomic number and high density that is highly noxious in context of environmental aspect. Flowers et al. (2010) found that the increase in industrialization all over the world resulted in the extensive elevation in the release, use, and production of heavy metals in the environment. Considerable increase in toxic heavy metal like cadmium, copper, manganese, chromium, arsenic, lead, mercury, selenium, and uranium has contaminated the agricultural soil and water and thereby adversely affected plants and animals directly as well as indirectly (Yadav 2010).

Uptake of heavy metals in plant occurs either by simple diffusion or with the investment of energy, and furthermore, metabolism and sequestration of the noxious elements are necessary for the detoxification (Alkio et al. 2005). Plants follow general physiological tolerance mechanism against salt and heavy metal stress along with some special mechanisms like phytostabilization and phytoextraction that are included under the broad term phytoremediation. Halophytes are the unique plants having special pollutant-degrading enzymes that act as a natural defense system, helping the plant to become natural cleanser of the ecosystem leading to

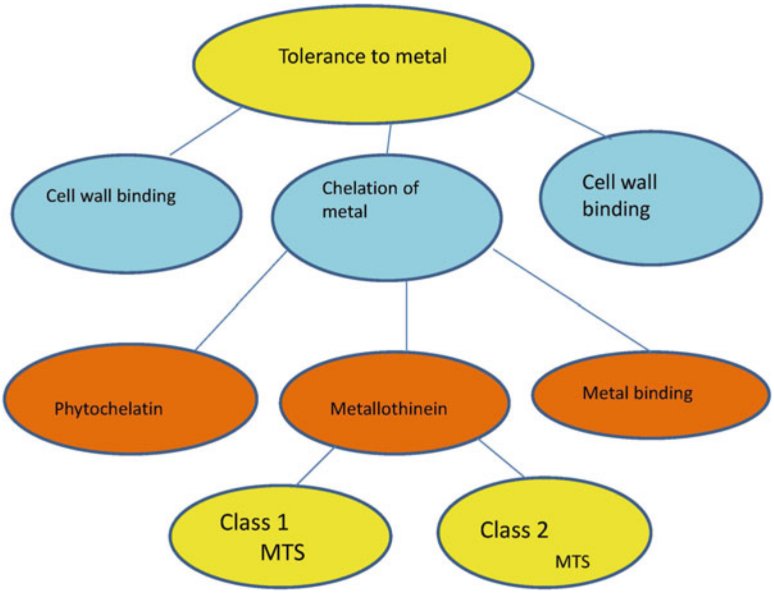

Fig. 2.4 Showing the tolerance mechanism of heavy metals in plants

phytoremediation (Aken 2008). The ability of formation of osmoprotectants is an advantage for halophytes to tolerate metal stress. So these plants are most suited to abiotic stresses including heavy metal tolerance (Jordan et al. 2002).

Phytochelatins are low molecular weight polypeptides having the formula (cGlu-Cys). Phytochelatins are synthesized from the amino acid glutathione and are utilized in metal detoxification by sequestration of metal in the vacuole (Fig. 2.4). Tennstedt et al. (2009) have shown that metallophytes don't use this strategy to avoid metal stress, whereas non-metallophytes synthesize phytochelatins to protect themselves from metal toxicity.

Special attention is going to be paid toward the removal of toxic substances from the environment and plantation or the use of those plants that can tolerate or significantly reduce the toxic form to less toxic (Zabłudowska et al. 2009). Pivetz (2001) states that phytoremediation includes various mechanisms like extraction, degradation, containment, or all of these. Along with phytoremediation, alternative methods of remediation are phytostabilization and phytoextraction as shown in Fig. 2.4. These methods are environmentally friendly, economical, and performed with ease (Szabados and Savoure 2009). Phytostabilization is the stabilization of heavy metals in the plant's rhizosphere and checking the migration of these into soil and water thus preventing the leaching of heavy metals to the surrounding environment. Lokhande et al. (2011) say that phytoremediation is considered as a group of strategies for the removal of toxicity of metals as well as stabilization at the rhizosphere, and the selection of plant depends on the type of contamination site.

2.7 Importance of Halophytes

In dry regions, for the irrigation of crops, groundwater or rainwater is used. Growing halophytes in such areas is a better option to use in salinized soil. With increase in population pressure, availability of fresh water becomes an expensive commodity. Therefore, halophytes are the best option to conserve fresh water as halophytes can be irrigated with saline water. Halophytes that are developing in estuaries, deserts, and seashores are major sources of the food, forage, and fuel. The eelgrass (*Zostera marina*) and salt grass seeds are ground to make flour. Some species like *Salicornia* are latent source of the vegetable oil. Mangrove (halophytic tree) can be harvested for fuel. Since ancient times, for the basket making and roofing, a marsh plant common reed (*Phragmites australis*) is used.

2.8 Future Prespective of Study

Due to the increasing salinity by expanding of the world population and more irrigation, approximately 400 million hectares of the land are exaggerated day by day. Therefore, we need ample food to fulfill the food requirements. Crops are not able to grow on the saline area, but halophytes are among the unique group of plants which are salt-loving plants that compete out of any type of hostile saline environments. Halophytes are considered ideal plants for growing in highly polluted soil because of their good phytoextraction and phytostabilization ability. Halophytes are highly adapted to cope with salinity stress because of highly organized defense system and mechanisms.

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Chapter 3
An Overview of the Germination Behavior of Halophytes and Their Role in Food Security

Gül Nilhan Tuğ and Ahmet Emre Yaprak

Contents

Abstract Halophytes, as differently oriented salt-tolerant plants, can provide a solution for our future food security. Lately, much attention is being paid toward the salt tolerance mechanism of halophytes, and attempts are made to provide fundamental knowledge for their genetical, agricultural, biotechnological aspects. As a dominating rule in the plant world, the most fragile and vulnerable developmental stage is germination. This holds true for the halophytes as well. Pre-germination adaptations and seed characteristics are important for the next generations. Adaptation mechanisms change with taxa, habitat type, and life span. Annual halophytes have dormancy mechanisms to avoid germination during unavailable period. Seed polymorphism is also one of the adaptations of halophytes against salinity and environmental fluctuations. For perennial halophytes, vegetative reproduction and long life span decrease the dependence on seed dormancy. Both annual and perennial halophytes guarantee their next generations by producing long-

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term or short-term seed banks. Evaluation of our knowledge related to these mechanisms can provide information for their propagation on saline habitats and reclamation of our degraded saline soils. They can provide a source for industrial products as well. Their evaluation can be used to put forward solutions for the food security of humans and animals.

Keywords Halophytes · Annuals · Perennials · Seed banks · Germination · Food security

3.1 Introduction

Global changes, mainly caused by human impact, occur in a short period concerning normal changes, and all the organisms are facing some difficulties to adapt to these rapid changes. One of the major changes is the climatic fluctuations. As a result of two important warming periods, between 1920 and 1945 and 1976 up to date, the world temperatures increased by 0,6 °C during the last 100 years. At the latter period, the warming has doubled as compared to the former one (Climate Change 2001). Extreme fluctuations in climate influence both humans and natural ecosystems. These influences are expected to get worse. Increases in global temperatures have led to the disappearance of some species because of abiotic stress and have triggered migration of some to the places outside their habitats (Öztürk et al. 2015). The movement of peregrine species causes an extra stress over the local ones. This situation not only influences the wild species but also the agricultural crops. Normally warm temperatures induce the growth and development of plants, but extreme values influence the productivity. Many agricultural plants are showing early flowering and maturations simply because of an increase in warmer periods (Craufurd and Wheeler 2009). Therefore, food security is becoming one of the major problems resulting from global warming.

"Food security exists when all people, at all times, have physical and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life" (World Food Summit 1996). In view of this, the food security means the availability of enough food from household to global level (Pinstrup-Andersen 2009). Global climate change severely influences the food security. This is mainly due to the influence of climate change on biological systems, which in turn affects food availability as well together with the sustainability and maintenance of food production, the stability of food security, and other aspects (Ericksen 2008; Thornton et al. 2014). Therefore, climate change has potential to slow down the progress of our globe leading toward hunger (Wheeler and von Braun 2013). According to the FAO's dimensions of food security, about two billion of the global population from over seven billion is food insecure, and the most severe situations are met in some parts of Africa and South Asia (von Grebmer et al. 2012).

One of the adverse effects of climate variability and change is caused by natural or human-induced phenomena which have a great impact on agriculture. These changes influence crop production systems for food, feed, or fodder; affect livestock health; and alter the pattern and balance of food and food products in several ways (Wheeler and von Braun 2013). Alternative food sources could be the answer for improvement of food security. Especially during the last few decades, the concern about food security has increased, and new food sources or production methods have followed.

Soil salinization is a large-scale worldwide problem and accepted as one of the major problems of loss of agricultural soils (Ashraf et al. 2009). Soil salinity mainly occurs in arid and semiarid regions, but lately because of both climate change and wrong irrigation practices, it also occurs in subhumid and humid areas (FAO 2017). The presence of soluble salts, either in soil or irrigation water, limits the growth and distribution of plants. Soils having excessive soluble salts include both saline and sodic soils and cause loss of plant productivity (Sen et al. 2002; Kasera and Mohammed 2010). Some plants, halophytes, have some adaptations or resistance against these conditions and can be irrigated with brackish or saline water having salinity ratio of seawater (Parida and Das 2005; Kasera and Mohammed 2010). Halophytes, which can germinate, grow, and reproduce under saline conditions over 0,5% NaCl (Chapman 1974), are one of the possible answers for a world without hunger. Morphological, physiological, and phenological adaptations are induced by the saline environment (Abdelly et al. 2006, 2008; Hakeem et al. 2013; Hasanuzzaman et al. 2013; Kafi and Öztürk 2011; Khan et al. 2016; Öztürk et al. 2006, 2008a, b, 2016, 2018).

There are different ways to classify halophytes. Waisel (1972) has divided them in two categories: ones that require salt for survival and/or maximum growth and the other ones that show resistance against salt. In addition, they have different mechanisms to deal with toxic levels of salt accumulated in their tissues: salt-enduring halophytes, salt-excluding halophytes, and salt-evading halophytes (Waisel 1972). Halophytes can also be divided into two categories on the basis of salt accumulation and secretion (Sen and Rajpurohit 1982; Sen et al. 2002): salt-accumulating halophytes and salt-secreting halophytes. Salt-accumulating halophytes increase the osmotic potential of cell sap by the accumulation of ions. They are mainly succulents which enables them to dilute the toxic ions in cell content, for example, *Salsola* spp., *Salicornia* spp., *Halocnemum* spp., *Heliotropium curassavicum*, *Zygophyllum simplex*, etc. Salt-secreting halophytes have salt glands, and secretion of salt ions regulates their ion content of cells. They are mainly non-succulent species *Tamarix* spp., *Atriplex* spp., etc.

In the life cycle of plants, the most vulnerable stage is the germination of seeds, which determines the establishment of any plant in certain areas. All the plants respond similarly to the salinity which delays germination because of salt stress (Keiffer and Ungar 1997; Khan and Ungar 1997). As glycophytes, halophytes show higher germination ratio in distilled water or the water with low salinity, but the germination ability under salinity shows great variation between different species (Baskin and Baskin 1998; Khan and Ungar 1996). In general, seeds are located near the soil surface, where salinity is high (Ungar 1979). The salts get deposited until the rainy season or melting of snow at the soil surface due to evaporation, which leach in the soil from the surface and provide more suitable conditions for germination (Ungar 1979, 2001; Keiffer and Ungar 1997). Higher levels of salt can induce seeds to remain dormant in a saline environment when they meet unfavorable edaphic condition (Khan and Ungar 1997). If the seeds of high salt-tolerant species, for example, *Salicornia europaea* and *Suaeda calceoliformis*, are removed to fresh water after being exposed to a high-salinity solution, germination is stimulated (Keiffer and Ungar 1997).

The inhibitory effect of salinity on germination is receiving much attention, especially during the last few decades. This inhibition is mainly caused by the osmotic effect of soluble salts, not their toxic effect in many halophytes like *Atriplex prostrata* (Egan et al. 1997) and *A. halimus* (Bajji et al. 2002). However, it has been found that the influence of NaCl on germination is more severe than other osmolytes (Katembe et al. 1998; Tobe et al. 1999). Therefore, the influence of salinity, whether it has an osmotic effect and/or ion toxicity, depends on the plant species (Petruzzelli et al. 1992; Poljakoff-Mayber et al. 1994; Song et al. 2005).

In general, halophyte seeds stay viable after prolonged exposure to hypersaline conditions (Keiffer and Ungar 1995, Keiffer and Ungar 1997; Gulzar and Khan 1994; Macke and Ungar 1971; Breen et al. 1977) and show quick recovery under suitable temperature conditions (Keiffer and Ungar 1997; Gulzar and Khan 2001; Khan and Ungar 2001; Gulzar et al. 2001). Depending on the species, a longer exposure and unfavorable temperature conditions can prevent their recovery from salinity stress (Keiffer and Ungar 1997; Gulzar et al. 2001). For some species, hypersaline conditions and unfavorable temperatures cause high seed mortality, but during germination and growth periods, they are highly salt tolerant (Khan and Gulzar 2003).

Halophytes have evolved in different families and different ecosystems. They show different adaptation mechanisms as well as different anatomical, physiological, and morphological characteristics. It is not easy to classify them according to their characteristic structures, because many far groups share the same or very similar adaptation mechanisms and even in the same family ecological changes cause different morphological adaptations. Seed-related characteristics are one of these, and generally, all share the same structures, but even similar species have different seeds. In general, all have small seeds with small endosperm, but some have perisperm instead of endosperm. Both hard-seeded and membraneous seed coat can be observed even in the same species. Salt tolerance depends on many factors like seed age, size, and morphology and the season of maturation and storage conditions, both in natural habitat and under laboratory experimentations. Halophyte species evolve with some tolerance or resistance mechanisms to deal with the extreme saline conditions. The seeds of halophytes have some adaptations to survive, germinate, and develop at high-salinity levels. The species can be annual or perennial, but all have some characteristics, and some are shared between them. To understand the tolerance or resistance mechanism for salt accumulation, most of the information comes from Chenopodiaceae family where the halophytes are concentrated.

3.2 Seed Characteristics of Halophytes for Germination

Survival of organisms in unpredictable and stressful habitats depends on the plasticity or adaptation capacity of organisms. During the evolutionary process, plants of extreme or unstable stressful environments have developed a number of morphological and/or physiological adaptations at different stages of their life cycles or in different parts. Seeds are one of the important structures for plants to settle or disperse in any area, and the presence of species depends on the survival or germination capacity of seeds.

Halophytes have different tolerance mechanisms to adapt to the high salinity, and these tolerances can be specialized for each life cycle phase. Germination is the most fragile phase for all plants as well as halophytes. The germination success and survival of seedlings depend on the adaptation mechanisms of seeds. Dormancy, seed coat permeability, maintenance of the viability of seeds at high salinity, seed bank formation, seed heteromorphism, perianth residues on seeds, and fast germination are the adaptations of seeds against salinity. These adaptation mechanisms protect seeds and seedlings from toxic effects of salinity by causing a delay of germination, fast germination, or dormancy.

3.3 Seed Morphology

Bromham (2015) has stated that halophytes have independently evolved in many lineages. They are widely distributed across the flowering plant families and have many different mechanisms for salinity adaptations. Although seed germination ecology of halophytes has been studied in detail, the relationships between seed morphology and salinity tolerance have not been evaluated till recently (Song et al. 2005, 2017; El-Keblawy and Bhatt 2015).

Seed coats simply form a barrier against environmental stress and provide a protection for the embryo. All the characteristics of seed coats possess some kind of adaptation mechanisms against extreme environmental conditions. Although halophytes have evolved independently in different families, studies are concentrated mainly on the Chenopodiaceae family, but the ecological conditions of variable saline areas result in variable seed morphology. Seed coat may be hard or membraneous; in some cases, seeds just have perisperm without endosperm, some have waxes over the surfaces, and some disperse with some perianth residues that all give some adaptive trait to the seed (Fig. 3.1).

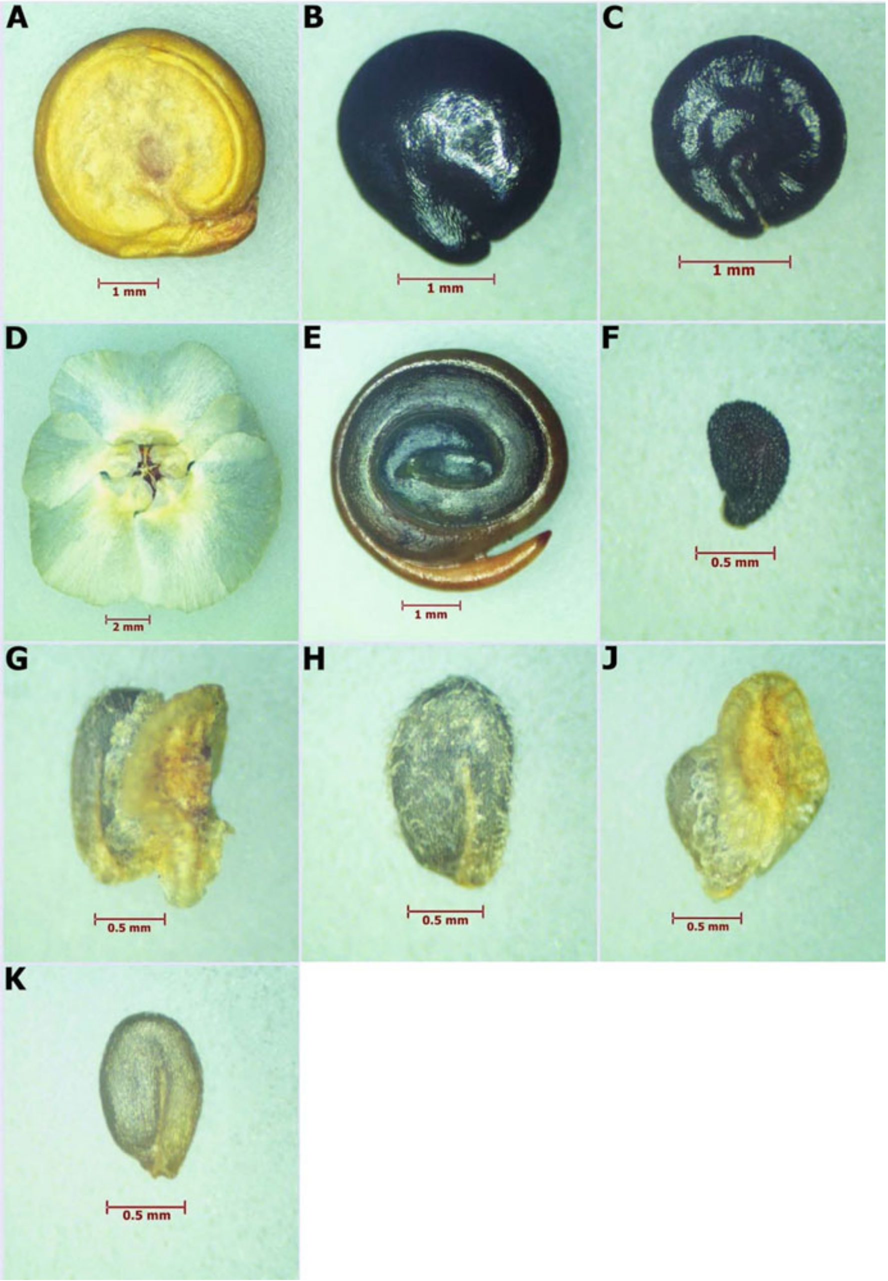

Fig. 3.1 Seed morphology of some halophytes. Heteromorphic seeds of *Atriplex aucheri* (**a**–**c**). Winged seed of *Salsola grandis* (**d**). Spirally coiled embryo of *S. grandis* (**e**). Seed of *Microcnemum coralloides* with hard seed coat (**f**). Dimorphic seeds of *Salicornia freitagii* central seed with and without perianth segment (**g**–**h**) and lateral seeds with and without perianth segment (**j**–**k**)

3.4 Adaptation Mechanisms

3.4.1 Seed Coat Permeability

Seed coats of halophytes can be evaluated in two different structures: hardseededness which forms an impermeable seed coat and membraneous seed coat which provide permeability. Hardseededness or impermeable seed coat provides a physical barrier against salinity, so halophyte seeds avoid toxic effects of salt ions (Nichols et al. 2008, 2009). It also delays germination, provided it occurs under conditions that are more suitable; so seedlings can survive and develop to form mature plants.

Hard seed coats cause physical dormancy in seeds, for example, *Saponaria halophila* (Çolak et al. 2017), *Melilotus siculus*, *Medicago polymorpha*, *Trifolium tomentosum* (Nichols et al. 2009), *Sphaerophysa kotschyana* (Yıldıztugay and Küçüködük 2012), *Kosteletzkya virginica* (Poljakoff-Mayber et al. 1994), *Microcnemum coralloides*, *Arthrocnemum*, *Halocnemum*, and *Suaeda* species (personal observations).

Generally, first rains are not strong enough for leaching of salts from the surface of the soil and are insufficient for inhibition and germination of impermeable seeds. If germination occurs at this very first precipitation, high seedling death occurs. Plants having delayed seed coat softening possess advantage under these conditions (Nichols et al. 2008, 2009). Impermeable seed coats also protect seeds from high surface salinity levels over the dry season. During this dry season, seed coat becomes soften and ready to germinate with the favorable rainy season (Taylor et al. 1991). Lignified palisade cells provide impermeability and inhibition of water and oxygen penetration inside the seed. This type of seed coat also causes physical dormancy (Baskin et al. 2000; Baskin 2003; Yıldıztugay and Küçüködük 2012). Seed coat impermeability also helps in the maintenance of the seed bank in the soil.

Other general morphological characteristics of seed coat are being permeable and membraneous. The permeability of seed coat provides germination soon after the precipitation and decreases in soil salinity. It also increases the risk of seed or seedling death due to toxic effects of salts (Munns 2002; Nichols et al. 2009). Some of the species having membraneous seed coat also produce impermeable seeds; they also show adaptation of seed polymorphism. For example, *Suaeda aralocaspica* is an annual halophyte producing two different types of seeds: hardseeded and membraneous seeds, which differ in morphology, dormancy, and germination. *S. aralocaspica* also produces two types of seeds with different colors and permeabilities. Highly permeable brown seeds are nondormant and show rapid germination when water is available. Black seeds are also water permeable, but their permeability is less than that of brown seeds, and they have non-deep physiological dormancy (Wang et al. 2008, 2012, 2017).

Mucilageous substances secreted during germination are another adaptation of seed coat, especially in dry areas. Mucilage provides resistance against drought by storing a high amount of water. Hydration of seed is provided by polysaccharides in the mucilage (Clarke et al. 1979; Goldstein and Nobel 1991; Morse 1990; Nobel et al. 1992, Bhatt et al. 2016). This characteristic is observed in the seeds of halophyte *Kosteletzkya virginica* (Gallagher 1985; Islam et al. 1982; Ghanem et al. 2010).

3.4.2 Maintenance of Viability at High Salinity Before the Start of Germination

The ability to maintain seed viability at high-salinity conditions is an important characteristic of halophyte seeds as compared with glycophytes. Halophyte species maintain seed viability and provide viable seed bank for the next generation (Ungar 1982; Chapman 1974; Kasera and Mohammed 2010). Germination of halophyte seeds is also inhibited by high salinity; however, these seeds remain viable and survive until the alleviation of salinity stress (Keiffer and Ungar 1997; Khan and Ungar 1997; Jutila 1998; Ungar 2001). Seed viability during and before germination is provided by mechanical characteristics of seed coat or compartmentalization of Na^+ in the seed coat. *Suaeda physophora* and *Haloxylon ammodendron* store Na^+ in the cells of the seed coat and protect the embryo from ion toxicity (Song et al. 2005). Black seeds of *Suaeda corniculata* are dormant under hypersaline and drought periods, and when the conditions are suitable, their viable seeds germinate after exposure to hypersalinity (Khan and Ungar 1997; Hanslin and Eggen 2005; Song et al. 2005; Cao et al. 2012).

3.4.3 Seed Bank Formation

Seed banks are important for the spatial and temporal distribution of plants. Especially under variable environmental conditions, seed banks increase/facilitate growth rate of populations and so reduce extinction risks (Kalisz and McPeek 1993; Fisher and Mattheis 1998; Adams et al. 2005; Moody-Weis and Alexander 2007). Seed banks can be persistent or transient. Persistent seed banks are particularly important for annual species. Seed banks are evolutionary responses to changing/fluctuating environmental conditions. Species of extreme environments produce a seed bank for securing next generation.

Under unfavorable conditions, halophyte seeds remain ungerminated and enter a persistent or transient dormancy phase until the conditions become favorable (Ungar 1978, 1987a, b, 1995; Jutila 1998; Ungar 2001). Halophytes prefer to form seed bank especially in hypersaline conditions and generally germinate under moderate saline conditions without forming a seed bank. Environmental variables induce seed dormancy, and the longevity of seeds in seed bank is determined by environmental conditions (Bekker et al. 1998; Ungar 2001). Seed banks provide storage of genetic information by dormant seeds, which will germinate and provide genetic diversity when the salinity alleviates.

Perennial species have the opportunity to reproduce several times or vegetatively through their life span; they do not depend on soil seed bank as annuals. Because of their semelparous characteristics, it is an advantage for annuals to produce persistent or transient soil seed bank (Redfield 1972; Badger and Ungar 1990, 1994; Egan and Ungar 1999a, b; Ungar 2001). Seed bank formation is more significant for the survival of annual species than perennials. So annual species produce large seed banks, but perennials do not need to produce persistent seed banks.

Therophyte *Spergularia marina* forms a seed bank in the soils of salt marshes in Ohio (Ungar 1995). Although the density of seeds in seed bank changes, it is still enough to form the next generation. According to Ungar and Woodell (1993, 1996), although the aboveground vegetation was dominated by perennial species, annuals dominated the seed bank. However, these results can change, depending on the species composition and the ability of species seed bank formation.

The findings on the seed bank dynamics are variable between populations and years, and although it is persistent in 1 year or one place, another year or another place, it can be transient (Jefferies et al. 1981, 1983; Philipupillai and Ungar 1984; Ungar 1987b). For example, *Salicornia europaea* forms a small seed bank in salt marshes at Nod marsh on the Norfolk Coast of England but does not form a seed bank at Stiffkey salt marsh on the same coast (Jefferies et al. 1981; Ungar and Woodell 1993, 1996). Also in Canada La Perouse Bay, and in Hudson Bay and Ohio, *S. europaea* formed a persistent seed bank (Jefferies et al. 1983; Philipupillai and Ungar 1984; Ungar 1987a), but it forms transient seed bank on British salt marsh (Jefferies et al. 1981). (It is most likely that these are different *Salicornia* species or microspecies; the problem has arisen due to taxonomical difficulties of genus *Salicornia*). *Atriplex prostrata* and *Salicornia europaea* form a persistent seed bank, but they also produce dimorphic seeds, and seeds forming seed bank are the ones small in size (Wertis and Ungar 1986). Germination differences and differences in seed bank formation ability of dimorphic seeds of *Suaeda corniculata* increase the fitness of the species to fluctuating environmental conditions.

Species forming transient seed bank are *Haloxylon recurvum* (Khan and Ungar 1996), brown seeds of *Suaeda corniculata* subsp. *mongolica* (Cao et al. 2012), *Heliotropium currassavicum*, *Polycarpaea spicata*, *Halopyrum mucronatum*, *Cyperus conglomeratus* (Aziz and Khan 1996), *Kochia americana*, *K. scoparia* (Gul and Weber 2001) etc. Species forming persistent seed bank are *Suaeda fruticosa* (Khan 1993), *Spergularia marina* (Ungar 2001), black seeds of *Suaeda corniculata* subsp. *mongolica* (Cao et al. 2012), *Cressa cretica* (Aziz and Khan 1996), *Holosteum umbellatum*, *Allenrolfea occidentalis*, *Salicornia rubra*, *S. utahensis*, and *Suaeda depressa* (Gul and Weber 2001).

Although seed banks generally occur in the soil, some species form an aerial seed bank until the release of seeds; these are stored in the maternal plant (Günster 1992). When the conditions become favorable for seedling settlement, seeds are released (Lamont et al. 1991). Osmotic shock effects and/or specific ion toxicity causes death of some halophyte seeds deposited in saline soils. Aerial seed banks increase survival and protection of seeds. Seeds from aerial seed banks disperse gradually and increase the extent of seed dispersal. Generally, seeds with lower tolerance against salinity stress retain in the aerial seed bank longer than the seeds with high tolerance (El-Keblawy and Bhatt 2015). According to the findings of El-Keblawy and Bhatt (2015), *Halocnemum strobilaceum* and *Halopeplis perfoliata* form aerial seed banks. It has been observed that *H. strobilaceum* is more tolerant against salinity stress than *H. perfoliata*, and seeds are stored in the aerial seed bank for 9 months in *H. strobilaceum* and for 17 months in *H. perfoliata*.

3.4.4 Seed Heteromorphism

Seed heteromorphism is defined as “the production of seeds of different form or behavior by single individuals” (Venable 1985). It has been recorded in 18 angiosperm families. Such seeds generally differ in color, size, and shape and also their dispersal mechanisms, dormancy, and germination characteristics (Baskin and Baskin 1998; Wei et al. 2007). This difference can be due to morphological features of seeds, perianth residuals on seed, or the structural differences of flowers. Heteromorphic seeds are reported from different families, but they are mainly concentrated in Asteraceae, Chenopodiaceae, and Poaceae (Imbert 2002). Generally, one seed morph is dormant, while the other is not, or one is more tolerant to high salinity than the other.

In the genus *Salicornia*, there are two types of flowers in each cyme: two lateral and one central. Central flowers give larger seeds which are dispersed with perianth segment, and lateral flowers produce small seeds loosely attached to perianth segments. These morphological differences cause variations in germination behavior (Davy et al. 2001; Ungar 1979). Although some debates on the salinity tolerance differentiation between central and lateral seeds do exist. The findings of germination trials for *Salicornia perennans* and *S. freitagii* are not meaningful. Some differences do exist between seed morphs against salinity response, but lateral seeds of both species have dormancy (Personal observations).

Germination characteristics of heteromorphic seeds of *Arthrocnemum indicum* (Khan and Gul 1998), *Suaeda moquinii* (Khan et al. 2001), *S. salsa* (Li et al. 2005), *S. aralocaspica* (Wang et al. 2017), *S. corniculata* ssp. *mongolica* (Cao et al. 2012), *Salicornia europaea* (Philipupillai and Ungar 1984), *Atriplex canescens* (Bhatt and Santo 2016), *Halogeton glomeratus* (Cao et al. 2012), and *Salicornia ramosissima* (Ameixa et al. 2016) have been studied at length. According to these studies, it can be said that production of heteromorphic seeds provides an advantage in different ways because each morph has its germination characteristics.

The waxes of seed coat can also be different in heteromorphic seeds and provide advantages in germination. These studies are new and still more is needed. However, it was found that the dimorphic seeds of *Salsola soda* have different wax contents in the seed coat of brown and black seeds. Black seeds contain more waxes than brown seeds, which may inhibit water uptake and germination. According to Song et al. (2017), seed coat of black seeds provides more protection under hypersaline conditions, which can be the reason for high wax content.

3.4.5 Perianth Color and Residues on Seeds

For the control of seed germination level and timing in many species inhabiting extreme environments, the perianth residues on seeds after dispersal is a common strategy (Takeno and Yamaguchi 1991; Wei et al. 2007; Xing et al. 2013). This phenomenon is widely common in the family Chenopodiaceae (Salsoloidae). Presence of wings on seeds reduces both germination percentage and rate of *Hammada salicornica* (Bahrani and Niknejad-Kazempour 2007), *Salsola rubescens* (El-Keblawy et al. 2014), *S. ikonnikovii* (Takeno and Yamaguchi 1991), and *S. grandis* (Çınar et al. 2016).

Perianth residues cause a delay of germination, for example, *S. grandis* (Çınar et al. 2016) seeds without perianth segments or removal of perianth segments by hand provide more rapid and easy germination which results in high germination rate.

Presence of perianth segments acts as a barrier for water absorption and also radicle emergence; thereby it inhibits the germination of winged seeds. This mechanical barrier also has an inhibitory effect on germination due to the chemical content of the wings. However, there has not been much information on the chemical content of seed wings. These chemicals, for example, could be an abscisic acid which could thus be the reason for low germination rate and percentage (El-Keblawy et al. 2014). Environmental conditions, e.g., heavy rains, can leach salinity and also the chemicals in wings and also mechanically corrupt the wing, and removal of chemical substances from the wings can result in an increase in the germination rate and percentage (El-Keblawy and Al-Shamsi 2008; Gul et al. 2013; El-Keblawy et al. 2014).

Presence of perianth residues and perianth color influences both germination rate and salinity tolerance in *Salsola rubescens* (El-Keblawy et al. 2014). This species is a perennial halophyte with two seed morphs: red-winged and yellow-winged. These wings are the perianth segments attached to the seeds. Even the color of the perianth residues influences the germination characteristics of *S. rubescens*. For example, red-winged seeds are more tolerant to salinity than yellow-winged ones. This mechanism is related to the response to light during germination (El-Keblawy et al. 2014). Different wing colors result from pigmentation; red color is mainly associated with anthocyanin production (Tanaka et al. 2008). There is a positive correlation between anthocyanin accumulation and increase in abscisic acid (Pirie and Mullins 1976; Hattori et al. 1992; Chen et al. 2012a, b). Abscisic acid is also related to the salinity tolerance (Lin et al. 2007; Chen et al. 2012a, b). These can be the answers to the question “how perianth color influences the germination?”.

3.4.6 Fast Germination

Species germinating in less than 4 days are accepted as "fast-germinating seeds," and if germination occurs in less than 1 day, these seeds are classified as "very fast germinating seeds" (Grime et al. 1981). Embryo and seed coat specializations result in very fast germination and favor the heteromorphic seed production (Parsons 2012). There is a strong relationship between very fast germination and extreme stressful habitats. Many halophyte seeds do not have endosperm but have spirally folding embryo which is coated by a pericarp (Tobe et al. 2000). Fast germination provides seedling establishment during transient favorable conditions. Fast germination is another adaptation to salt stress and occurs in the seeds with membraneous seed coat, without endosperm. They generally have a spiral or horseshoe-shaped embryos like *Salsola* spp. and *Salicornia* spp.

Salsola grandis seeds normally have wings, but if these wings are removed, they germinate within few hours (Çınar et al. 2016). *Haloxylon persicum* and *H. ammodendron* seeds do not have any endosperm; their seeds have spiral embryo coated by a pericarp (Tobe et al. 2000); and they germinate within an hour (Sharma and Sen 1989; Song et al. 2005). Many species from Chenopodiaceae family do not have true endosperm and embryo which could fill the seed coat (Wallace et al. 1968). Especially the ones with spiral embryo which have very fast germination rate, uncoiling of the embryo with water addition results in the germination. For *Salsola tragus* germination takes place in less than 29 min, and in *Anabasis aretioides* it takes 10 min (Grenot 1974). Central seeds of *Salicornia* spp. have horseshoe-shaped embryos and they germinate within few hours. Uncoiling of embryo also anchors the seedling in the soil and spreads the cotyledons (Grenot 1974; Wallace et al. 1968).

3.4.7 Dormancy

Seed dormancy is the inhibition of complete germination of viable seed under favorable conditions (Bewley 1997; Koornneef et al. 2002). It is controlled by several environmental factors. Dormancy is simply to overcome stressful conditions and is not the absence of germination (Vleeshouwers et al. 1995; Fenner and Thompson 2005; Finch-Savage and Leubner-Metzger 2006). It is the suppression of germination of viable seeds which is blocked by different factors (Nonogaki 2014; Hilhorst 1995; Bewley 1997; Li and Foley 1997; Finch-Savage and Leubner-Metzger 2006). The adaptation mechanisms are closely related with seed dormancy. One or more adaptation mechanisms work together in this case. To breakdown the dormancy, all factors causing dormancy should be removed. Halophyte seeds remain dormant under unfavorable (hypersaline, dry, cold) conditions. Increase in water potential results in a breakdown of dormancy (Ungar 1982, 1996). However, in some cases, increase in water potential is not enough if it is caused by a combination of more than one dormancy types.

Dormancy can be due to morphological, physical, physiological factors or a combination of these (Nikolaeva 2004). Based on Nikolaeva's system, Baskin and Baskin (2004) have proposed a classification for this with five classes of seed dormancy: physiological, morphological, morphophysiological, physical, and the combination of physical and physiological. Physical dormancy is one of the most dominant dormancy types mainly caused by water impermeable hard seed coats. For breaking down any kind of dormancy, there should be a trigger like a mechanism like an increase in water content that will result in the imbibition of seeds, leaching of germination inhibiting chemicals from soil or seed coat, or changes in environmental conditions, e.g., temperature and/or light or some hormonal activities. Dormancy can be caused by other adaptation mechanisms against salinity, for example, seed coat structure, perianth residuals. Dormancy and related studies are conducted under laboratory conditions, and there is not much knowledge about the processes in nature. *Salsola affinis* produces seeds with different morphological characters. Wei et al. (2007) have defined three seed morphs, and each has different germination characteristics. Although two of them do not possess any dormancy, one of them has non-deep dormancy which needs cold stratification for germination.

In some cases, seed coat-imposed dormancy and physiological dormancy occur simultaneously, and breaking down of one kind is not enough for the seed to germinate. *Atriplex triangularis* has seed heteromorphism, and small seeds show dormancy. It is caused by both impermeable seed coat and presence of inhibitory substances (Kelly et al. 1992). For breaking down dormancy, there are treatments to be used. Depending on the germination season, if it is spring cold or if it is autumn warm, stratification is required (Baskin and Baskin 1998). As explained before perianth residues block the entrance of water through seed coat and also prevent the emergence of the radicle. The inhibitory substances contained in the perianth residues inhibit germination until they leach from the tissues. Salinity-induced dormancy is alleviated by growth regulators and compatible osmotic compounds like betaine or proline (Poljakoff-Mayber et al. 1994; Pujol et al. 2000).

3.5 Physiological Aspects of Halophyte Germination

Germination of halophytic seeds is controlled by a number of environmental factors, temperature, light, water, etc. It has been reported that halophyte seeds generally show the best germination under fresh water conditions or below the salinity levels of 100 mM NaCl (Berger 1985; Ungar 1996; Carter and Ungar 2003; Wei et al. 2008; Gul et al. 2013). Because of different adaptation mechanisms and also different tolerance levels, salinity concentration that inhibits the germination changes within the species. Salt-accumulating stem-succulent halophytes are more tolerant to high-salinity levels than the salt-secreting halophytes during the germination period. Even at salinities over 1 M NaCl which is over the seawater salinity, seeds of salt-accumulating halophytes can germinate (Khan and Gul 2006). However, the salinity threshold for seeds of some species is less than almost 250 mM

NaCl, for example, *Halopeplis perfoliata*, *Arthrocnemum australicum*, *Salicornia fraitagii*, *S. perennans*, *S. rubra*, *and Haloxylon stocksii* (Clarke and Hannon 1971; Khan and Ungar 2000; Khan and Ungar 1996). Khan and Gul (2006) have provided detailed information on the response of halophytes to changing salinity levels.

Although halophyte seeds have some adaptations to germinate under saline conditions, they show highest germination ratio at low salinities such as fresh water. But they also have high recovery ratio after exposure to high, even toxic levels of salinity. The ability to recover germination is important for seedling establishment. Generally, germination in nature takes place when the soil salinity levels decrease because of the leaching of salts by precipitation.

Ion exclusion from roots (Tester and Davenport 2003) or accumulation of ions at vacuoles (Greenway and Munns 1980) cannot be the case for germinating seeds or seedlings which makes them more vulnerable to high salinities than the adults. But especially seeds remain viable and have the ability to recover for germination at high salinities. This indicates that seeds can be more tolerant than the growing plants by using their adaptation mechanisms. As mentioned before, the temperature is also important for germination, especially for breaking dormancy. Thermoperiod affects the salt tolerance of halophytes (Morgan and Myers 1989; Khan and Ungar 1996). Every species has its optimum temperature range to germinate. The optimum temperature of each species generally depends on the optimum temperatures of the distribution area.

Growth regulators are important intrinsic factors for seed germination. According to Bewley and Black (Baskin and Baskin 2004), breaking down of dormancy depends on the removal of some growth inhibitors like ABA. Growth promoters such as gibberellins, ethylene, and cytokinins increase the germination ratio of some species when the soil salinity decreases. Influence of growth regulators changes with species, it is not easy to generalize the influences, and there should be more detailed studies to understand the mechanisms and the effective factors of halophyte seed germination physiology.

3.6 Biotechnological Approaches in Germination Studies of Halophytes

Halophyte seeds have many desirable germination adaptations which can be useful for agricultural plants, such as maintenance of the viability of seeds at high salinity and fast germination in favorable conditions. In many plants, salt sensitivity is most evident at the seed germination and seedling stages. Many halophytic species are reported to germinate best under distilled water or at lower salinities, so they are not obligate halophytes during germination stages (Ungar 1974; Khan and Ungar 1996; Baskin and Baskin 1998). But still, halophytes tolerate higher salinities during germination than glycophytes and most of the conventional crops. Halophyte seeds have other adaptations like being dormant in high salinities, high recovery

Table 3.1 Some examples on the genetic modification studies

Gene Donor	Gene	Gene acceptor	References
Salicornia brachiata	*SbSOS1*	*Nicotiana tabacum*	Yadav et al. (2012)
Leptochloa fusca	*LfNHX1*	*N. tabacum*	Rauf et al. (2014)
Halostachys caspica	*HcVP*, *HcVHA-B*	*Arabidopsis thaliana*	Hu et al. (2012)
Spartina alterniflora	*SaINO1*	*A. thaliana*	Joshi et al. (2013)
Eutrema halophilum	*ThMSD*	*A. thaliana*	Xu et al. (2014)
S. brachiata	*SbASR-1*	*N. tabacum*	Jha et al. (2012)
S. alterniflora	*SaARF*	*A. thaliana*	Karan and Subudhi (2014)
Pennisetum glaucum	*PgNHX1*	*Brassica juncea*	Rajagopal et al. (2007)
Aeluropus littoralis	*AlSAP*	*N. tabacum*	Saad et al. (2010)
Salsola soda	*SsNHX1*	*Medicago sativa*	Li et al. (2011)

ratios, and fast germination in favorable conditions (Keiffer and Ungar 1997; Khan and Ungar 1997, 2001; Gulzar and Khan 2001; Gulzar et al. 2001; Hanslin and Eggen 2005; Song et al. 2005; Cao et al. 2012).

There are mainly two biotechnological approaches to increase the ability of plants to germinate in saline conditions, namely, marker-assisted selection and genetic modification. Marker-assisted selection has allowed identification of quantitative trait loci in germination stage (Foolad et al. 1998; Mano and Takeda 1997; Quesada et al. 2002) and applied to many crops by different scientists with a huge variety of molecular methods (Foolad et al. 1998, 1999; Mano and Takeda 1997; Quesada et al. 2002) to obtain germination success of crops in saline environments, but marker-assisted selection is limited with genetic variability of the species, and co-introduction of undesired traits is also a problem for selection.

Many genetic modification studies have been undertaken to improve germination success of plants in saline environments. Even though it is possible to use non-halophytic plant genes with overexpressing, in such studies halophytes are reliable and important potential gene sources. Many studies have been reported regarding the overexpressing of some halophyte genes in glycophytes with promoted seed germination under saline conditions (Table 3.1). Considering halophytic plant diversity and different adaptation mechanisms, many more gene sources should be available for transgenic halophyte seeds.

3.7 Conclusions

During the last few decades, halophytes have attracted much attention. Many reviews have been published on the halophytes and their germination physiology (Ungar 1978, 1982, 1987b; Baskin and Baskin 1998, 2004; Baskin et al. 2000; Gul et al. 2013; Khan 1993; Khan and Gul 2006). All these reviews cover details on the halophyte seed germination ecology and physiology. In the present review, we are focussing on all kinds of seed adaptations including pre-germination stages of halophyte seeds and usability of these adaptations for food security.

Classification of halophyte seed adaptations can be done on different ways, such as morphological, physiological, and ecological, but it is not easy since most species have more than one adaptation mechanisms. Halophytic habitats are so diverse, and each habitat type has its challenges for seeds such as from daily fluctuating tidal salt marshes to extremely arid salt deserts. High variability in environmental conditions and taxonomical diversity of halophytes result in enormous diversity in seed adaptation mechanisms which makes classification of adaptation mechanisms quite complex. Moreover, one adaptation mechanism generally is not enough for survival under these extreme conditions.

The adaptation mechanisms of halophyte seeds are classified here into seven main groups: these are seed coat permeability, maintenance of viability at high salinity before the start of germination, seed bank formation, seed heteromorphism, fast germination, perianth color and residues on seeds, and dormancy. All these provide new opportunities for the use of saline soils to overcome food security.

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Chapter 4
Reactive Oxygen Species Production and Scavenging During Seed Germination of Halophytes

Aysha Rasheed, Sarwat Ghulam Rasool, Bilquees Gul, M. Ajmal Khan, and Abdul Hameed

Contents

Abstract Reactive oxygen species (ROS) are excited or partially reduced forms of atmospheric oxygen, which are continuously produced during aerobic metabolism like many physiochemical processes operating throughout seeds' life. ROS were previously known merely as cytotoxic molecules, but now it has been established that when tightly regulated to low levels they perform numerous beneficial functions in plants including many critical roles in seed physiology. This ROS homeostasis is achieved owing to the presence of a well-coordinated antioxidant system, which is composed of many enzymatic and nonenzymatic components. ROS reportedly facilitate seed germination via cell wall loosening, endosperm weakening, signaling, and/or decreasing abscisic acid levels. Most of the existing knowledge about ROS homeostasis and functions is based on the seeds of crops and model plants. This information about the seeds of non-crops such as halophytes is limited to just a few studies. Furthermore, mechanisms underlying ROS functions such as downstream targets, cross talk with other molecules, and alternative routes are still obscure. The objective of this article is to present an overview about (i) general mechanisms of

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ROS homeostasis in plants, (ii) ROS homeostasis in dry seeds, (iii) ROS metabolism in germinating seeds under optimal conditions, and (iv) ROS flux in germinating seeds under stress conditions with special emphasis on halophytes.

Keywords Antioxidant defense system · Halophyte · Oxidative damage · Salinity · Seed germination · Reactive oxygen species

Abbreviations

$^{\bullet}OH$	Hydroxyl radical
ABA	Abscisic acid
AOI	Active oxygen intermediates
AOS	Active oxygen species
APX	Ascorbate peroxidase
AsA	Ascorbate
CAT	Catalase
DHAR	Dehydroascorbate reductase
GPOX	Guaiacol peroxidase
GPX	Glutathione peroxidase
GR	Glutathione reductase
GSH	Reduced glutathione
GSSG	Oxidized glutathione
GST	Glutathione S-transferases
H_2O_2	Hydrogen peroxide
MDAR	Monodehydroascorbate reductase
NaCl	Sodium chloride
NADPH	Nicotinamide adenine dinucleotide phosphate
$O_2^{\bullet -}$	Superoxide radical
O_2	Oxygen
$^1O_2$	Singlet oxygen
POD	Peroxidase
Prx	Thiol peroxidase type II peroxiredoxin
ROI	Reactive oxygen intermediates
ROS	Reactive oxygen species
SOD	Superoxide dismutase

4.1 Introduction

Reactive oxygen species (ROS) are excited or partially reduced forms of atmospheric oxygen, generated in all living cells by the transfer of one, two, or three electrons to oxygen to produce a superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide

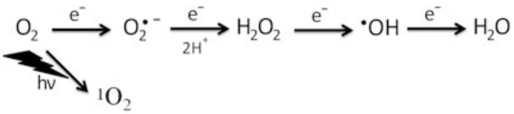

Fig. 4.1 Formation of common ROS

(H_2O_2), or hydroxyl radical ($^{\bullet}OH$), respectively, or by the energetic excitation of oxygen to produce singlet oxygen ($^1O_2$) (Fig. 4.1). Different terminologies such as active oxygen species (AOS), reactive oxygen intermediates (ROI), active oxygen intermediates (AOI), and sometimes oxygen free radicals are also used for ROS (Gutteridge and Halliwell 2000; Apel and Hirt 2004; Ray et al. 2012; Suzuki et al. 2012; Diaz-Vivancos et al. 2013; Waszczak et al. 2018). ROS appeared on Earth about 2.5 billion years ago along with atmospheric oxygen and since then have played a key role in the evolution of both prokaryotic and eukaryotic organisms (Anbar et al. 2007; Ślesak et al. 2012).

Although conventionally reported as toxic chemical species, under optimal conditions ROS are generally formed in low quantities and serve as signaling molecules for many cell processes (Suzuki et al. 2012; Baxter et al. 2013; Mittler 2017; Turkan 2017). Being signaling molecules, ROS are quite versatile because of their reactivity, diverse production sites, and their potential permeability for biological membranes (Møller et al. 2007; Møller and Sweetlove 2010; Farmer and Mueller 2013). It has been well-established that ROS have large number of beneficial/regulatory roles in living organisms including plants, animals, and other eukaryotes (Halliwell 2006; del Río 2015; Choudhury et al. 2017; Mittler 2017; Turkan 2017). For instance in higher plants, ROS have a vital role in the regulation of different developmental processes, stress signaling, interactions with other organisms, systemic responses and programmed cell death, etc. (Gutteridge and Halliwell 2000; del Río 2015; Choudhury et al. 2017). ROS are produced as metabolic by-product primarily in chloroplasts, mitochondria, and peroxisomes but are also reported to be synthesized in many other cell compartments where there are proteins or any other molecule with a redox potential high enough to excite or donate an electron to atmospheric oxygen (Fig. 4.2; Apel and Hirt 2004; Farmer and Mueller 2013; Mittler 2017). Under optimal conditions, a synchronized action of different antioxidant enzymes and substances helps plant cells to maintain ROS homeostasis (Foyer and Noctor 2005, 2009; Gill and Tuteja 2010; Mittler 2017). However, under stress conditions, production of ROS overwhelms the capacity of cell's intrinsic antioxidant defense to detoxify them; as a result, oxidative damage to different cell components such as membrane lipids, proteins, and nucleic acids occurs (Jithesh et al. 2006; Ozgur et al. 2013; Shabala 2017). These deleterious effects of ROS are often termed as oxidative stress (Inzé and Van Montagu 1995; Mittler 2002; Shabala 2017). Currently, a large number of articles including many reviews exist on ROS homeostasis and redox metabolism in the vegetative tissues of the plants (Foyer and Noctor 2009; Gill and Tuteja 2010; Choudhury et al. 2017; Turkan 2017; Czarnocka and Karpiński 2018). However, there is generally a dearth of knowledge about production, scavenging, and roles of ROS in seeds, especially during their germination stage (Bykova et al.

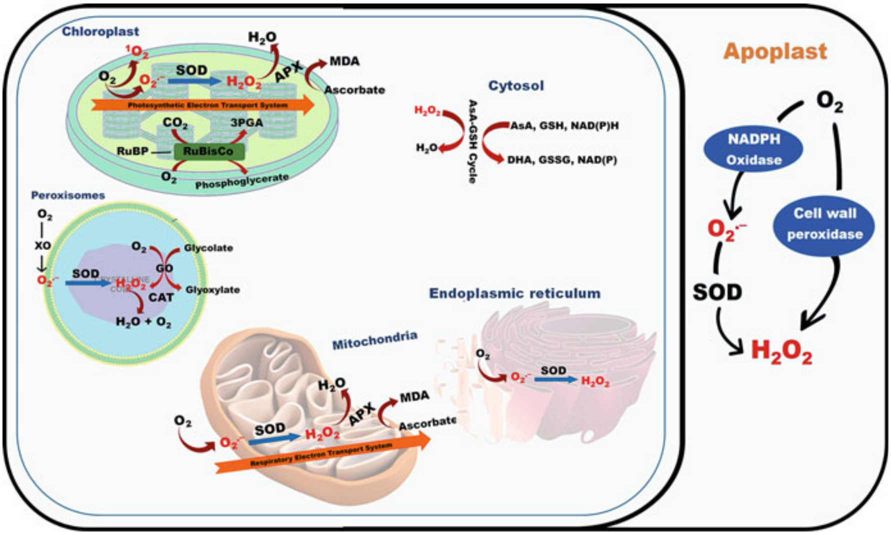

Fig. 4.2 General outline of ROS production and scavenging in plants. ROS are produced at several sites in the plant cells such as chloroplasts, mitochondria, peroxisomes, apoplast, endoplasmic reticulum, etc.

2015; Pehlivan 2017). This information is even scarcer for the seeds of halophytes (Kranner and Seal 2013), which are naturally salinity tolerant plants of saline habitats and hold immense potential to become non-conventional crops for arid saline lands in the future (Panta et al. 2014; Shabala 2017). The aim of this article is to present an overview of the findings on (i) general mechanisms of ROS homeostasis in plants, (ii) ROS production and scavenging in dry seeds, (iii) ROS metabolism in germinating seeds under optimal conditions, and (iv) ROS flux in germinating seeds under stress conditions.

4.2 ROS Production and Scavenging in Plants: General Outline

Plants metabolize atmospheric oxygen (O_2) in a number of processes including photosynthesis, photorespiration, and respiration; consequently, ROS are continuously produced as a by-product of aerobic metabolism (Foyer and Noctor 2005). During these aerobic processes, formation of ROS by activation of O_2 occurs by two mechanisms: (i) stepwise monovalent reduction of O_2 leads to the formation of $O_2^{\bullet -}$, H_2O_2, and ${}^{\bullet}OH$ and (ii) energy transfer to O_2 that leads to the formation of ${}^1O_2$. In green tissues of the plants, main sites for ROS production are the chloroplasts, which produce $O_2^{\bullet -}$, H_2O_2, and O_2^1 as a by-product of photosynthesis (Miller et al. 2010), whereas mitochondria produce $O_2^{\bullet -}$ and H_2O_2 as a by-product of respiration and peroxisomes generate H_2O_2 as a by-product of photorespiration (Miller et al. 2010). ROS are also produced due to the activation of the apoplast and plasma membrane-bound ROS-producing enzymes such as NADPH oxidases, various peroxidases, and superoxide dismutases (SODs) (Mittler 2002; Apel and Hirt 2004; Miller et al. 2010; Mittler et al. 2011; Czarnocka and Karpiński 2018). NAD(P)H-dependant electron transport involving Cty P450 in endoplasmic reticulum could be another source of $O_2^{\bullet-}$ production (Mittler 2002). Under stress conditions, accumulation of $O_2^{\bullet-}$ and H_2O_2 in the presence of heavy metals (e.g., Fe^{2+} and Cu^{+}, etc.) generates hydroxyl radical ($^{\bullet}OH$) via Haber-Weiss reactions, which is considered the highly toxic ROS and has been reported in many organelles such as chloroplasts and apoplasts (Koppenol 2001; Demidchik 2015).

Under optimal conditions, ROS content is tightly regulated to low levels via a well-coordinated antioxidant system, which is composed of many enzymatic and nonenzymatic antioxidants (Mittler 2002; Apel and Hirt 2004; Czarnocka and Karpiński 2018). Enzymatic components of antioxidant defense include superoxide dismutases (SODs), catalases (CATs), and enzymes of Foyer-Halliwell-Asada pathway, while key nonenzymatic components are ascorbate, glutathione, tocopherol, and phenolic compounds (Jithesh et al. 2006; Sharma et al. 2012). Many of these antioxidants such as SODs and CATs are believed to be originated as early as 4.1–3.6 billion years ago, even prior to the great oxidation event (Inupakutika et al. 2016), that made it possible for the organisms to deal with ROS which appeared on Earth about 2.5 billion years ago along with atmospheric oxygen (Anbar et al. 2007; Inupakutika et al. 2016).

Superoxide dismutases (SODs; EC 1.15.1.1) act as “the first line of defense against ROS” by converting $O_2^{\bullet-}$ into H_2O_2. Three major types of SODs, i.e., cytosolic Cu-Zn SOD, mitochondrial Mn-SOD, and chloroplastic Fe-SOD, have been reported from plants (Alscher et al. 2002). Often a positive relationship between SOD activity and salinity tolerance is reported in both glycophytes and halophytes (Jithesh et al. 2006; Prashanth et al. 2008; Ozgur et al. 2013; Bose et al. 2014). However, halophytes are known to possess comparatively higher levels of SOD activity/expression as compared to the glycophytes. For example, SOD activity invoked promptly and to a higher level in *Cakile maritima* (halophyte) as compared to *Arabidopsis thaliana* (glycophyte) upon salt exposure (Ellouzi et al. 2011). Similarly, SOD activities in mangrove *Rhizophora stylosa* were more than 40 times than those of peas (Cheeseman et al. 1997). Hence, a quick and stronger induction of SOD activity in halophyte might be a key player in stress signaling in halophytes.

Catalases (CATs; *EC* 1.11.1.6) are haem-containing tetrameric antioxidant enzymes involved in detoxification of H_2O_2 into water and oxygen (Willekens et al. 1997). CATs perform multifaceted roles in plants such as in photorespiration (Canvin 1990), scavenging of H_2O_2 during β-oxidation of fatty acids in germinating seeds (Willekens et al. 1995), and stress tolerance (Anjum et al. 2016). Often multiple isoforms of CATs are found in plants, which are mainly localized in peroxisomes in most plants (Jithesh et al. 2006; Su et al. 2014) and also in mitochondria of some plants (Scandalios 1990; Shugaev et al. 2011). The reaction catalyzed by CATs is very fast with reaction rate constant of $K \approx 10^7\ M^{-1}\ s^{-1}$which means each unit of CAT can detoxify millions of molecules of H_2O_2 per second (Deisseroth and Dounce 1970). Degradation constant of the CAT protein is 0.263 day^{-1} (Eising and Süselbeck 1991), while K_M value of CATs for H_2O_2 ranges between 40 and 600 mM (Del Río et al. 1977; Arabaci 2011). CATs, unlike other antioxidant enzymes, detoxify H_2O_2 in an energy-efficient manner, as they do not need reducing equivalent for activity, hence considered indispensable for ROS quenching under stress conditions (Anjum et al. 2016). Jithesh et al. (2006) reviewed that exposure to salinity may lead to all the possible (i.e., rise, decline, and unchanged) responses of CAT activity/expression in halophytes. However, halophytes generally tend to possess higher CAT activity/expression levels than the glycophytes (Bose et al. 2014). For instance, halophyte *Hordeum marinum* showed higher constitutive levels of CAT compared to *H. vulgare* (Seckin et al. 2010).

Enzymes of Foyer-Halliwell-Asada pathway (also known as ascorbate-glutathione cycle), namely, ascorbate peroxidase (APX; EC 1.11.1.11), monodehydroascorbate reductase (MDAR; EC 1.6.5.4), dehydroascorbate reductase (DHAR; EC 1.8.5.1), and glutathione reductase (GR; EC 1.8.1.7) with the help of some antioxidant metabolites (i.e., ascorbate, glutathione, and NADPH), also play an important role in detoxification of H_2O_2 (Fig. 4.3; Noctor and Foyer 1998; Jithesh et al. 2006). In plants, this antioxidant pathway reportedly operates in the cytosol, mitochondria, plastids, and peroxisomes (Jimenez et al. 1998; Noctor and Foyer 1998; Jithesh et al. 2006; Das and Roychoudhury 2014). This pathway is very efficient and helps in fine-scale homeostasis of H_2O_2, as APX (the first enzyme of the pathway) has a higher affinity for H_2O_2 (at μM level) than the CATs (at mM level) (Gill and Tuteja 2010). Hence, enzymes of Foyer-Halliwell-Asada pathway especially APXs are considered important component of plants' stress tolerance machinery (Mittler 2002; Jithesh et al. 2006; Bose et al. 2014). For instance, an

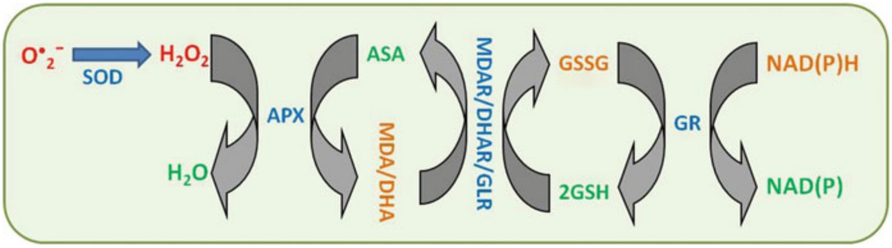

Fig. 4.3 An outline of Foyer-Halliwell-Asada pathway (also known as ascorbate-glutathione cycle) that quenches ROS (i.e., $O_2^{\bullet-}$ and H_2O_2) in the cytosol, chloroplast stroma, and mitochondria of plant cells. SODs convert $O_2^{\bullet-}$ into H_2O_2, which is detoxified into water by the action of APX that consumes ascobate (AsA). Oxidized forms of ascorbate [monodehydroascorbate (MDA) and dehydroascorbate (DHA)] are recycled back to AsA by MDAR (monodehydroascorbate reductase) and DHR (dehydroascorbate reductase) or GLR (glutaredoxin) at the expense of glutathione (GSH). Oxidized glutathione (GSSG) is reduced back to GSH by the action of glutathione reductase (GR) that consumes NAD(P)H as regeneration power

increase in APX and GR was found in response to salinity in halophytes *Bruguiera parviflora* (Parida et al. 2004) and *Salicornia brachiata* (Parida and Jha 2010). Many other antioxidant enzymes such as glutathione peroxidase (GPX; EC 1.11.1.9), glutathione *S*-transferases (GST; EC 2.5.1.18), thiol peroxidase type II peroxiredoxin (Prx; EC 1.11.1.15), and guaiacol peroxidase (GPOX; EC 1.11.1.7) have also been reported from plants and contribute toward ROS homeostasis (Jithesh et al. 2006; Ozgur et al. 2013; Bose et al. 2014).

To keep ROS levels within the tolerable range, plants also utilize low-molecular-weight nonenzymatic antioxidants such as ascorbate (AsA, a sugar derivative also known as vitamin C), glutathione (GSH; a thiol tripeptide γ-glutamyl-cysteinyl-glycine), and tocopherols (Foyer and Halliwell 1976; Jithesh et al. 2006; Ozgur et al. 2013). Often a positive relationship between plant salinity tolerance and levels of these antioxidants are reported. AsA and GSH are the most common nonenzymatic antioxidants of plants, which are found in all major compartments of the plant cells where they can scavenge ROS directly as well as with the help of Foyer-Halliwell-Asada pathway and many other antioxidant enzymes (Ozgur et al. 2013). Their role in salinity tolerance is well-established. For example, levels of AsA and GSH increased with increasing salinity in the halophytic species *Sphaerophysa kotschyana* (Yildiztugay et al. 2013) and *Limonium stocksii* (Hameed et al. 2015). Tocopherols (also known as vitamin E) are lipid-soluble molecules, which exist in four (i.e., α-, β-,γ-, and γ-) forms and are known as an active antioxidant defense for biological membranes (Falk and Munné-Bosch 2010; Ozgur et al. 2013). Among the four isoforms, α-tocopherol is the predominant form in plants, which is synthesized in plastids and plays an important role in quenching ROS especially $^1O_2$ (Bose et al. 2014; Ozgur et al. 2013). Its role in salinity tolerance of plants including halophytes is also frequently reported (Seal et al. 2010; Ellouzi et al. 2011; Ozgur et al. 2013). In addition, many other substances such as phenolic compounds, proline, glycine-betaine, polyamines, polyols, many sugars, and ferritin (iron-binding proteins) have also been reported as nonenzymatic antioxidants of plants (Jithesh et al. 2006; Ozgur et al. 2013; Bose et al. 2014).

A coordinated action of aforementioned enzymatic and nonenzymatic antioxidants keeps the levels of various ROS within low/tolerable range, which in fact is essential for the regulation/signaling of various plant processes (Fig. 4.4; Jithesh et al. 2006; Ozgur et al. 2013; Bose et al. 2014). For instance, ROS are involved in regulation of seed germination and dormancy (Schopfer et al. 2001; Oracz et al. 2007), growth and development (Gapper and Dolan 2006; Gechev et al. 2006), stress acclimation (Gechev et al. 2006), and programmed cell death (Jabs 1999; Dangl and Jones 2001; Van Breusegem and Dat 2006). However, these benefits are strictly dose-dependent (Fig. 4.4; Gechev et al. 2006; Quan et al. 2008). Under environmental stresses production of ROS exceeds the capacity of cells to detoxify them; as a result higher cellular levels of ROS cause oxidative damage to various cellular components like nucleic acids, membrane lipids, and proteins (Beckman and Ames 1998; Apel and Hirt 2004; Ozgur et al. 2013; Bose et al. 2014).

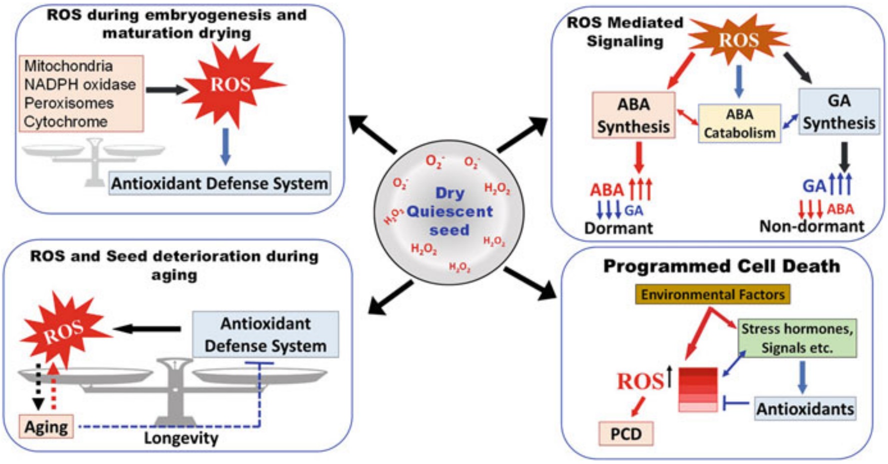

Fig. 4.4 Model indicting the dual roles of ROS in plants. Under optimal conditions, low levels of ROS perform various positive functions in plants, while under environmental stresses, their production overwhelms the capacity of cells to detoxify them; as a result their accumulation causes oxidative damages to lipids, proteins, and nucleic acids

4.3 ROS Production and Scavenging in Dry Seeds

Seeds are the perpetuation units of plants and composed of an embryo, food-laden tissues, and protective coverings (Bewley and Black 1994; Matilla et al. 2005; Khan and Gul 2006; Kranner et al. 2010a, b). Seeds by protecting the embryo and being able to travel long distances ensure the establishment of next generation, thereby the continuity of a plant species on the temporal and spatial scale (Hilhorst 1995; Koornneef et al. 2002; Gul et al. 2013). Seeds of many plant species are extremely tolerant to harsh environmental conditions such as high salinity and drought as long as they are in the dry quiescent state. Hence, seeds of most species can last in soil for a long period (weeks, months, or even years) in the dry state of metabolic quiescence while retaining their ability to germinate (Bewley and Black 1994; Rajjou and Debeaujon 2008; Gul et al. 2013). Seeds of most plants including those of halophytes are orthodox in nature with low ($\leq 5\%$) moisture content (Roberts 1973). Development of orthodox seeds includes the embryogenesis, accumulation of food reserve, and desiccation or maturation drying which results in a mature quiescent seed (Müntz 1982; Bewley and Black 1994). Production of ROS is obligatory at every step from seed development to seed germination and also during seedling establishment (Bailly 2004; Bailly et al. 2008; Pehlivan 2017). Hence, an efficient antioxidant system is essential for seed development, longevity, and germination (Bailly 2004; Kranner et al. 2010a, b; Hameed et al. 2014).

A growing body of literature indicates the presence of ROS in the “dry” orthodox seeds (Fig. 4.5; Bailly 2004; Bailly et al. 2008; Kranner et al. 2010a, b; Hameed et al. 2014; Pehlivan 2017). Although an ample number of articles exist now about ROS

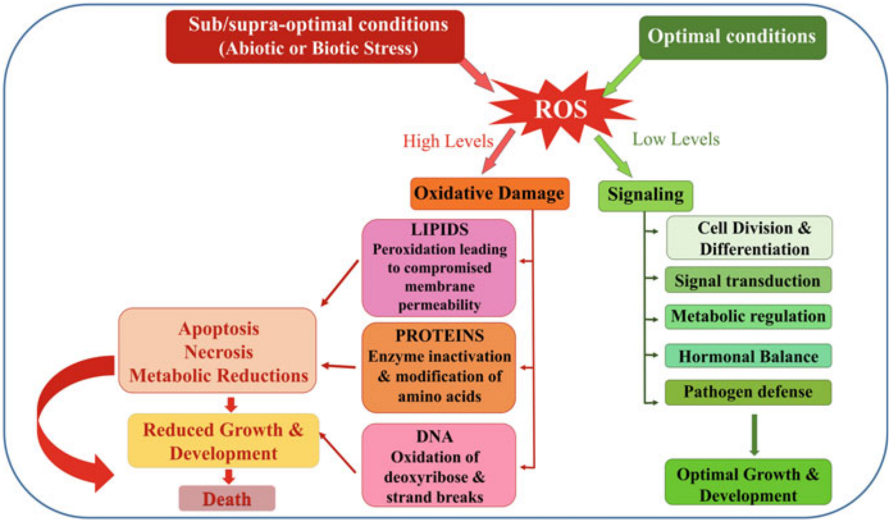

Fig. 4.5 Production and functions of ROS in dry quiescent seeds of orthodox nature

production in the seeds of crop plants (Bailly et al. 2008; Pehlivan 2017), this information about the seeds of halophytes is scant (Kranner et al. 2010a, b; Hameed et al. 2014). Hameed et al. (2014) reported that H_2O_2 and malondialdehyde (MDA, a common indicator of oxidative membrane damage) were present in freshly collected dry seeds of two halophytes *Suaeda fruticosa* and *Limonium stocksii*. Bailly et al. (2008) reviewed that the H_2O_2 content of the seeds first declines during maturation drying (i.e., seed development), remains constant afterward during quiescence or dormancy stage, and finally increases with after-ripening (i.e., dormancy breakage) and with aging (i.e., deterioration). Owing to low (5–15%) moisture content, enzymatic processes are not active in dry orthodox seeds. Hence, nonenzymatic processes such as Amadori and Maillard reactions and lipid autoxidation may be responsible for ROS production and MDA accumulation in a dry state (McDonald and Vanlerberghe 2004; Varghese and Naithani 2008; Bailly et al. 2008).

Dry seeds are generally devoid of AsA and APX owing to their depletion during maturation drying stage. However, there may be present an ASA-independent antioxidant system comprised of components like SOD, CAT, GSH, tocopherols, etc. (De Tullio and Arrigoni 2003; Bailly 2004; Chen and Arora 2011). However, such information about halophyte seeds is limited to just a few studies (Kranner et al. 2010a, b; Hameed et al. 2014). Hameed et al. (2014) reported that the dry seeds of *S. fruticosa* and *L. stocksii* were devoid of AsA but had GSH, SOD, CAT, GPX, and GR. Weitbrecht et al. (2011) indicated that owing to low moisture in dry seeds, antioxidant enzyme activities are limited/impossible in most parts of the seeds, and GSH plays key antioxidant function.

The ROS signaling pathways in quiescent seeds are not yet fully understood, and it is still fascinating how seeds sense ROS in the "dry" (i.e., maturation, seed bank/

storage) states (Fig. 4.5). Many recent studies have shown that ROS play crucial roles in releasing seed dormancy and the mechanism involved in this process might be the oxidation of certain proteins during after-ripening (Oracz et al. 2007; Kumar et al. 2015). Bahin et al. (2011) showed that the interaction of ROS and phytohormones alleviated the seed dormancy in *Hordeum vulgare* seeds. Similar cross talk of ROS with the phytohormones was reported for the seeds of *Bunium persicum* (Amooaghaie and Ahmadi 2017) and *Avena fatua* (Cembrowska-Lech et al. 2015). ROS also play a pivotal role in protection against pathogens, as their accumulation in infected cells acts as safeguard for the seeds either by affecting pathogens directly or indirectly by provoking the hypersensitive reaction leading to programmed cell death (Grant and Loake 2000). Besides the aforementioned positive impacts, ROS are also implicated in seed deterioration and result in the loss of viability during the aging (either natural or accelerated aging) (Bailly 2004; Bailly et al. 2008). Hence, seeds' intrinsic antioxidant constituents are of immense importance for the longevity of the seeds in soil seed bank and also for *ex situ* seed conservation banks (Bailly et al. 2008; Kranner et al. 2010a, b; Donà et al. 2013).

4.4 ROS Production and Scavenging in Germinating Seeds Under Optimal Conditions

Seed germination is a complex process of transformation of dry seeds from quiescent to metabolically active state that demands energy and hence is accompanied by rapid oxygen consumption for respiratory oxidative phosphorylation (Bewley and Black 1994). This reactivation of metabolism upon water uptake especially the oxidative phosphorylation and transition of damaged mitochondrial membranes from gel to liquid-crystalline state result in an oxidative burst by the production of ROS (Crowe and Crowe 1992; Tommasi et al. 2001; Nonogaki et al. 2010; Pergo and Ishii-Iwamoto 2011). Generally, about 2–3% of the oxygen used by the mitochondria can be transformed into superoxide and hydrogen peroxide (Oracz et al. 2007). Peroxisomes of germinating seeds also generate ROS, as fatty acid β-oxidation during conversion of stored lipids into sugars produces H_2O_2 and oxidation of xanthine into uric acid by xanthine oxidase produces superoxide in the peroxisomal matrix (Corpas et al. 2001; Bailly 2004). Plasma membrane-bound NADPH oxidases are another source of ROS in imbibed seeds, as they transfer electrons from cytoplasmic NADPH to oxygen that leads to the formation of superoxide radical and subsequently H_2O_2 (Colville and Kranner 2010).

To deal with continuously producing ROS during germination, nondormant imbibed seeds utilize a well-coordinated antioxidant defense system (Bailly 2004; Bailly et al. 2008; El-Maarouf-Bouteau and Bailly 2008; Miller et al. 2010; Hameed et al. 2014). However, generally little is known about antioxidant defense mechanism of halophyte seeds (Kranner and Seal 2013; Hameed et al. 2014; Rasheed et al. 2016). Activities of SOD, APX, and GR increased, while CAT and GPX activities decreased with time in water-imbibed seeds of two halophytes *S. fruticosa* and *L. stocksii* (Hameed et al. 2014). The dry seed of *Spinacia oleracea* maintained a SOD- and CAT-based antioxidant system which was replaced by APX-based system in osmoprimed germinating seeds (Chen and Arora 2011), while peroxidase (POD) activity was not detected during seed germination in *Chenopodium murale*, indicating the little role of peroxidases during seed germination (Bogdanović et al. 2008). In case of germinating sunflower seeds, CAT and GR activities increased before radicle protrusion (Bailly et al. 2000).

Ascorbate (AsA), although absent in dry orthodox seeds, seems to be synthesized during germination (De Gara et al. 1997; Bailly 2004; Bailly et al. 2008; Hameed et al. 2014). For example, AsA was detected in germinating seeds of halophytes *C. rubrum* (Dučić et al. 2003), *S. fruticosa*, and *L. stocksii* (Hameed et al. 2014) soon after attaining complete hydration. Rise in AsA content may be a result of its de novo synthesis (Tommasi et al. 2001) and/or recycling from the oxidized form (De Tullio and Arrigoni 2003). Besides antioxidant function, AsA is also a cofactor for enzymes involved in the synthesis of germination-regulating hormones like gibberellins and ethylene (De Tullio and Arrigoni 2003) and is also implicated in promoting cell division essential for seedling formation (Noctor and Foyer 1998; De Tullio et al. 1999; De Tullio and Arrigoni 2003). Reduced glutathione (GSH) content also increased in seeds of pine (Tommasi et al. 2001) and pea (Spragg et al. 1962) during the initial 24 h of germination. GSH content peaked at the time of radicle emergence in *Chenopodium rubrum* (Dučić et al. 2003). Similarly, GSH content also increased with time in germinating unstressed seeds of *S. fruticosa* and *L. stocksii* (Hameed et al. 2014). Tommasi et al. (2001) and Hameed et al. (2014) reported a decline in the content of the oxidized form of glutathione (GSSG) alongside increased GSH that indicates the prevalence of an efficient recycling machinery of GSH from GSSG.

ROS production during germination has conventionally been considered detrimental for seed germination; however, an increasing body of evidence suggests that they play important roles during germination (Fig. 4.6; Bailly et al. 2008; Soundararajan et al. 2016). ROS accumulation during early phase of germination creates an “oxidative window” (sensu Bailly et al. 2008) under optimal conditions that facilitates seed germination via cell wall loosening (Müller et al. 2009), signaling (El-Maarouf-Bouteau and Bailly 2008), and/or decreasing ABA levels (Fig. 4.6; Wang et al. 1995, 1998). According to Levine et al. (1994), H_2O_2 production in low quantity during seed germination protects emerging seedlings from pathogens.

4.5 ROS Production and Scavenging in Germinating Seeds Under Stress Conditions

All environmental stresses such as salinity, drought, heat, cold, heavy metals, high irradiance, and biotic stresses lead to excessive production of ROS, which cause oxidative damage to key cell components such as membrane lipids, proteins, and nucleic acids (Jithesh et al. 2006; Gill and Tuteja 2010; Kranner et al. 2010a, b;

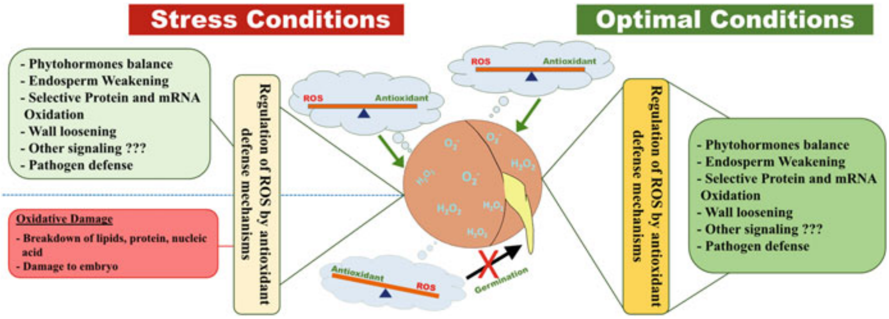

Fig. 4.6 Roles of ROS and antioxidants in germinating seeds under optimal and stress conditions. Change (i.e., dark vs light) in the intensity of colors (green, red, yellow) indicates the intensity of the phenomenon in different box

Choudhury et al. 2017). Generally, germination of the seeds is inhibited under stress or non-optimal conditions, and often this inhibition is linked to oxidative stress (Fig. 4.6; McDonald 1999; Tommasi et al. 2001; Lee et al. 2010; Xu et al. 2013). Thus the success of seed germination is dependent on the efficiency of an antioxidant defense system that operates during germination (De Gara et al. 1997; Bailly 2004). Most studies are related to ROS production in seeds of crops during storage under non-optimal conditions such as high temperature (Rajjou and Debeaujon 2008; Rajjou et al. 2012). Generally, little is known about stress-related ROS homeostasis in germinating seeds (Kranner et al. 2010a, b) especially of halophytes (Hameed et al. 2014; Rasheed et al. 2016).

Exposure to salinity caused an increase in endogenous H_2O_2 and malondialdehyde in two halophytes *S. fruticosa* and *L. stocksii* (Hameed et al. 2014) as well as in seedlings of *Sorghum bicolor* (Chai et al. 2010). Wang et al. (2009) showed that after 4 days of salinity treatment (300 mM NaCl), seeds of *Medicago sativa* and *Melilotus officinalis* had much higher malondialdehyde contents than in those of the control, whereas malondialdehyde content of germinating seeds of *Salsola drummondii* did not vary with increases in salinity, but sub-/supra-optimal temperature, and dark resulted in higher malondialdehyde as compared to optimal temperature and 12 h photoperiod, respectively (Rasheed et al. 2016). Hence, ROS production and oxidative damage responses of the halophyte seeds seem to vary with species and type of stresses; however, current knowledge is just confined to few studies and warrants the importance of more studies in this regard.

An increase in the activities of different antioxidant enzymes is often ascribed important for successful seed germination especially under stress conditions (Bailly 2004; Kranner and Seal 2013; Hameed et al. 2014; Panuccio et al. 2014; Rasheed et al. 2016). For instance, an increase in the activities of SOD and CAT after 48 h of exposure to NaCl was reported in germinating seeds of *Cucumis melo* (Pinheiro et al. 2016). SOD, CAT, and APX activities increased in germinating seeds of *Chenopodium quinoa* 3 days after sowing in various NaCl solutions (Panuccio et al. 2014). Similarly, an increase in CAT and GPX activities was reported in the germinating seeds of *Suaeda fruticosa* and *Limonium stocksii* under saline treatments (Hameed et al. 2014). Similarly, an increase in SOD, CAT, GPX, and APX activities was observed in the germinating seeds of *Salsola drummondii* under non-optimal temperatures and dark but not under saline conditions (Rasheed et al. 2016). Hence, an induction of antioxidant enzyme activities particularly of CAT appears key to successful seed germination under stress conditions.

Generally, little is known about the variations in the content of different nonenzymatic antioxidants of germinating seeds under stress conditions. This information about halophyte seeds is confined to just a few studies. Hameed et al. (2014) indicated that salinity inhibited seed germination of coastal halophytes *Suaeda fruticosa* and *Limonium stocksii* by decreasing ascorbate-dependent antioxidant system. Similarly, there was some decline in AsA content of germinating seeds of *Salsola drummondii* under high salinity and non-optimal temperatures (Rasheed et al. 2016). In the absence of AsA, GSH acts as the key antioxidant in orthodox seeds and thereby appears important for seed germination (Bailly 2004; Tommasi et al. 2001; Kranner and Seal 2013; Hameed et al. 2014). However, environmental stresses may cause a decline in its levels. For instance, GSH decreased with increasing salinity in germinating seeds of *L. stocksii*, *Suaeda fruticosa* (Hameed et al. 2014), and *Melilotus officinalis* (Wang et al. 2009). GSH content did not vary with variations in salinity, temperature, and light in *Salsola drummondii* (Rasheed et al. 2016). In contrary, total antioxidant capacity and total phenols increased in germinating seeds of *Chenopodium quinoa* 3 days after sowing in various NaCl solutions (Panuccio et al. 2014). Hence, it appears that responses of different nonenzymatic antioxidants of germinating seeds may vary with species and stresses, thus demanding more research for a better understanding.

4.6 Conclusions

Production of ROS is ubiquitous to aerobic metabolism and is therefore observed during every stage of a plant's life cycle and throughout seeds' life. ROS, although conventionally known for their cytotoxic effects, have emerged as key signaling molecules implicated in regulating a number of plant processes including seed germination/dormancy. It is believed that tightly regulated levels of ROS constitute an "oxidative window" (*sensu* Bailly et al. 2008) that facilitates the germination of most seeds. Seeds' antioxidant defense system which is composed of both enzymatic and nonenzymatic antioxidants plays a pivotal role in the tight regulation of ROS levels. ROS reportedly facilitate seed germination through cell wall loosening, endosperm weakening, signaling, and/or decreasing abscisic acid levels. Therefore, it appears that ROS and antioxidants play a broader role in seed biology than often acknowledged. Despite an increasing amount of literature on ROS homeostasis during seed germination and dormancy loss, generally, there is a dearth of this knowledge about the seeds of non-crop plants such as halophytes. In addition, detailed mechanisms of ROS functions such as downstream targets, cross talk with other molecules and alternative routes, etc. also need to be clarified.

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Chapter 5
Halophyte Growth and Physiology Under Metal Toxicity

Anita Kumari, Sunita Sheokand, Pooja, Ashwani Kumar, Anita Mann, Neeraj Kumar, Sarita Devi, Babita Rani, Arvind Kumar, and B. L. Meena

Contents

Abstract Heavy metals are present in low concentration in soil as their natural constituents. However various anthropogenic, industrial activities and agricultural practices have resulted in an increase in the concentration of heavy metals to toxic levels and thus become a limiting factor, affecting the sustainability of agricultural production. Environmental degradation due to increase in heavy metal is a serious

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issue which requires immediate remediation. To add to the problem large areas of agricultural land with heavy metal pollution are also affected by salinity particularly in arid and semiarid regions. Heavy metals inhibit plant growth and development and may be lethal at high concentrations. Heavy metal toxicity leads to a reduction of assimilation rate, respiration, nutrient uptake and increased oxidative stress. Oxidative stress damages various metabolic pathways which in turn affect the physiological and biochemical processes and cause a reduction in plant growth and productivity. Halophytes are salt-tolerant plants which can grow and reproduce in saline areas where glycophytes cannot survive. Due to special adaptive mechanism present in halophytes, they can be grown in saline soils which are also heavy metal-contaminated. However halophytes are also adversely affected by higher concentration of heavy metals (Cd, Cr, Pb and Ni). Halophytes have additional advantages as compared to glycophytes like higher tolerance to heavy metal and increased heavy metal uptake. Various studies revealed that halophytic plants are also tolerant to other abiotic stresses like temperature, drought and heavy metals. This may be due to the activated antioxidative system against ROS-induced oxidative stress. So the halophytic plants can be used for phytoremediation purpose in salt and heavy metal-contaminated soil. Among the halophytic flora, species having high biomass and deep root system are most suitable.

Keywords Growth · Halophytes · Heavy metals · Metallothioneins · Osmoregulation · Oxidative metabolism · Phytochelatins · Phytoremediation

Abbreviations

ABC transporters	ATP-binding cassette transporter
APX	Ascorbate peroxidase
As	Net assimilation rate
Ca	Calcium
CAT	Catalase
CAX	Cation exchanger
Cd	Cadmium
$CdCl_2$	Cadmium chloride
Chl	Chlorophyll
Co	Cobalt
Cr	Chromium
Cu	Copper
Cys	Cysteine
GB	Glycinebetaine
GPX	Glutathione peroxidase
GR	Glutathione reductase
gs	Stomatal conductance
GSH	Reduced form of glutathione
H_2O_2	Hydrogen peroxide

Hg	Mercury
HM	Heavy metal
K^+	Potassium ion
KCl	Potassium chloride
LOX	Lipoxygenase
MDA	Malondialdehyde
Mg	Magnesium
MTs	Metallothioneins
N	Nitrogen
NaCl	Sodium chloride
NADPH	Reduced form of nicotinamide adenine dinucleotide phosphate
$NaNO_3$	Sodium nitrate
Ni	Nickel
O_2^-	Superoxide anion
OH^-	Hydroxyl radical
PAs	Polyamines
Pb	Lead
PCD	Programmed cell death
PCs	Phytochelatins
POX	Peroxidase
PS II	Photosystem II
ROS	Reactive oxygen species
S	Sulphur
SO_4^2	Sulphate
SOD	Superoxide dismutase
V	Vanadium
Zn	Zinc

5.1 Introduction

Plants that can grow and reproduce in saline areas are known as halophytes. They are characterized to survive in saline areas containing high salt concentrations that are toxic to many crop plants (Flowers and Colmer 2008). These plants also have abilities for adaptation to other abiotic stresses like temperature, high light intensities, heavy metals, etc. (Lokhande and Suprasanna 2012; Walker et al. 2014). This potential of halophytes in agriculture and plant biology in terms of salt tolerance is beneficial in other abiotic stresses also (Wang et al. 2014). The main mechanism (physiological and molecular) that confers heavy metal tolerance in halophytes involves reduction in transport of heavy metals to the aerial plant parts, compartmentalization of toxic ions and synthesis of osmoprotectants (Manousaki and Kalogerakis 2011a, b) and an efficient and active antioxidant system (Zhu et al. 2004). These mechanisms have also been observed in hyperaccumulator plant. Thus the basic tolerance mechanism in halophytes and heavy metal-tolerant plants is mostly common (Shevyakova et al. 2003). According to reports of the United

Table 5.1 Sources of heavy metals

Metal	Source
Arsenic (As)	Pesticides, fungicides, geogenic/natural processes, smelting operations, thermal power plants, fuel burning
Cadmium (Cd)	Welding, electroplating, phosphatic fertilizers, pesticides, zinc smelting, waste batteries, nuclear fission plant, paint sludge
Chromium	Mining, electroplating, textile, tannery industries, industrial coolants, chromium salts manufacturing, leather tanning
Copper (Cu)	Electroplating, mining, pesticides
Lead (Pb)	Paint, pesticides, batteries, automobile emission, lead acid batteries, paints, coal burning, ceramics, bangle industry
Manganese (Mn)	Welding, fuel addition
Mercury (Hg)	Batteries, thermal power plants, fluorescent lamps, hospital waste (damaged thermometers, barometers, sphygmomanometers), electrical appliances, etc.
Nickel (Ni)	Electroplating, batteries, smelting operations, thermal power plants, battery industry
Vanadium (Va)	Spent catalyst, sulphuric acid plant
Molybdenum (Mo)	Spent catalyst
Zinc (Zn)	Refineries, brass manufacture, smelting, electroplating

Source: Gautam SP, CPCB, New Delhi

Nations Food and Agriculture Organisation and United Nations Environment Programme, about 4 million square kilometre land, 20% of all agricultural land and 50% crop land throughout the world are saline (Shabala 2012).

All living organisms require participation of some metal ions to develop and survive properly. The metals include both essential and non-essential elements along with toxic heavy metals. Those elements which have a density of more than 4 g/cm^3 are defined as heavy metals (Hawkes 1997); however chemical properties are also important factors for being a heavy metal. However over the years due to an increase of industrial activities and prolonged use of fertilizers, fungicides and pesticides, heavy metal concentration is increasing in salt marshes and other saline areas (Defew et al. 2005; Han et al. 2012b). The toxic heavy metals have adverse impact on environment and human health due to their persistence in soil for longer periods and accumulation in soil and groundwater (Wong et al. 2002). The major sources of heavy metals from industry are given in Table 5.1.

Heavy metals include both essential and non-essential elements and among non-essential Cd, Pb and Hg are toxic even at low concentrations. The European Environment Agency (2007) reported the presence of toxic levels of heavy metals (Cd, Cr, Cu, Pb and Zn). Saline areas in the eastern coastal region of China contain heavy metal-contaminated areas due to accumulation of industrial effluents, fertilizers, etc. (Shi et al. 2009; Han et al. 2012a). Paul (2017) recently reviewed the research on increasing heavy metal pollution in river Ganga of India. Presence of heavy metals like Cd, Cr, Co, Cu, Fe, Mn, Ni, Pb and Zn also has been reported by Ajmal et al. (1984) in the water and sediments of river Ganga, Prasad et al. (1989) in Varanasi-Mirzapur region, India and Singh et al. (1993) in Kanpur of Uttar Pradesh, India. However a considerable variation in heavy metals levels was observed in different sampling stations.

Mangrove (wetland halophyte) ecosystems also contain high concentration of heavy metals as they are connected to canals and rivers contaminated with industrial and agricultural effluents. Heavy metals are also polluting the urban aquatic system (Sun et al. 2016). Sediments are the basic repositories of different metals including toxic heavy metals (Zachmann et al. 2009). Lagoons and lakes from all over the world, Egypt, Portugal, Indonesia and Mexico, are polluted with heavy metals (El-said et al. 2014; Mil-Homens et al. 2014; Syakti et al. 2015; Arcega-Cabrera et al. 2015). Kamala-Kannan et al. (2008) observed that Pulicat Lake of India received mismanaged and untreated effluents from 25 industries and became polluted with heavy metals. Banerjee et al. (2017) also reported the extent up to which Chilika Lake of Orrisa, India, was contaminated mainly with Hg, Cd, Co and Pb heavy metals. The largest ship-breaking yard in the world present in the western coast in the Gujarat India produces a large amount of waste products like petroleum, its byproducts and heavy metals (Tewari et al. 2001; Srinivasa Reddy et al. 2003). Shackira and Puthur (2013) detected the higher concentration of Cd in sediments and Zn, Fe, Ni, Cu, Cr and Pb in water samples in the wetlands of Kadalundi-Vallikkunnu Community Reserve (KVCR).

Heavy metal toxicity adversely affects the plant growth and development. Cu, Cr, V and Co are redox-active heavy metals which produce ROS and cause oxidative stress. Heavy metals have an affinity for S and N atoms in amino acid side chains, thus interacting and attacking the proteins (Wei et al. 2003). Heavy metals can displace the essential cation from specific binding sites (Sharma and Dietz 2009). Among non-redox heavy metals, Pb, Cd, Ni, Al, Mn and Zn do not produce ROS directly but can induce cell death due to oxidative stress caused by generation of ROS via different indirect mechanisms. These include NADPH oxidase-dependent H_2O_2 accumulation, O_2^- formation in mitochondria and generation of hydroperoxy fatty acids (Garnier et al. 2006). These heavy metals also reduce the antioxidant pools and thus increase the ROS production (Hossain et al. 2012). This leads to disturbance in various physiological processes of plants and results in growth and yield reduction.

In this chapter we will discuss the main features of halophytic plants in relation to their growth and physiology in heavy metal-contaminated soils. We will also discuss the tolerance of halophytic plants towards salt and heavy metals and their possible interaction. In the last section, we will also discuss phytoremediation of heavy metals by use of halophytic plants.

5.2 Heavy Metal Absorption in Halophytes

Plants growing in contaminated areas absorb toxic metals along with essential nutrient elements from the soil. However metal uptake depends on the age and growth stage of the plant including metal characteristics and its bioavailability (Cacador et al. 2000). Bioavailability is influenced by the concentration of heavy metals as well as the soil characteristics like composition, acidity as well as the redox potential of the rhizosphere (Lombi et al. 2001). Root activity and root-associated microorganisms also have a direct effect on the bioavailability of heavy metals (Carvalho et al. 2006). Plants roots secrete many organic compounds into the surrounding medium which enhances the metal availability and facilitates their uptake by roots (Hall 2002; Haoliang et al. 2007). These root secretions include both low and high molecular weight compounds (Watanabe and Osaki 2002; Rascio and Navari-Izzo 2011). The low molecular weight compounds are organic acids and amino acids, while high molecular weight compounds consist of mucilages and ectoenzymes (Marschner et al. 2007). As halophytes are the habitat of saline soils, salinity also influences heavy metal speciation and uptake. Salinity positively affects the metal mobility as there is interaction of heavy metals and salt-derived ions; however there is a competition between salt-derived cations and heavy metals for absorption sites (Acosta et al. 2011). It has been reported in many studies that salinity results in higher Cd adsorption in sunflower by Li et al. (1994) and Muhlingh and Lauchli (2003) in wheat. In contrast Chai et al. (2013) reported that salinity stress resulted in reduced heavy metal accumulation in halophytic plants Spartina alterniflora. Another Halophytic plant *Atriplex halimus* when exposed to 50 μM $CdCl_2$ for 12 and 14 days along with treatment of 50 mM NaCl, KCl or $NaNO_3$ observed for reduced Cd uptake and accumulation in shoots and roots with chloride salinity and while increased Cd accumulation in leaves with $NaNO_3$ (Lefèvre et al. 2009). In salt marshes salinity stress influenced heavy metal uptake in plants (Fitzgerald et al. 2003; Kadukaova and Kalogerakis 2007).

Metal mobility is generally determined by the concentration of heavy metal and type salts in the saline media. For example, Ca^{2+} increases the mobility of metal higher than Mg^{2+}. This is due to difference in the size and atomic mass of these cations and Ca^{2+} is being more heavier has high ability for metal mobilization. In soil Cd can undergo for complex formation with chloride ions like $CdCl_n^{2n}$ ionic species, Cd^{2+} ions and $CdCl^+$ complex ($CdCl_3^-$ and $CdCl_4^2$). The mobility of these complexes is higher than free bivalent with less retaining capacity in soil and organic matter (Garcia-Miragaya and Page 1976). If soils are sulphate dominated, then its impact on metal (Cd) mobility is very less due to the reason that complex formation of SO_4^{2-}-Cd does not occur easily (Bingham et al. 1986). The absorption cadmium-chloride complex by plants is an open question because size of cadmium-chloride complex makes it less suitable for absorption. The absorption of Cd^{2+} may be easily done by non-selective transporters for Ca^{2+}.

Heavy metal uptake translocation and vacuolar sequestration can be correlated with expression levels of membrane transporters (Rascio and Navari-Izzo 2011). Park et al. (2012) reported that ABC transporters play an important role in heavy metal detoxification by transporting the phytochelated metal complex into vacuole for sequestration. However, no much data are available for transporters in halophytes. In *Suaeda salsa* Li et al. (2012) studied the scanning technique for ion-selective electrode and found different rates of cadmium fluxes at different regions of the root apex. The Cd^{2+} absorption was found maximum near the root tips in the rhizosphere (within 150 μm of the tip). Further Ca^{2+} channel blockers inhibited the Cd^{2+} influx into roots. Soil salinity has been reported to increase the bioavailability of Cd in metal-contaminated soil. After absorption, Cd enters the vascular tissue by the symplastic pathway and is transported throughout the roots (Li et al. 2012). In halophytes movement of heavy metals from roots tissue to shoot is limited due roots capacity to accumulate a higher content of heavy metals than shoots (Sousa et al. 2008; Han et al. 2012a, b). Once absorbed by plant, these heavy metals have adverse effects on growth and other physiological and biochemical processes.

5.3 Halophyte Growth Under a Metal-Contaminated Environment

Heavy metals adversely affect the growth, development and metabolic pathways in plants (Arduini et al. 1996). The growth of halophytic plants *Atriplex hortensis* and *A. rosea* was adversely affected in terms of reduced dry weight of root and shoot when grown in heavy metal-contaminated soil (Sai Kachout et al. 2009, 2015). Tolerance of root and shoot portion of halophyte *Atriplex* differed with varied concentrations of polluted soil, and the adverse impact was more on shoot growth than root growth. Heavy metals inhibited the elongation of cells thus resulting in inhibition of growth in *Atriplex* (Adid and Okamote 1993). Cadmium negatively influenced the growth of *Atriplex halimus* by decreasing dry weight, shoot length, specific leaf area (SLA) and thus relative growth rate (RGR) (Nedjimi and Daoud 2009; Redondo-Gomez et al. 2010; Mesnoua et al. 2016). Cadmium content significantly increased in both root and shoot with increasing Cd concentration in soil and 75% of absorbed heavy metal was retained by roots (Nedjimi and Daoud 2009). Mesnoua et al. (2016) reported no survival of *A. halimus* at 1350 μM Cd, while 28% of the plants could survive only up to 22 days after treatment with 400 and 650 mM Cd. The phytotoxicity threshold for shoot of *A. halimus* was between 420 and 650 mg kg^{-1} and for roots between 1100 and 2660 mg kg^{-1}. Bankaji et al. (2016) observed the reduced root and shoot growth in halophyte *Atriplex halimus* when plants were treated with cadmium or chromium for 1 month with and without NaCl (200 mM) treatment. Ghnaya et al. (2005) observed the effects of cadmium (0, 50, 100, 200 and 300 μM) on the growth of *Sesuvium portulacastrum* and *Mesembryanthemum crystallinum.* The herbaceous perennial halophyte *S. portulacastrum* was more tolerant than annual halophyte with more accumulation of Cd in root than shoot. Reductions in growth parameters under heavy metal stress also have been reported by Shevyakova et al. (2003) in *M. crystallinum* and Li et al. (2005) in *Arabidopsis thaliana*. Thus it can be concluded that reduction in plant growth under heavy metal stress may be result of direct effect due to accumulation in plant tissues and/or indirect effect due to interference with absorption and transport of water and minerals ions. Chai et al. (2013) also have observed reduction in plant growth parameters like plant biomass (root and shoot) and height in halophyte *Spartina* *alterniflora* under moderate Cd exposure (1 mm) due to the enhancement of toxic effects of NaCl on $CdCl_2$ stress. However at higher Cd stress (3 mM Cd) NaCl treatment did not increase toxic effects of Cd stress. This halophyte *Spartina alterniflora* can tolerate salt stress up to 600 mM NaCl, and their growth was very well at 100 mM NaCl (Ma et al. 2011). The possible explanation for this is not further enhancement in phytotoxicity that may be due to NaCl-induced growth stimulation of halophytic plants resulting in a dilution of toxic effect, and when combined with Cd, the phytotoxicity did not intensify (Zaier et al. 2010). Eid (2011) reported that halophytic plants including monocotyledonous and dicotyledonous *Sporobolus virginicus*, *S. patens*, and *A. nummularia* showed more tolerance in response to heavy metals when grown in soil under combined treatment of Zn, Cu and Ni (25 mg/kg soil each). In this study they observed no significant decrease in plant biomass. Under high Cd stress, plant growth is inhibited due to reduction in cell division and cell growth, damaged cell organelles and alteration in carbohydrate metabolism (Prasad 1995). High tolerance to heavy metals like Pb, Zn, Cd and Ni has also been shown by two halophytic plant species *Atriplex hortensis* and *Atriplex rosea* (Sai Kachout et al. 2012). Another halophyte *A. atacamensis* showed tolerance up to 1000 mM arsenic (As). Under high arsenic treatment, plants close their stomata efficiently to reduce loss of water and also accumulate osmoprotectants like glycinebetaine (Vromman et al. 2011). These specific features of halophytic plants make them able to grow under combined stress of heavy metal and salinity.

5.4 Heavy Metals and Physiological and Biochemical Processes

Heavy metals resulted in alteration of different metabolic processes of plants like nutrient absorption and transport, photosynthesis and respiration (Sandalio et al. 2001), cause oxidative stress and activate antioxidative defence system (Rodriguez-Serrano et al. 2006). In response to stress condition, halophytic plants also develop modifications like salt glands (trichomes) and leaf succulence.

5.4.1 Indices of Stress

The formation of malondialdehyde (MDA), the end product of oxidation of membrane lipids, is the main effect of heavy metal toxicity in plants (King et al. 2012). It is a product of polyunsaturated membrane fatty acids after decomposition (Gupta et al. 2009). The MDA content increases significantly in response to oxidative stress under abiotic stress conditions (Weber et al. 2004). Bankaji et al. (2016) reported increase in MDA levels in root tissue of halophyte *A. halimus* when irrigated with Cd, and Cu added solution, indicating oxidative damage induced changes. Shackira and Puthur (2017) reported a significantly higher MDA content in roots of *Acanthus ilicifolius* L. plants, upon treatment with Cd. They observed that maximum lipid peroxidation in the root on the 9th (27.13 μM/gDW MDA content) and 12th days (26.31 μM/gDW MDA content) (twofold) as compared to the untreated plants; beyond this, MDA content exhibited a significant decrease up to the 15th day (23.1 μM/gDW). Cd-induced oxidative stress-mediated enhanced production of MDA has reported in a mangrove, *Bruguiera gymnorrhiza* (Tao et al. 2012). Sai Kachout et al. (2015) suggested that heavy metal-polluted soil (25%, 50%, 75% and 100%, with Cu, Pb, Ni and Zn) gradually increased MDA content especially in *Atriplex rosea* than *A. hortensis*. These peroxides oxidize and damage the membranes of chloroplast. The lipid peroxidation further induces free radical chain reactions that result in oxidative stress which in turn damages the cell membrane proteins, DNA (Stocker and Keaney 2004).

5.4.2 Oxidative Metabolism

Heavy metals and saline condition cause oxidative stress by overproduction of reactive oxygen species (ROS). However these ROS are also produced naturally in the cell, but their production is significantly increased under stress conditions. ROS are extremely reactive and cause oxidative stress in plants by damaging cell proteins, lipids, carbohydrates and nucleic acids. Plants have antioxidative defence system to protect themselves from oxidative stress damage. The ROS like O_2^-, OH^-, H_2O_2 are highly reactive and can damage proteins by oxidizing specific amino acids like histidine, methionine and tryptophan. ROS weaken the membranes and make them leaky by disrupting their structure through oxidation of membrane lipids (Demidchik 2014). Mittler (2002) has also discussed in his review that some heavy metals induce oxidative stress by generating free radicals that further cause damage to various physiological processes. The redox-active metals directly produce ROS by taking part in Haber-Weiss or Fenton reaction, while non-redox-active metal ROS production is not direct; however, they induce secondary oxidative stress by disturbing enzymatic pathways. Another free hydroxyl radical (OH^-) is reported to cause oxidative stress and signal programmed cell death (Demidchik et al. 2010; Demidchik 2014). These ROS also disrupt the cell homeostasis by the activating Ca^{2+} and K^+ channels of plasma membrane, leading to Ca^{2+} influx and K^+ efflux in response to oxidative stress under heavy metal treatment (Rodrigo-Moreno et al. 2013; Demidchik 2014). Regulation of plasma membrane channels is of considerable importance in the case of halophytes as they regulate the concentration of Na and K in the cells (Flower et al. 2010).

Enzymatic and non-enzymatic antioxidant defence system is present in plants that can scavenge ROS produced due to heavy metal stress. The activation of antioxidative defence system is a very important mechanism to reduce the oxidative damage and protect plant under stress conditions (Qiu et al. 2008; Dazy et al. 2009; Kumari et al. 2010). The non-enzymatic system consists of antioxidative metabolites like glutathione (GSH), ascorbate, carotenoids, etc. In the enzymatic system, antioxidative enzyme superoxide dismutase (SOD) functions as first line of defence against cellular injury by heavy metal stress as it is the major O_2^- scavenger and generates H_2O_2 and O_2 (Grateao et al. 2005). Action of SOD results in the formation of relatively less toxic H_2O_2 (hydrogen peroxide) from O_2^- (superoxide radical). H_2O_2 must be converted to H_2O in subsequent reactions by the action of intracellular enzymes. According to Noctor and Foyer (1998), CAT, APX and GPX are considered the most important enzymes for this function (Noctor and Foyer 1998). As the rate of H_2O_2 production increases by SOD action, the H_2O_2 scavenging enzymes GPX, APX, CAT and POX activities are induced, which help in removal of H_2O_2 from the cells. The inductions of antioxidative enzymes have been reported in a number of halophytes. Shackira and Puthur (2017) recently observed higher ROS production as evidenced from increased MDA content under cadmium stress (40 μM) in halophyte *Acanthus ilicifolius* L. and also an increase in activity of antioxidative enzyme SOD. This SOD being a most important and effective intracellular metalloenzyme is ubiquitous in all cellular compartments affected by ROS-induced oxidative stress (Gill and Tuteja 2010; Lutts and Lefevre 2015). Zhang et al. (2011) reported in mangrove *Sonneratia apetala* an increase in GPX and SOD activities under heavy metals including Cd, present in the wastewater (growing medium). Two- and threefold increase in GPX activity was recorded in the roots of *B. gymnorrhiza* and *K. candel*, respectively, upon Cd treatment (Zhang et al. 2007), whereas Shackira and Puthur (2017) recorded ninefold increase in the GPX activity in *A. ilicifolius*. The higher increase in GPX activity points towards its more important role than other antioxidative enzymes (SOD, CAT and APX) in the detoxification mechanism of *A. ilicifolius* under Cd stress. Similarly higher antioxidative enzyme activity under Cd stress has been reported in other halophytic plants including *Kosteletzkya virginica* (Rui-Ming et al. 2013), *Salicornia brachiata* (Sharma et al. 2010; Wang et al. 2014) and *Spartina alterniflora* (Chai et al. 2013). Enhanced expression levels of CAT genes under Zn, Pb and their combination were observed in shoots of *Suaeda salsa* (Wu et al. 2013). They also observed the increased activities of SOD, CAT and GPX under Zn and Zn + Pb treatments.

As far as non-enzymatic antioxidants are concerned, ascorbate is a ubiquitous soluble antioxidant in plant cells, which can directly scavenge ROS and act as a reducing substrate for APX and GPXs to detoxify H_2O_2 (Mittler 2002). Shackira and Puthur (2017) reported in *A. ilicifolius* under Cd treatment that from 3 days onwards, ascorbate content exhibited an increasing trend over the control plants throughout the treatment period in the root tissue. The highest accumulation of ascorbate content was recorded on the 9th day of treatment, i.e. a 21-fold increase over the control plants reduced significantly to 15-fold 15 days after Cd treatment. The observed significant increase in the ascorbate content in *A. ilicifolius* under Cd bioaccumulation may reduce or neutralize the toxic effects of ROS produced in the root cells as was found for the halophytic plant *Kosteletzkya virginica* (Rui-Ming et al. 2013).

Glutathione (GSH) is an antioxidative metabolite that acts as a ROS scavenger by chelating metal ions (Yadav 2010). Though salinity stress also induces oxidative damage in plants, it is observed to reduce Cd-induced oxidative stress in some

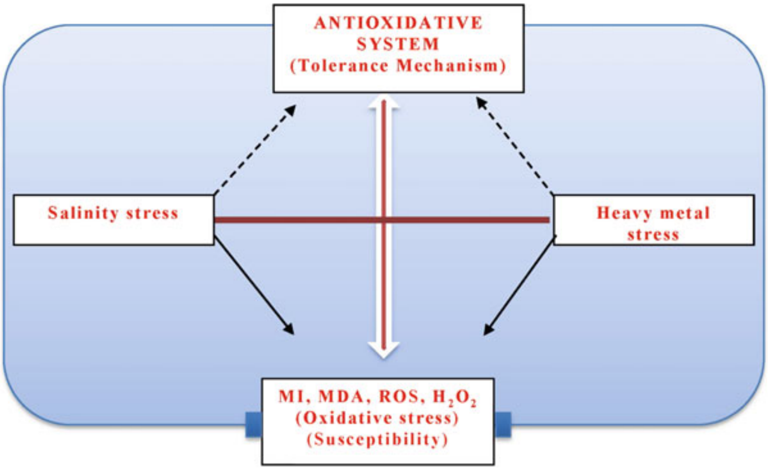

Fig. 5.1 Effect of salinity (S), heavy metal (HM) and their combination (S+HM) on oxidative metabolism in halophytic plants. Bold arrow indicates a higher effect of combined stresses (S+HM), light arrow indicates a mild effect of individual stress (S, HM) and dashed arrow indicates a lower effect of individual stress

halophytes. Han et al. (2013) reported an increase in alpha tocopherol and ascorbic acid under Cd stress in NaCl-treated plants to reduce toxic effects of Cd. Salinity stress also increased the glutathione content, and it is precursor for phytochelatin synthesis (PC) (discussed in another subsection) under heavy metal stress. PCs are involved in vacuolar compartmentalization of heavy metals and help plant to tolerate oxidative stress induced by heavy metals. Halophytic plants are able to maintain their GSH pool more efficiently under heavy metal stress as compared to glycophytic plants, so they can grow in contaminated areas.

Carotenoids as antioxidants are able to protect plants from oxidative damage and photochemical damage (Sengar et al. 2008). Carotenoids have efficiency to quench oxidizing free radicals and excited molecules of photosynthetic pigment, which causes cellular damage through oxidative stress and disrupts metabolism (Candan and Tarhan 2003). Reduction in carotenoid content under heavy metal stress was observed in *Atriplex halimus* (Mesnoua et al. 2016). However, effect on carotenoid content was less than chlorophyll (Chl) content. Carotenoid production is depending on type of heavy metal (Fargasova 1998; Singh and Tewari 2003).

Heavy metal and salinity both induce oxidative stress individually as well as in combination, but in halophytic plants, salinity stress-induced oxidative metabolism helps in coping with heavy metal stress by reducing the toxic effects (Fig. 5.1). Wali et al. (2014) confirmed reduction in oxidative stress (less H_2O_2 content) under heavy metals with NaCl treatment in *Sesuvium portulacastrum* through in vivo tissue fluorescence imaging. Han et al. (2012b) also observed that salinity protected halophytic species *K. virginica* against Cd stress via reducing oxidative stress and managing hormonal status and showed that the combined treatment of Cd an NaCl have negative synergistic effects. In Hasna et al. (2013) study pretreatments of salinity, drought and cadmium stress treatment in halophyte *Cakile maritima* resulted in reduced oxidative damage and reduction in H_2O_2 and MDA content, under salt treatment (100–800 mM NaCl), particularly at high NaCl concentrations indicating towards acclimatization response.

5.4.3 Photosynthesis

Photosynthesis is the most essential process in plants for the biomass production and yield. Photosynthetic rate decreased under heavy metal treatments (Mesnoua et al. 2016). It may be due to deteriorative effects of heavy metal on the photosynthetic pigment and their functionality (Broadley et al. 2007). Heavy metals adversely affect the photosynthetic pigment by inhibiting the reductive steps in the biosynthetic pathways; this may be due to high redox potential of many heavy metals (Chandra and Kang 2016). In many other halophytic species, decrease in photosynthetic rate (As) and stomatal conductance (gs) under Cd toxicity has been recorded in different studies (Redondo-Gomez et al. 2010; Ying et al. 2010). The reduction in As may be due to closing of the stomatal pores or decrease in density of stomatal pores, intercellular CO_2 concentration or pigment content (Cornic 2000; Flexas and Medrano 2002; Chen et al. 2011; Mesnoua et al. 2016). Heavy metals have been reported to suppress the activity protochlorophyllide reductase which converts protochlorophyll to chlorophyll (De Filippis and Pallaghy 1994). Cd toxicity caused marked changes in chloroplast ultrastructure and resulted in abnormal shape and enlarged thylakoid (Najeeb et al. 2011). One of the reasons for disturbances in chloroplast structure may be due to increased lipid peroxidation of membranes (Parmar et al. 2013) resulting from enhanced lipoxygenase (LOX) activity (Remans et al. 2010). Lipoxygenase induces oxidation of polyunsaturated fatty acid of chloroplast membrane resulting in production of free radicals. Many researchers observed increased lipid peroxidation with enhanced lipoxygenase activity in arabidopsis, barley, lupine and phaseolus under heavy metal stress (Maksymiec and Krupa 2006; Tamas et al. 2009). Heavy metal stress might disturb the proper complex between photosynthetic pigments and proteins of photosystem (Ouzounidou et al. 1997; Wang et al. 2014). Chai et al. (2013) have also observed reduction in chlorophyll content (chlorosis) in *Spartina alterniflora* leaves when exposed to Cd stress (1 and 3 mm) at 30 days of exposure.

In halophytic plant, *A. halimus*, Mesnoua et al. (2016) recorded a significant decrease in photosynthetic pigment concentration and intrinsic water use efficiency (iWUE) with higher Cd concentration in growth culture. The chlorophyll fluorescence is a non-destructive method to study the effects of abiotic stress on photosynthetic performance in vivo (Baker 2008). The chlorophyll fluorescence is the ratio of Fv/Fm and maximum quantum efficiency of PSII, and decrease in it indicates a decrease in normal photosynthesis due to photoinhibition and damage in photosynthetic apparatus. Mesnoua et al. (2016) observed that chlorophyll fluorescence (Fv/Fm) in halophyte *Atriplex halimus* affected by Cd stress at midday due to enhanced photoinhibition induced by light stress. The reduction in Fv/Fm at midday showed dynamic photoinhibition in *Atriplex halimus* at the higher light flux. This photoinhibition may be due to reduction in a number of open reaction centres as a result of saturation of photosynthesis by light. The photoprotective mechanism is increased thermal dissipation that protects photosynthetic apparatus from oxidative damage (Maxwell and Johnson 2000). However, as a consequence of Cd toxicity, the PSII disruption depends on the irradiance conditions such as 'sun reaction' and 'shade reaction'. Sun reaction during high light intensity resulted in direct damage to PSII reaction centre. On the contrary, during 'shade reaction', light-harvesting complex II (LHCII) gets disrupted due to exchange of Mg^{2+} with Cd in chlorophyll pigment and becomes the main cause of damage in PSII activity during dark phase (Kupper et al. 2007).

5.4.4 Mineral Nutrition

Mineral uptake is affected under heavy metal treatments due to interaction between nutrients and heavy metals. This interaction is also affected by other factors like presence of chelates, pH and ion concentration (Yadav et al. 2014). Symptoms of heavy metal toxicity are related to essential macro- and micronutrient interactions (Kabata-Pendias and Pendias 2001; Pal et al. 2006). Reduced Fe and Zn contents were observed under Cd stress in *Artemisia aucheri* (Vahedi 2013). They also observed an increase in N content with high Cd treatment and a decrease in P and K content at lower Cd treatments, and an enhanced content was observed at a higher concentration of treatment. This may be due to reduced plant growth at higher Cd treatment. Mesnoua et al. (2016) also observed decrease in macronutrient (K, P, Mg) and micronutrient (Fe, Mn) content under Cd stress in root and shoot tissue of *A. halimus.* Disturbed mineral nutrition under Cd stress has been reported in various halophytic plants (Ghnaya et al. 2005; Han et al. 2012a; Chai et al. 2013). Heavy metal Cd interferes with nutrient uptake by changing membrane permeability and by effecting transport process of elements. Chai et al. (2013) observed a significant reduction in K^+ content in shoot of Cd-treated halophytic plants. This may be due to interference of Cd^{2+} in K^+ nutrition up to certain limits. The reduction in micronutrient like Mn in plants may be due to interference with the expression of transporter gene or competition for transporter as suggested by Kupper and Kochian (2010).

High Na^+/K^+ ratio adversely affects the membranes protein synthesis and enzyme activities (Brady et al. 1984). Along with Cd stress, the salinity stress (NaCl) reduced Na^+/K^+ ratio significantly, so as to recover enzyme activities, protein synthesis and reduced membrane permeability (Li et al. 2010). Bankaji et al. (2016) reported in *A. halimus* halophyte that heavy metal stress resulted in unbalanced nutrient uptake by reducing translocation of ions from root to shoot. Sghaier et al. (2015) reported NaCl stress reduces the concentrations of K^+, Ca^{2+} and Mg^{2+}, while arsenic stress does not have significant impact on the concentration of these ions.

5.4.5 Osmoregulation

Harmful effects of abiotic stresses are tolerated by osmotic adjustment mechanism in plants (Flower and Colmer 2008). In order to maintain favourable water status and to prevent cellular organelles from harmful ions, these halophytic plants synthesize various osmoprotectants (Lefevre et al. 2009). The important osmoprotectants are sucrose, trehalose, proline, polyols, proline, glycinebetaine, alanine betaine, etc. (Rhodes and Hanson 1993). These substances help in plant survival and protection during stress conditions (Parida and Das 2005; Ashraf and Foolad 2007). Proline concentration in chloroplast, cytosol and vacuole has shown its significant effect on osmotic adjustment. Proline has a positive role in heavy metal stress tolerance by enhanced production and accumulation which subsequently affect the osmotic adjustment (Shevyakova et al. 2003; Chen et al. 2004; Gouia et al. 2003; Ashraf and Foolad 2007; Lefevre et al. 2009; Nedjimi and Daoud 2009; Jisha and Puthur 2014). Proline as an osmoprotectant helps in antioxidant defence mechanism, metal binding and signalling under heavy metal stress (Sharma and Dietz 2006; Majumdar et al. 2010). Shackira and Puthur (2017) recently reported a 13 times higher proline content in the root of *A. ilicifolius* under 12 day Cd treatments. Proline also helps in detoxification of oxidative stress and stabilization of proteins and acts as a signalling molecule (Szabados and Savour 2009). It was found that proline acts as ROS scavenger during Cd toxicity in *Mesembryanthemum crystallinum* a facultative halophyte (Shevyakova et al. 2003). Shackira and Puthur (2017) also reported antioxidant and osmoregulatory properties of proline in *A. ilicifolius* plants against metal stress. In many halophytic species, high proline levels have been observed during heavy metal stress (Ashraf and Harris 2004). High level of proline in *Armeria maritima*, *Deschampsia cespitosa* and *Silene vulgaris* helps in metal tolerance (Sharma and Dietz 2006). Wang et al. (2009) and Hong et al. (2000) reported that reactive oxygen species accumulation due to Hg toxicity may be scavenged by proline but decrease in proline content increases ROS levels.

Glycinebetaine (GB) is an important quaternary ammonium compound and acts as osmoprotectant under stress conditions (Ashraf and Foolad 2007). Lefevre et al. (2009) studied that the presence of cadmium also triggers glycinebetaine overproduction in *Atriplex halimus*. Subbarao et al. (2001) reported accumulation and synthesis of GB. It protects the cytoplasm from dehydration and ion toxicity and stabilizes macromolecular structure for metabolic functioning, protecting chloroplast and PSII. Moghaieb et al. (2004) reported accumulation of proline and glycinebetaine during osmotic adjustment in *S. europaea* and *S. maritime*. Pinitol a sugar alcohol also helps in osmotic adjustment and free radical scavenging (Choudhary et al. 2007). Han et al. (2012b) studies showed that NaCl and Cu increased the synthesis of these ammonium compounds in *Kosteletzkya virginica.*

Polyamines (PAs) are small aliphatic amine involved in biological functions during plant development and growth. They play a protective role in repair or prevention injuries induced by stress conditions through direct interaction with numerous biochemical and physiological pathways (Lutts et al. 2013). Lefevre et al. (2009) observed increased polyamine content such as spermine, putrescine and spermidine in response to metal stress conditions. Vromman et al. (2011) also observed increased polyamine concentration in *Atriplex atacamensis* exposed to high dose of arsenate. Moreover, increased amino acid synthesis stabilizes various macromolecules structurally and acts as potential ligands for metal ion binding (Pohlmeier 2004). Total amino acid level significantly increased in *A. ilicifolius* root plays a role in modulating Cd detoxification and removing ROS under stress conditions (Shackira and Puthur 2017).

5.4.6 Phytochelatins and Metallothionein

Phytochelatins (PCs) have an important role in tolerance of plants under heavy metal stress conditions. PCs are peptide having (g-Glu-Cys)n-Gly as basic structure where *n* may vary from 2 to 11 (Clemen 2006). PCs are synthesized by g-glutamyl cysteine dipeptidyl transpeptidase from reduced glutathione (Cobbett 2000). The expression of this is constant but may be regulated by presence of metals and metalloids at transcription and translational level (Heiss et al. 2003). For Cd stress tolerance active PC genes, PC-dependent Cd sequestration considered essential (Cobbett and Goldbrough 2002). They transport the free metal ions into the vacuoles and thus remove their toxic effects from cytosolic reactions. ABC-type transporters are involved in transport of Cd-PC complex from cytosol to vacuoles (Sanitá di Toppi and Gabbrielli 1999).

Phytochelatins may also involve in transport of metals from roots and shoots (Mishra et al. 2006). Clemens (2006) correlated the production of PCs with accumulation and transport of metal. Under stress conditions genes responsible for GSH synthesis activated and resulted in increased GSH production in *Arabidopsis thaliana* and subsequently may help in detoxification of Cd (Semane et al. 2007; Xiang and Oliver 1998). Zeng et al. (2009) observed higher PCs production in the root during Cd stress and form complex with PC contributed towards Cd tolerance in roots. Cobbett and Goldsbrough (2002) observed binding affinity of GSH and PCs with heavy metals like Cd, As, Ni, Hg. *Avicennia germinans* tolerance in polluted environment may be due to over expression of AvPCS coding gene under the high concentration of Cu^{2+} and Cd^{2+} ions (Gonzalez-Mendoza et al. 2007). Freeman and Salt (2007) showed that GSH accumulation increased the antioxidative system and growth during Ni, Cd and Co exposure. A change in GSH production and localization has been well reported under salt stress (Hasegawa et al. 2000; Rouhier et al. 2008). Glutathione (GSH) production in halophytic and metal-accumulating plants that shared a common tolerance mechanism and enhanced glutathione level (GSH) and related enzyme activities has been reported in a number of halophytes. Jha et al. (2011) reported that overexpression of glutathione transferase of *S. brachiata* enhanced salt tolerance in tobacco up to 300 mM NaCl. Similarly Lokhande et al.

(2011) also observed the role of glutathione and ascorbate for salinity tolerance by balancing redox reactions.

Metallothioneins (MTs) are cysteine-rich metal-binding proteins found in all organisms including plants, animals and microorganisms. They form complex with metals by as they have affinity with sulphur present in cysteine residue (Cobbett and Goldsbrough 2002). Carpene et al. (2007) observed that in plants, mainly four types of MTs are present based on arrangement of cysteine in protein formation. MTs are involved in various functions like detoxification of heavy metals, complexation with cytosolic Zn and metal secretion via trichomes on leaves (Coyle et al. 2002). Upregulation of genes coding for MT under heavy metal (Cd, Cu, Pb) stress has been reported in *Bruguiera gymnorhiza* (Huang and Wang (2009). Type 2 metallothionein (MT2) was mainly observed in leaves and type 1 (MT1) in roots. Chaturvedi et al. (2012) observed the upregulation in expression of type 2 metallothionein in *Salicornia brachiata* (SbMT2) by Zn and Cu but not affected by Cd. They also reported that this MT might be induced under other abiotic stresses like salinity and heat but downregulated under cold stress.

5.4.7 Plant Modifications

Halophytic plants have developed modifications like leaf succulence, salt bladders, salt glands and trichomes, for coping with high salt levels. As a secondary tolerance mechanism, halophytes excrete toxic ions through salt glands or trichomes (Lefevre et al. 2009). Salt glands and salt bladders transport ions from mesophyll cells of leaf to its surface. Here ions form crystals and are removed by wind, rain, etc. Salt glands are very specialized organs with several external cells specially designed to remove salts from tissue and salt bladders are modified epidermal hair cell. These salt bladders accumulate salt and may burst to release their salt contents outside the plants, thus preventing the plants from the deleterious effects of excess salts. All halophytes may not have specific salt glands, and they are mainly reported in plants from the families of Poaceae, Tamaricaceae, Frankenaciaceae and Chenopodiaceae. The plants with salt glands modification on leaves can excreate half of the absorbed salt to outside environment and thus help in salt tolerance (Glenn et al. 1999). It is proposed that salt-tolerant species with capability to exclude salt also possess the ability to exclude other ions including heavy metals like Zn, Cd, Cu or Pb through the phytoexcretion mechanism (Kadukova et al. 2008; Manousaki and Kalogerakis 2011a). Lefevre et al. (2009) observed in *A. halimus* L. when exposed to 50 mM cadmium chloride more than 30% of accumulated Cd was found in trichomes present at leaf surface and thus excreted about one third of the absorbed Cd through trichomes. Weis and Weis (2004) observed that heavy metal excretion in *Spartina alterniflora* was above 260 g Pb and Cu/hectare/year in contaminated area. Redondo-Gomez (2013) also observed that a number of other plants species of *Spartina* were capable to excrete heavy metals in the form of salt crystals through salt glands. *Limoniastrum monopetalum* also have shown tolerance to higher levels of Cd and Pb by excreting them as ions through salt gland (Manousaki et al. 2013). Manousaki et al. (2008) have reported that *Tamarix smyrnensis* plants excrete 3.4 times higher Cd when grown in saline soil as compared to nonsaline soils. Thus these special structures help in metal detoxification through phytoextraction.

Many halophytes do not have the special salt glands or trichomes but may have leaf succulence which is another tolerance mechanism. The accumulation of salts in the vacuoles leads to increase in succulence of plants, a common feature of halophytic plants (Flowers et al. 1977). Succulence has a dilution effect on the toxic ions thus decreasing their effects. Succulence also has a positive effect on plant water content. Succulent halophytes are distinct as they have thick leaves and stems, larger mesophyll cells and smaller intercellular spaces. In succulent leaves the mitochondria are larger in number and size as the additional process of salt compartmentalization and excretion required more energy. Salt stress-related increase in leaf succulence was observed in many halophytes (Munns and Tester 2008; de Vos et al. 2013; Katschnig et al. 2013). The expanded cells of succulent shoots provide sufficient space for accumulation of toxic ions. Wang et al. (2012) studied a heavy metal-resistant halophyte plant *Sesuvium portulacastrum* which showed leaf succulency in response to ion toxicities. According to Munns and Tester (2008), the leaf succulence trait in halophytes is mainly induced due to osmotic components of salt stress. Wang et al. (2012) reported that sodium ions are more effective in creating leaf succulence than potassium ions and the Cl^- are mainly responsible for toxicity under NaCl stress. Leaf succulence increases vacuole storage capacity and free and chelated forms of ions may accumulate in the vacuoles thus preventing the other cell organelles from the toxic effects. Hence, this mechanism helps in salinity and metal detoxification.

5.5 Phytoremediation Potential of Halophytes

Heavy metals are among the stubborn soil pollutants present in the environment. The majority of heavy metals released in environment are from industrial activities (Table 5.1). Excessive use of metal containing pesticides and fertilizers also results in accumulation of heavy metals in the soil. The concentration of heavy metals like Cd is continually increasing in the soil (Ghosh et al. 2013). The rise of heavy metal concentration in soil raises the risk of heavy metals entering in the food chain. It is therefore imperative to find ways and means of cleaning up the soil.

Phytoremediation is an eco-friendly, economic and cost-effective technology for removal of toxic heavy metals from the soil. The other traditional methods used for removal of heavy metal from soil are cumbersome and expensive. The approaches proposed for the phytoremediation of heavy metals are use of natural hyperaccumulator plants with very high metal-accumulating capacity and use of high-biomass plants. The hyperaccumulator plants generally have slow growth potential and low biomass and may accumulate only a specific element. Being hyperaccumulators, these plants ultimately result in slow and quantitatively low amounts of heavy metal extraction from the soil. In high-biomass plants, heavy metals absorbed from soil are translocated and distributed to different parts of plants, i.e. root, shoot, leaves, etc. (Chen et al. 2004; Manousaki et al. 2007). This process reduces the metal concentration in the contaminated site and also stabilizes the soil by different mechanism. These approaches are referred as ‘phytoextraction’ or ‘phytostabilization’. The selection of plant species for phytoremediation is on the basis of type and concentration of heavy metal contamination in soil. Phytoextraction involves the uptake and subsequent accumulation of toxic substances from the soil/environment into plant biomass. Phytostabilization takes place by decreasing the mobility of toxic substances in soil, for example, decreasing the leaching of toxic substances from the soil. Both phytoextraction and phytostabilization can be used at highly affected sites with plants able to tolerate high concentration of toxic heavy metals/salts. For this plant may or not be a hyperaccumulator. Majority of plants used in environmental restoration are glycophytic, and metal phytoremediation by halophytic plants has been less studied. Halophytic plants generally have special mechanisms for salt uptake and tolerance, and thus possibilities exist for heavy metal uptake and tolerance also (Flowers et al. 2010; Taamalli et al. 2014; Wang et al. 2014). Moreover, it has been reported that salinity stress can increase the heavy metal mobility in soil and also their translocation from root to shoot (Acosta et al. 2011; Manousaki et al. 2014). Now researchers are focusing on the halophytes for phytoremediation, and some researchers have used halophytic plants for phytoremediation of heavy metal-contaminated saline soil (Zaier et al. 2010; Milic et al. 2012; Manousaki et al. 2014; Santos et al. 2015; Christofilopoulos et al. 2016; Santos et al. 2017). Anjum et al. (2014) have suggested that halophytic plant may survive better on heavy metal-contaminated soil and can offer greater potential for phytoremediation. The tolerance to heavy metal of halophytes may be related to their salt tolerance characteristics (Wang et al. 2014). This could be because halophytes and heavy metal-tolerant plants have many common features (Shevykova et al. 2003; Van Oosten and Maggio 2015). Based on these studies, it has been proposed that halophytic plants are naturally better adapted to heavy metal stress, than glycophytic plants (Manousaki and Kalogerakis 2011a, b; Wang et al. 2014).

Researchers have reported many halophytic species suitable for phytoextraction and phytostabilization under heavy metal- and salinity-contaminated soils, e.g. *A. halimus* (Manousaki and Kalogerakis 2009), *S. portulacastrum* (Ayyappan et al. 2016), *S. alterniflora* (Nalla et al. 2012) and *T. Africana* (Santos et al. 2017). Lutts et al. (2004) observed that *Atriplex halimus* showed accumulation of 830 mg kg^{-1} Cd and 440 mg kg^{-1} Zn in shoot tissue and can be considered as a good candidate for phytoextraction purpose. However, Manousaki and Kalogerakis (2009) reported that metal accumulation capacity in shoots of *A. halimus* was relatively low, but its high biomass and growth rate may be the positive factors for considering this halophyte suitable for phytoextraction. Ghnaya et al. (2005) also have reported that *S. portulacastrum* and *M. crystallinum* were effective for Cd phytoextraction from saline soils and among these two species, *S. portulacastrum* was found more tolerant to Cd stress than *M. crystallinum*; although the tolerance levels varied, *S. portulacastrum* was significantly more tolerant to Cd than

M. crystallinum. However Thomas et al. (1998) have also reported that the halophyte *M. crystallinum* is more tolerant to Cu toxicity than glycophyte *A. thaliana*. Zaier et al. (2010) have reported that the *S. portulacastrum* when grown in a Pb-containing nutrient solution accumulated more Pb in the shoots (3.4 mg g^{-1} DW) as compared to *Brassica juncea*. Mazharia and Homaeed (2012) compared the capacity of halophytic and hyperaccumulator plants for Cd phytoextraction and found that halophyte *Chenopodium botrys* has six times higher capacity to export Cd (180 g Cd ha^{-1}) than hyperaccumulator *Noccaea caerulescens*. Another halophytic plant *Leptochloa fusca* showed high accumulation of Zn (335 mg g^{-1} shoot DW) (Eisa and Eid 2011). Amari et al. (2016) reported that *M. crystallinum* is more tolerant to nickel than *B. juncea* when grown on Ni-polluted soils and there is higher Ni accumulation in aboveground part which could be contributing towards tolerance. Thus this halophyte *M. crystallinum* could be used for phytoextraction of Ni-polluted sites due to its capacity to accumulate moderate amounts of Ni in aboveground tissues. Metal-accumulating capacity has also been reported in various other halophytic plants like *Salsola soda*, *Salicornia europaea*, *Suaeda maritima*, etc. Different halophytic species have different phytoremediation potential based on accumulation and translocation mechanisms. Based on previous literature, the halophytic plants found suitable for Pb phytoremediation are *Aster tripolium*, *Salicornia europaea*, *Chenopodium album* and *Atriplex vesicaria* (Fitzgerald et al. 2003; Khodaverdiloo and Taghlidabad 2013). Salt marsh plant *Triglochin striata* was observed as a phytostabilizer as it has potential to limit metal in belowground tissue like roots and rhizomes. On the other hand, *Phragmites australis* was reported as a phytoextractor as it accumulates metal in aboveground tissues, while some halophytes like *Juncus maritimus* and *Spartina patens* accumulate heavy metals in both root and shoot tissues (Almeida et al. 2011). The phytoremediation potential of halophytes is mainly due to the plants ability to accumulate and retain in their tissue by activating heavy metal detoxification mechanism (Sousa et al. 2008). It has been proposed that halophytic plants use a non-selective salt tolerance mechanism for detoxification and they can sequester harmful toxic ions into vacuoles and/or salt glands/trichomes (Shevyakova et al. 2003). Salt glands help to excrete toxic ions to outside environment through leaves (Lefevre et al. 2009). These salt glands are not always specific for Na and Cl but may take up heavy metals also, and these heavy metals are concentrated and excreted as a possible metal detoxification mechanism on the surface of leaves (Kadukova et al. 2008; Lefevre et al. 2009). Halophytic plants *Atriplex halimus* and *Tamarix smyrnensis* were reported to have salt gland on their leaf surface which accumulate Cd and Pb indicating their phytoextraction potential (Manousaki et al. 2008; Manousaki and Kalogerakis 2009). Based on present literature, a list is given in Table 5.2 for halophytic plants used for phytoremediation.

Table 5.2 Examples of halophytic plant species used for the purpose of phytoremediation

Plant species	Phytostabilization/ phytoextraction/ phytoexcretion of heavy metals	References
Sesuvium portulacastrum	Cd, Ni, Cr, P and Zn	Ghnaya et al. (2007), Zaier et al. (2010), Lokhande et al. (2011), Mnsari et al. (2015) and Ayyappan et al. (2016)
Mesembryanthemum crystallinum	Cd	Ghnaya et al. (2007)
Halimione portulacoides	Cd, Cu, Pb, Zn, Co and Hg	Andrades-Moreno et al. (2013), Castro et al. (2009) and Sousa et al. (2008)
Spartina maritima	As, Cd, Cu, Fe, Mn, Pb and Zn	Cambrolle et al. (2008), Manousaki et al. (2008) and Reboreda and Caçador (2008)
Spartina densiflora	As, Cu, Fe, Mn, Pb and Zn	Cambrolle et al. (2008)
Spartina alterniflora	Cu	Chai et al. (2014)
Spartina patens	Zn, Cu and Ni	Eid and Eisa (2010)
Arthrocnemum macrostachyum	Cd and Cr	Redondo-Gomez et al. (2010)
Triglochin maritima	Hg	Castro et al. (2009)
Juncus maritimus	Hg, Al, Cd, Cr, Cu, Fe, Mn, Ni, Cu and Zn	Almeida et al. (2006) and Castro et al. (2009)
Avicennia marina	Cu, Zn Cd	Hagemeyer and Waisel (1988) and Lutts et al. (2004)
Armeria maritima	Cu, Zn Cd	Hagemeyer and Waisel (1988) and Lutts et al. (2004)
Atriplex halimus, Atriplex halimus subsp. Schweinfurthii	Cd, Pb and Zn	Lefevre et al. (2009), Lutts et al. (2004), Manousaki and Kalogerakis (2009) and Nedjimi and Daoud (2009)
Atriplex nummularia	Zn, Cu and Ni	Eid and Eisa (2010)
Atriplex lentiformis, A. undulate	Zn, Cu, Pb, and Cd	Eissa (2015)
Aster tripolium	Cu and Pb	Fitzgerald et al. (2003)
Commelina communis	Cu	Wang and Zhong (2011)
Elsholtzia splendens	Cu	Jiang et al. (2008)
Sarcocornia perennis	Fe, Mn and Hg	Castro et al. (2009) and Lilebo et al. (2010)
Tamarix smyrnensis	Pb and Cd	Kadukova and Kalogerakis (2007), Kadukova et al. (2008) and Manousaki et al. (2008)
Tamarix aphylla	Cu, Zn and Cd	Hagemeyer and Waisel (1988) and Lutts et al. (2004)
Sporobolus virginicus	Zn, Cu and Ni	Eid and Eisa (2010)
Salicornia europaea	Cd	Ozawa et al. (2009)
Salicornia perennis	Cd, Zn, Cu, Co	Lefevre et al. (2010)
Salicornia brachiata	Cd, Ni, AS	Xu et al. (2010)

(continued)

Table 5.2 (continued)

Plant species	Phytostabilization/ phytoextraction/ phytoexcretion of heavy metals	References
Salicornia ramosissima	Cd	Pedro et al. (2013)
Suaeda salsa	Pb, Zn	Wu et al. (2013)
Phragmites australis	Cd	Nunes da Silva et al. (2014)
Acanthus ilicifolius	Cd	Shackira and Puthur (2017)

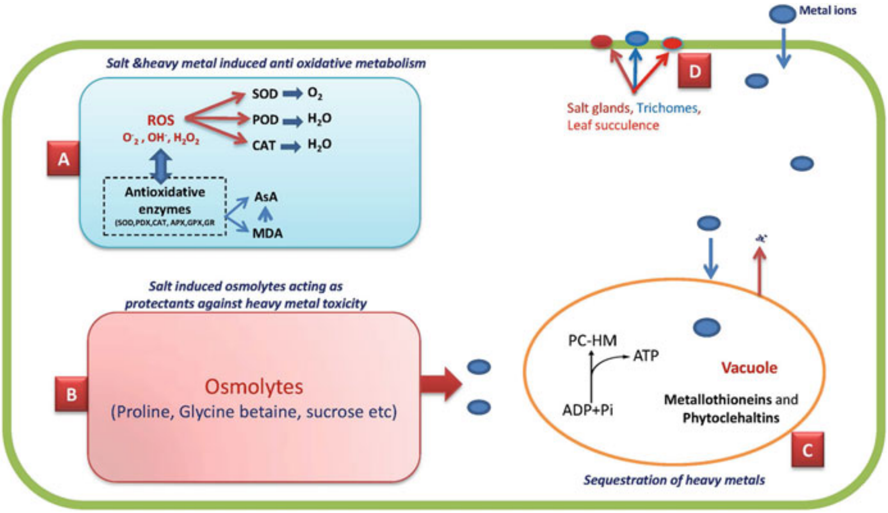

Fig. 5.2 Mechanisms of heavy metal tolerance in halophytes

5.6 Conclusion and Future Perspective

Adaptive mechanisms that allow halophytes to survive in highly saline conditions may not be exclusive to salts only but may also confer tolerance to toxic ions like heavy metals. Halophytes have a better antioxidative metabolism as compared to glycophytes. Antioxidative metabolism prevents the heavy metal-induced oxidative stress and thus maintains integrity of cellular organelles. The photosynthetic rate is maintained in halophytes under heavy metal stress as compared to glycophytes. In Fig. 5.2, various mechanisms of tolerance in response to heavy metal for halophytic plants have been shown. Osmoprotectants like proline and glycine betaine may also contribute to tolerance to heavy metals, as they also result in secondary water stress. Morpho-physiological adaptation like salt glands, trichomes and leaf succulence helps in heavy metal excretion and accumulation in leaves. Halophytes are also a suitable candidate for heavy metal phytoremediation depending upon the specific properties like large biomass production, deep rooting system and heavy metal accumulation in different parts of plant. Most of the halophytes have been found to be suitable for phytoextraction and phytostabilization.

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Chapter 6

Oxidative Stress and Antioxidant Defence Under Metal Toxicity in Halophytes

Anita Kumari, Vinod Goyal, and Sunita Sheokand

Contents

Abstract Halophytes are diverse group of plants with tolerance to high salinity due to specific mechanisms of salt uptake and tolerance. Saline areas are being affected by heavy metal pollution also due to many reasons like industrialization, etc. in the recent years. Use of halophytic species for heavy metal remediation is of significant importance as these plants are naturally present in soils characterized by excess of

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salts. They possess specific mechanisms for uptake, detoxification and extrusion of salts. These mechanisms could help in heavy metal remediation also. Halophytes are constitutively better equipped to cope with oxidative stress as reactive oxygen species (ROS) are overproduced when plants are exposed to high salt concentrations. Halophytes have higher antioxidant metabolism compared with glycophytes. Heavy metal stress also results in overproduction of ROS. ROS scavenging proteins are particularly critical for plants under salt and heavy metal stress to maintain redox homeostasis. Sulphur metabolism also plays a role in heavy metal detoxification. Heavy metal accumulators have increased cysteine biosynthesis induced by heavy metals. Highly reactive heavy metals such as Cr, Cu and Fe are directly involved in redox reactions and generate ROS, while the redox inactive heavy metals can induce indirect ROS through decrease in antioxidant activity. The oxidative damage caused by overproduction of ROS in heavy metal-contaminated soils of halophytes will be discussed. The antioxidant metabolism of halophytes in terms of heavy metal tolerance also will be discussed as some adaptations to these stresses are common. The role of osmolytes, phytochelatins and metallothionein in heavy metal tolerance will also be discussed.

Keywords Antioxidants · Halophytes · Heavy metals · Osmoprotectants · Oxidative metabolism · Salinity and sulphur metabolism

6.1 Introduction

Halophytic plants are a group of plants that can grow and survive under high salinity conditions. These plants need saline habitat to complete their life and grow naturally on saline soil (Rozema et al. 2013). According to Flowers and Colmer (2008), halophytes normally survive at 200 mM NaCl and can tolerate even higher salt concentrations. Halophytic plants can be grown on soil and water that are unsuitable for glycophytes (Flowers et al. 2010). Plants are exposed to different kinds of stresses like drought, salinity, high temperature, heavy metals, toxic ions, etc., and the major reason behind these toxicities may be human activities or natural abundance. Heavy metals are of more concern because they are nondegradable and have a longer half life, i.e. persist for longer time in the environment. The trace elements which have a density of more than 4 g/cm^3 are defined as heavy metals (Hawkes 1997). Trace elements of periodic table include both essential and non-essential elements along with toxic heavy metals. For example, copper is an essential micronutrient involved in various physiological reactions via Cu^{2+} enzymes, while cadmium is a non-essential heavy metal causing the disturbances in cell functioning. Cd^{2+} ions interact with thiol groups of cell constituents and result in growth reduction by disturbing photosynthesis, ion and water transport as well as enzymatic activities. Heavy metals not only affect the plant growth and productivity but also the human health (Lopez-Climent et al. 2011). High levels of heavy metals result in the oxidative stress through the production of reactive oxygen species (Mittler 2002). ROS react with other cellular components like lipids, proteins, photosynthetic pigments and DNA which results in membrane damage, lipid peroxidation, degradation of metabolites, inactivation of enzymes and even cell death (Nagarani et al. 2012). Heavy metals may interact with proteins through affinity for S and N atoms in side chains of amino acids (Wei et al. 2003). They can also bind with the sulphydryl groups of enzymes and structural proteins. Heavy metals cations can displace an essential cation in specific binding sites (Sharma and Dietz 2009).

Halophytes are many times exposed to heavy metal toxicity particularly in the mangrove ecosystem. They act as a major sink for a number of pollutants from nearby drainage and rivers of mangrove-growing area (MacFarlane and Burchett 2001). Heavy metal pollution of mangrove ecosystem in India is due to urban and agricultural runoff, industrial waste, boating and recreational activities including chemical spills, leachates from domestic garbage dumps, sewage water treatment plants and mining, etc. (Lokhande et al. 2011). Many estuary salt marshes and large area of oasis farmlands of arid and semiarid regions are affected by both salinity and heavy metal stress (Defew et al. 2005; Han et al. 2012). In India, ship scraping industry also causes pollution by producing waste products like crude petroleum and heavy metals as byproducts (Tewari et al. 2001; Srinivasa Reddy et al. 2003). Banerjee et al. (2017) reported that Chilika Lake of Orrisa (India) is polluted by heavy metals like Hg, Cd, Co and Pb. Shackira and Puthur (2013) detected significantly higher concentrations of Cd than other heavy metals in the sediment and the water samples in Kadalundi-Vallikkunnu Community Reserve wetlands. Mandal et al. (2009) have reported arsenic pollution in West Bengal (Sunderban region) due to industrial effluents, agricultural runoff and sewage discharge.

The halophytic plants possess morphological, anatomical and physiological adaptations allowing them to survive in soils with high concentrations of salinity (Flowers and Colmer 2008). These adaptations include ion compartmentalization, osmotic adjustment, ion transport and uptake, redox energy balance, activation of antioxidative defence system, succulence, salt accumulation or extrusion (Lokhande and Suprasanna 2012). These adaptations help halophytic plants to cope with other abiotic stresses like temperature, high light intensities, heavy metals, etc. (Lopez-Chuken and Young 2005; Ruan et al. 2010; Lokhande and Suprasanna 2012; Walker et al. 2014; Panda et al. 2017). There are some specific adaptations to maintain oxidative status in halophytic plants as compared to glycophytic plants to tolerate saline environments (Ellouzi et al. 2011). A better antioxidant system enables them to tolerate heavy metal stress also. Therefore, it has been proposed that heavy metal-accumulating plants and halophytic plants share a number of common processes (Shevyakova et al. 2003). Oxidative metabolism-induced tolerance mechanism has been studied under heavy metal stress in halophyte *Salicornia brachiata* (Sharma et al. 2010), *Kosteletzkya virginica* (Han et al. 2012, 2013), *Atriplex halimus* L. (Bankaji et al. 2016) and *S. maritima* (Panda et al. 2017). Halophytes have been proposed as potential candidates for removal of heavy metals from contaminated soil due to common tolerance and detoxification mechanisms (Manousaki and Kalogerakis 2009). Ruan et al. (2008) reported that perennial halophyte *Kosteletzkya virginica* could be utilized for revegetation of salt-affected coastal tidal flats. These studies further confirm that the salt-tolerant species can better adapt to adverse environmental conditions including heavy metal stress (Chai et al. 2013; Lokhande et al. 2011). In general, plants have different mechanism to control heavy metal uptake. These include chelation and sequestration of heavy metal ions by specific ligands to maintain them at low and lesser harmful levels in the cell cytosol (Sbartai et al. 2012). The main chelating substances are phytochelatins (PCs) and metallothioneins, and this ubiquitous detoxification strategy has been described in a number of plants (Yadav 2010).

In the present chapter we will discuss the heavy metal-induced oxidative stress and their interaction with salinity in halophytes and how the antioxidant defence system helps in detoxification of heavy metals. Sulphur metabolism and osmotic adjustment in halophytes in response to heavy metals will also be discussed in detail.

6.2 Oxidative Metabolism in Halophytes Under Heavy Metal Stress

The halophytic plant displays a cascade of events upon heavy metal stress exposure that leads to disturbances in metabolic behaviour. These events include water deficit-induced stomatal closure, limited CO_2 availability, over-reduction of ETC chain in chloroplast (photosynthesis) and mitochondria (respiration) and generation of ROS (Lokhande and Suprasana 2012) causing oxidative stress. Heavy metal stress causes the imbalance of the redox metabolism and leads to oxidative stress (Schutzendubel and Polle 2002; Mittler et al. 2004). Oxidative metabolism will be studied under following subheadings.

6.2.1 Reactive Oxygen Species (ROS) Production

The overproduction of ROS like superoxide anion (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH^-) resulting in oxidative stress is among the initial heavy metal toxicity responses (Shahid et al. 2014). ROS are highly toxic, and their high concentration can oxidize cell constituents like DNA, carbohydrates, proteins and lipids (Mittler 2002; Mittler et al. 2010). The first step during the O_2 reduction is production of relatively short-lived, not readily diffusible hydroperoxyl (HO_2^-) and superoxide anions (O_2^-). Superoxide anions are very active and can oxidize specific amino acids like histidine, methionine and tryptophan (Lutts and Lefevre 2015). Further it may undergo spontaneous or enzymatic dismutation to produce H_2O_2; otherwise it may interact with plastocyanin or cytochrome f and reduce them, resulting in a superoxide-mediated cyclic electron flow around PS I (Hormann et al. 1993). H_2O_2 is a natural toxic plant metabolite, produced as a product of photorespiration. Both O_2^- and H_2O_2 cause membrane damage by attacking membrane lipids (Willenkens et al. 1995). The biological toxicity of H_2O_2 is due to oxidation of SH-group which is enhanced by a metal catalyst. Hydroxyl radical

(OH^{-}) is the most toxic ROS, due to high affinity for the biological molecules which results in oxidative damage to proteins and nucleic acids and induces lipid peroxidation (Demidchik 2014).

Among the heavy metals, Cu, Cr, Fe^{2+}, V and Co produce ROS (O_2^{-}, H_2O_2, OH^{-}) via Fenton-type reactions. Different researchers documented cellular injury by this type of mechanism like for Fe (Halliwell and Gutteridge 1986), copper (Li and Trush 1993), vanadate (Shi and Dalal 1993) and Cr (Shi et al. 1993). The other heavy metals also known as non-redox metals generate oxidative stress by indirect mechanisms, such as NADPH oxidase-dependent H_2O_2 accumulation and O_2^{-} formation in mitochondria and hydroperoxy fatty acids (Garnier et al. 2006). These non-redox heavy metals can cause indirect production of ROS through depletion of antioxidant pools (Hossain et al. 2012).

Han et al. (2013) reported nearby sixfold increase in O_2^{-} and threefold increase in H_2O_2 content in Cd (5 μM)-treated *K. virginica* plants; however salinity along with Cd reduced the toxic effects of Cd. H_2O_2 content increased with heavy metal treatments of Cd^{2+}, Ni^{2+} and As^{3+} in *Salicornia brachiata* (Sharma et al. 2010). A 1.5-fold increase with Cd (200 and 300 μM), 2.5-fold with Ni (200 μM) and no survival with 200 μM As^{3+} were reported. Panda et al. (2017) reported that levels of O_2^{-} go parallel with the SOD activity, i.e. with increase of superoxide O_2^{-} concentration, the SOD activity also increases indicating utilization of SOD in dismutation. Increase in ROS under heavy metals has been observed in halophytic plants *Kandelia candel* (Zhang et al. 2007), *Avicennia marina* (MacFarlane and Burchett 2001; Caregnato et al. 2008) and *Spartina alterniflora* (Chai et al. 2013). However Panda et al. (2017) reported that high concentration of salt (600 mM NaCl) and NaCl in combination with arsenic (As) resulted in a decline in O_2^{-} and H_2O_2 content in halophyte *S. maritima* seedlings. Vromman et al. (2016) also reported no significant changes of H_2O_2 level in *A. atacamensis* subjected to salinity and As treatments.

ROS have been considered as dangerous molecules and their levels need to be kept as low as possible. However many studies have proposed that ROS also play an important role in the plant defence system against pathogens (Bolwell et al. 2002) and PCD (programmed cell death) (Fath et al. 2002; Demidchik et al. 2010; Demidchik 2014) and also act as intermediate signalling molecule to regulate expression of genes (Neill et al. 2002; Vranova et al. 2002). In the view of multiple functions of these ROS, it is necessary to regulate their level in cell but not to eliminate them from cell completely. The role of H_2O_2 as a signalling molecule under abiotic stress including heavy metals has been reported by many researchers (Dat et al. 2000; Sexena et al. 2016). Salinity stress-induced ROS production in halophytes may be compensated by various adaptations including ion compartmentalization, strong antioxidant defence system, etc. Heavy metal stress also increases ROS production, and saline adaptation further helps them to cope with heavy metal stress. Sharma et al. (2010) reported reduced level of ROS in *Salicornia brachiata* plants treated with both heavy metal and salinity as compared to the plants treated with heavy metals only. Han et al. (2013) also reported no significant increase in O_2^{-} and H_2O_2 in *K. virginica* plants under salinity and salinity along with Cd treatments. ROS content decreased significantly in *S. maritima* when treated with high salinity in combination with heavy metal (As+NaCl), suggesting the presence of active and efficient ROS scavenging system present in this halophyte. The decreased level of H_2O_2 under combined treatment of As+NaCl may be attributed to the cumulative effects of both enzymatic and non-enzymatic antioxidants (Panda et al. 2017). On the other hand, Rangani et al. (2016) reported that significant levels of H_2O_2 in *S. maritima* under heavy metal (As) and/or salinity stress may be demonstrating its role in stress signalling.

6.2.2 Membrane Damage

High concentration of ROS in the cellular environment damages the cell structure and biomolecules by affecting cell membrane lipids, proteins and DNA resulting in lipid peroxidation (Schickler and Caspi 1999; Baccouch et al. 2001). Extent of lipid peroxidation is measured in terms of MDA content, a decomposition product of polyunsaturated fatty acids. ROS causes elimination of hydrogen from unsaturated fatty acids which lead to the formation of lipid radical. Lipid structure is destroyed due to a cascade of cyclic reactions leading to respective and lipid acid aldehydes and results in membrane deterioration. The lipid peroxidation leads to dimerization and polymerizations of membrane proteins which is considered to be most damaging to cell membranes (Demidchik 2014). This causes irreversible damage to cell membrane proteins and lipids and makes them leaky and alters their functioning (da Silva 2010). Shackira and Puthur (2017) observed significant increase of twofold in MDA content in roots of halophyte *Acanthus ilicifolius* L. plants, upon treatment with Cd. Chai et al. (2013) reported significant increase in MDA content and membrane electrolyte leakage when exposed to Cu^{2+} more than 200 mg kg^{-1} soil in halophyte *Spartina alterniflora* (Poaceae). Similarly an increase of lipid peroxidation under heavy metal stress condition has been reported by many workers like Tao et al. (2012) in mangrove, *Bruguiera gymnorrhiza*, Han et al. (2013) in *K. virginica* and Sai Kachout et al. (2015) in *A. rosea.* Bankaji et al. (2016) reported 1.6-fold and 5.9-fold increased MDA in root tissue of halophyte *Atriplex halimus* when irrigated with Cd (400 μM) and Cu (400 μM) solution, respectively, indicating oxidative damage-induced lipid peroxidation. Addition of 200 mM NaCl to the irrigation medium along with Cu^{2+} and Cd resulted in significantly lower values of MDA, i.e. NaCl treatment showed their protective effect in reducing oxidative damage caused by heavy metals. Similarly Han et al. (2012) also reported that the presence of NaCl reduced to some extent the oxidative stress-induced membrane damage in cadmium-treated plants that was manifested by less lipid peroxidation and protein oxidation. 50 mM NaCl treatment in the nutrient solution for 2 weeks had no influence on MDA content as compared to control plants in halophyte *K. virginica*, but an increase was observed with Cd treatment of 5 μM (Han et al. 2013). A reduction of about 25% in MDA content was observed when Cd treatment (5 μM) was given along with NaCl (50 mM), showing positive effects of exogenous NaCl on plant responses to Cd^{2+}. This effect has been reported in other halophytes

A. halimus and *Spartina alterniflora* also (Lefevre et al. 2009; Chai et al. 2013). The effect may be due to the dilution caused by salinity-induced growth stimulation in halophytes at moderate concentrations. There are many reports on significant increase in the MDA content in different plants when exposed to high salinity or As stress (Shaheen et al. 2013; Zhao et al. 2010; Tripathi et al. 2012). However Panda et al. (2017) reported no significant change in lipid peroxidation levels (MDA content) in *S. maritima* plants under salinity, As or combination of both. The total protein content and carbohydrate content in shoot parts of *S. salsa* seedlings upon zinc exposure were significantly decreased showing the upregulated protein biodegradation (Wu et al. 2013).

6.3 Antioxidant Defence System in Halophytes Under Heavy Metal Stress

Salinity- and heavy metal stress-induced oxidative damage is controlled by antioxidative defence system. This system is composed of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT) and enzymes of ascorbate-glutathione cycle including ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR) and antioxidative metabolites like ascorbate, glutathione, carotenoids, etc. The antioxidative defence system counteracts or neutralizes the harmful effects of ROS (Foyer and Noctor 2005; Asada 2006; Lokhande et al. 2011; Dar et al. 2017). Plants tend to increase phytochelatins synthesis (specific metal-binding proteins), glutathione and polymers of glutathione (precursors for phytochelatins synthesis) as a protective mechanism under heavy metal stress (Tripathi et al. 2007; Begum et al. 2016). Understanding the detoxification mechanism adopted by plants to alleviate or reduce oxidative stress is the key information to further manipulate heavy metal tolerance in halophytic plants. There is difference in spatial localization and biochemical properties of different antioxidative enzymes and metabolites. They also vary in terms of gene expression, and all these properties give a flexible and versatile defence system to cope with excess ROS levels (Vranova et al. 2002). Antioxidant enzymes reduce oxidative stress by interrupting the cascades of uncontrolled oxidation of membrane lipids by oxygen free radicals. Antioxidative enzymes may remove, neutralize or scavenge ROS and their intermediates (Foyer and Noctor 2005). A direct correlation among enzymatic and non-enzymatic antioxidant defence system capacity and salinity stress tolerance has been observed in several halophytic plant species like *Crithmum maritimum*, *Crithmum maritime*, *Sesuvium portulacastrum*, *Plantago* genus and *Mesembryanthemum crystallinum* (Ben Amor et al. 2005; Jitesh et al. 2006; Sekmen et al. 2007; Ashraf 2009; Lokhande et al. 2010, 2011). A well-expressed antioxidative defence mechanism in halophytes also helps in overcoming the heavy metal-induced oxidative stress. The various studies

Table 6.1 Examples of halophytic plant species showing the antioxidant defence system in response to heavy metal stress

Halophytic plant species	Antioxidant response	Heavy metal	Reference
Salicornia brachiata	CAT, SOD activities increased	Cd^{2+}, Ni^{2+} and As^{3+}	Sharma et al. (2010)
Suaeda salsa	SOD, CAT, GPX activities increased	Zn, Pb+Zn	Wu et al. (2013)
Suaeda salsa	POX activities increased	Zn	Wu et al. 2013
Suaeda salsa	CAT activities increased	Pb	Wu et al. (2013)
Atriplex halimus	CAT, APX, GPX activities decreased	Cd^{2+}	Bankaji et al. (2016)
Atriplex halimus	CAT, APX, activities decreased and GPX activity increased	Cu^{2+}	Bankaji et al. (2016)
Atriplex halimus L.	POX activity increased	Cd+Pb	Manousaki and Kalogerakis (2009)
Kosteletzkya virginica	Increase in GSH, α-tocopherol and ascorbic acid synthesis, increase in GR activity	Cd^{2+}	Han et al. (2013)
Kandelia candel,	SOD activity decreased, CAT activity increased	Pb, Cd, and Hg	Zhang et al. (2007)
Kandelia candel	Increased POX activity	Pb, Cd, and Hg	Schutzendubel et al. (2002)
Bruguiera gymnorrhiza	SOD activity decreased	Pb, Cd, and Hg	Zhang et al. (2007)
Avicennia marina	Increased POX activity	Cu, Pb and Zn	MacFarlane and Burchett (2001)
Avicennia marina	Increase in GPX activity	Zn, Cu and Pb	Caregnato et al. (2008)
Suaeda maritima	SOD activity decreased	As	Panda et al. (2017)
	CAT activity increased		

on the antioxidant response under heavy metal stress have been listed in Table 6.1. The role of antioxidative enzymes and metabolites are discussed below:

6.3.1 *Superoxide Dismutase*

Superoxide dismutase (SOD) (EC 1.15.1.1) is a metalloprotein and occurs universally in all plants in aerobic conditions. It acts as primary/first-line defence against ROS-induced damages (Liang et al. 2003). It catalyses the dismutation of O_2^- to H_2O_2 and molecular oxygen (Bowler et al. 1992; Hernandez et al. 2000; Gratao et al. 2005). It acts as a key antioxidative enzyme in aerobic cells as its activity determines the concentration of Haber-Weiss reaction substrate, i.e. superoxide radical and hydrogen peroxide (Sabarinath et al. 2009; Gill et al. 2015). This dismutation reaction is 1000 times faster than the spontaneous dismutation (Gill and Tuteja 2010; Das and Roychoudhury 2014). In plants three classes of SOD have been reported so far based on the metal cofactor. These are di-nuclear Cu/Zn SOD, mononuclear Fe SOD and Mn SOD (Perry et al. 2010). In plants Cu/Zn SOD isoforms are found primarily in the cytosol and chloroplast, Mn SODs are located in the matrix of mitochondria and peroxisomes and Fe SODs are located in the chloroplast (Racchi et al. 2001; Alscher et al. 2002). The upregulation of SOD activity in response to various stresses plays an important and crucial role in alleviation of oxidative stress for the plant survival (Boguszewska et al. 2010). SOD activity increased with increase in production of ROS (Abedi and Pakniyat 2010). SOD activity has been observed to increase in number of halophytes when exposed to different heavy metals.

Sharma et al. (2010) reported in halophytic plant *Salicornia brachiata* a twofold increase in SOD with Cd^{2+} (300 μM) and Ni^{2+} (300 μM) and 1.2-fold with As^{3+} (100 μM) treatment proving that SOD acts as a first line of defence. In *K. virginica* plants, Cd (5 μM)-induced SOD activity by twofold as compared to control plants and NaCl alone had a slight promotion in total SOD activity (Han et al. 2013). A twofold increase in SOD activity was observed in plant treated with both Cd and NaCl. This can be correlated with control of oxidative stress produced at cellular level under salt and Cd stress (Hernandez et al. 2001). Similar enhanced activity of SOD under increased concentration of Cd has been reported in halophytic plants like *Kandelia candel* and *Bruguiera gymnorrhiza* (Zhang et al. 2007), *Spartina densiflora* (Redondo-Gomez et al. 2011), *Salicornia brachiata* (Wang et al. 2014), *Atriplex halimus L.* (Mesnoua et al. 2016). da Silva (2010) reported slight increase in SOD activity in C3 halophyte limited to coastal salt marshes *Halimione portulacoides* up to 30 PSU of NaCl and 200 μM Zn treatment. Higher salinities (40 and 50 PSU) result in impaired ROS scavenging system with decreased SOD activity. Transgenic plants overexpressing SOD genes were found tolerant to oxidative stress in maize (Breusegem et al. 1999), salt stress in *Arabidopsis* (Wang et al. 2004) and drought stress in rice (Yang et al. 2009). Panda et al. (2017) reported a decrease of around 30% SOD activity under As (200 μM and 400 μM), NaCl (200 and 600 mM) and a combination of both (200 μM As+200 mM) treatment in *S. maritima* as compared to control plants. However, decrease in SOD activity in this halophyte under stress condition indicates its utilization in sequestration of stress-induced O_2^- radicals (Rangani et al. 2016). Wu et al. (2013) reported a slight increase in SOD activity with Pb, Zn and their combination in *Suaeda salsa*. The SOD dismutase O_2^- into H_2O_2 and H_2O_2 is further scavenged by other antioxidative enzymes like CAT and APX to reduce toxic effect of H_2O_2 on plants (Bose et al. 2014).

6.3.2 Catalase

Catalase (CAT) (EC 1.11.1.6) is a heme-containing enzyme that catalyses the conversion of H_2O_2 into H_2O and O_2 (Das and Roychoudhury 2014). Hydrogen peroxide (H_2O_2) concentration is expected to increase under normal and abiotic stress conditions either due to action of SOD or by biochemical pathways that directly produce it. H_2O_2 also acts as signalling molecule and takes part in a number of important functions of plant cell (Foyer and Noctor 2005). But there should be control on its buildup and total concentration in plant cell to protect from oxidative damage to membranes and proteins. Peroxisomes are the major sites of H_2O_2 production due to β-oxidation of fatty acids, photorespiratory oxidation and purine catabolism (Mittler 2002). There are different forms of catalase isozymes found in different cellular organelles, such as CAT 1 found in peroxisomes and cytosol which is expressed in pollens and seeds, CAT 2 expressed mainly in leaves but also in roots and seeds and CAT 3 localized in mitochondria and which is highly expressed in seeds and seedlings (Scandalias 1990; Sharma et al. 2012). Under the stressful environmental conditions, energy consumption along with increased production of H_2O_2 increases catabolism. CAT eliminates the H_2O_2 in an energy-efficient manner without consuming cellular reducing equivalents. According to Sandalio and Romero-Puertas (2015), catalase activity is mostly associated with peroxisome where it is involved in removal of H_2O_2 mainly formed during photorespiration.

Wu et al. (2013) reported an increase in CAT activity with an upregulation of CAT gene expression in response to Zn (100 μg L^{-1}), Pb (20 μg L^{-1}) and their combined effect in shoots of *Suaeda salsa*. Panda et al. (2017) observed a significant increase in CAT activity under As (200 μM and 400 μM), NaCl (200 and 600 mM) and a combination of both (200 μM As+200 mM NaCl) treatments with respect to control in *S. maritima*. A 142% increase was reported in seedlings treated with 400 μM arsenic. There is a negative correlation between activity of CAT and H_2O_2 concentration in cell showing an effective sequestration of H_2O_2 under stress conditions. Similarly increased CAT activity has also been observed in other halophytes when exposed to salinity and heavy metal stress *Kandelia candel* and *Bruguiera* (Zhang et al. 2007) and salinity *Salvadora persica* (Rangani et al. 2016). Salt stress (NaCl) alone had no effects on enzyme activity in *K. virginica* plants; in contrast Cd stress resulted in a threefold reduction in CAT activity. A sixfold decrease as compared to control plant was observed in CAT activity of plants treated with both Cd and NaCl (Han et al. 2013). The Cd-induced decrease in CAT activity has also been observed in halophyte *Salicornia brachiata* (Parida and Jha 2010), *Suaeda salsa* (L.), *Kochia scoparia* (L.) and *Beta vulgaris* (L.) (Takagi and Yamada 2013). Bankaji et al. (2016) also reported a significant decrease in CAT activity of *Atriplex halimus* (86.3–64.2%) when treated with Cd^{2+} or Cu^{2+} (400 μM), respectively. They reported a decrease in activity when Cd and NaCl (200 mM) were applied simultaneously to the growing medium as compared to those when applied individually. Similar responses were observed with Cu^{2+} in place of Cd^{2+} as a heavy metal. Similar increased activity of CAT antioxidant enzymes with increased concentration of Cd has been reported in other halophytic plants including *Atriplex halimus* L. (Mesnoua et al. 2016) and *Salicornia brachiata* (Sharma et al. 2010; Wang et al. 2014). The catalase activity increased with 20 PSU and 400 μM Zn treatment (da Silva 2010) in coastal salt marshes *Halimione portulacoides*. Sharma et al. (2010) reported 1.5- and fivefold increases in CAT activity with Cd (50 μM) and Ni and Zn (200 μM) representing its role in removing heavy metal-induced H_2O_2 levels.

6.3.3 Peroxidase

Peroxidase (POX) (EC 1.11.1.7) is a heme chloroplastic enzyme that detoxifies H_2O_2 in the cytosolic compartment of the cell under normal as well as stress conditions (Das and Roychoudhury 2014). They are non-specific in utilizing electrons donors for oxidation of H_2O_2. They use aromatic compounds like guaiacol and pyrogallol (Asada 1999) as reducing agents. MacFarlane and Burchett (2001) reported a significant increase of 21% in POX activity when exposed to Cu (200 μM) and increased proportionally up to 800 μM Cu treatment in a mangrove *Avicennia marina* indicating role of peroxidase in ROS amelioration. POX activity also increased under Pb and Zn treatments in *Avicennia marina*. Peroxidase plays an important and active role in the cytosol, vacuoles and also cell walls and is considered as an essential enzyme for the removal of H_2O_2 from cell (Das and Roychoudhury 2014). Wu et al. (2013) observed increased POX activity only with Zn treatment (100 μg/L) and not in Pb (20 μg L^{-1}). Similarly increase in POX activity was reported with Cd and Pb combined treatment not with individual treatments (Manonusaki and Kalogerakis 2009). Salt alone has no effect on enzyme activity in *K. virginica* plants (Han et al. 2013). However an increase of about 87% was observed in POX activity in Cd-treated plants. In the plants treated with both Cd and NaCl, POX activity was maintained at control levels. In *S. maritima* no significant change in POX activity was observed in NaCl-treated seedling, while As treatment enhanced the activity. A combined treatment of 200 μM As and 200 mM NaCl resulted in 54% increase in POX activity with respect to control (Panda et al. 2017) indicating the role of POX in antioxidative defence mechanism.

6.3.4 Ascorbate Peroxidase

Ascorbate peroxidase (APX) (EC 1.11.1.11) is a key enzyme of the ascorbate-glutathione cycle and catalyses the conversion of H_2O_2 to water. The ascorbate-glutathione cycle includes two antioxidant metabolites ascorbate and glutathione and enzymes APX, GR, DHAR and MDHAR. The activation of ascorbate-glutathione cycle is essential to control oxidative stress in plants (Gill and Tuteja 2010). It is an efficient pathway which detoxifies H_2O_2 by performing APX-induced dismutation of H_2O_2 into H_2O and DHA by using ascorbic acid as a reducing agent (Das and Roychodhury 2014). This mechanism was also found important under heavy metal stress (Tiryakioglu et al. 2006; Liu et al. 2007). Ascorbate peroxidase is the primary H_2O_2 scavenging enzyme in the chloroplast and cytosol of the plant cells (Asada 1999). APX uses ascorbate as it reduces substrate, and there are several isozymes of APX located in different cellular organelles like cytosol, microbodies, chloroplast, etc. (Madhusudhan et al. 2003; Pandey et al. 2017), and they are known with the name of their respective cellular locations like cytosolic, mitochondrial APX, etc. (Noctor and Foyer 1998; Sharma and Dubey 2004). APX acts by a series of coupled reactions (Asada 1994). It plays an important role in ROS scavenging as compared to other antioxidative enzymes as ascorbate, in addition to reacting with H_2O_2, may react with superoxide anion, singlet oxygen and hydroxyl radical (Shigeoka et al. 2002). Heavy metal-induced APX activity has been reported widely in literature (Sheokand et al. 2010; Kumari et al. 2017) under salinity (Kumari et al. 2010) and heavy metal stress. A reduced APX activity was observed in many crops under heavy metal stress (Smeets et al. 2008; Khan et al. 2009; Pinto et al. 2009).

In halophytic plant *K. virginica*, Han et al. (2013) reported a 35% reduction in APX activity with Cd (5 μM), and NaCl alone had no effects. Combined effect of both stress (Cd+NaCl) resulted in a significant reduction in APX activity (49%). In *S. maritima*, the APX activity decreased with salinity but remained the same as in control with heavy metal (As) treatment (Panda et al. 2017). Similarly Bankaji et al. (2016) reported a reduction of 64.3% and 21.4% in APX activity in leaves of *Atriplex halimus* with the treatment of either Cd^{2+} or Cu^{2+} (400 μM). A decrease in APX activity was observed when Cd and NaCl (200 mM) were applied simultaneously to the growing medium as compared to their individual application. Similar responses were observed with Cu^{2+} in place of Cd^{2+} as heavy metal. This decrease could be the result of damage caused by metal ion-induced ROS (Sai Kachout et al. 2009). Salinity- and As stress-induced H_2O_2 is reduced by APX scavenging thus to maintain the appropriate level of H_2O_2 to be used as signalling molecule. H_2O_2 is efficiently scavenged by the action of APX as observed by Panda et al. (2017) in halophyte *S. maritima*. They reported a negative correlation between APX activity and H_2O_2 concentration. Eyidogan and Oz (2007) suggested that the enhancement in APX activity under stress may be modulated by the overproduction of H_2O_2 under CAT deactivation.

6.3.5 Glutathione Peroxidase

Glutathione peroxidase GPX (EC 1.11.1.9) is an antioxidative enzyme that catalyses the reduction of hydrogen peroxide, using the glutathione (GSH) pool and thus protecting cells against oxidative damage (Helliwell and Gutteridge 1986). Superoxide radicals are converted to H_2O_2 by SOD (Dixit et al. 2001), and glutathione antioxidant acts as one of the important protective mechanisms (Bela et al. 2015). Cartegnato et al. (2008) reported a 230% and 300% increase in GPX activity when exposed to 100 μg ml^{-1} and 800 μg ml^{-1} Zn showing a positive correlation between GPX activity and Zn concentration in leaves of halophyte *A. Marina*. Wu et al. (2013) reported an increase in GPX activity in above ground part of halophyte *Suaeda salsa* seedling grown in Zn (100 μg L^{-1}), Pb (20 μg L^{-1}) or the combination of both metals. Similar results were observed by Mesnoua et al. (2016) in *Atriplex halimus* L. under Cd toxicity. Yildiztugay et al. (2014) observed increase in GPX activity in response to salinity stress (250–1500 mM NaCl) at 15 days in halophytic plants *Salsola crassa* showing that it contributes to tolerance mechanism under salinity-induced damage. On the other hand, Haluskova et al. (2009) observed only a slight increase in GPX activity with Pb, Ni and Zn and no effect with Co.

However, a decline of 75.8% in GPX activity under Cd^{2+} stress (400 μM) was observed in leaves of *A. halimus* (Bankaji et al. 2016). A decrease in GPX activity was also observed when Cd and NaCl (200 mM) were applied simultaneously to the growing medium as compared to individual treatment. Cu^{2+} (400 μM) treatment however resulted in a significant increase in GPX activity in NaCl plus Cu^{2+} as compared to only Cu^{2+} and only NaCl treatment. Increase in GPX activity may be due to the reason Cu acts as catalyst in the formation of ROS (via Fenton reaction) and causes GSH depletion. The other heavy metal like Cd does not produce ROS directly, but it increases lipid peroxidation and GSH depletion causing an indirect ROS production. Sai Kachout et al. (2009) reported that these ROS cause oxidative damage and alter the antioxidative enzymes activities. GPX may act as a secondary line of stress defence under Zn and NaCl treatments.

6.3.6 Glutathione Reductase

Glutathione reductase (GR) (EC 1.6.4.1) is an important enzyme of ascorbate-glutathione cycle. The monodehydroascorbate formed in the APX reaction can be regenerated to ascorbate by reduced GSH, which is oxidized to form glutathione disulphide (GSSG). For many cellular functions, reduced form of glutathione is required. The reduction of oxidized glutathione to reduced glutathione occurs via the action of GR enzyme in a NADPH-dependent manner (Noctor et al. 2012). Glutathione reductase plays a crucial role in providing protection against oxidative stress in plants by maintaining the endogenous pool of GSH. According to Pilon-Smits et al. (2000), this enzyme has very important function in heavy metal tolerance. Rodriguez-Serrano et al. (2006) reported enhancement in expression of GR coding genes including both transcriptional and post-transcriptional impacts under Cd stress. Han et al. (2013) reported an increase of about twofold in GR activity in Cd-treated plants; however NaCl alone treatment resulted in no significant changes in enzyme activities in *K. virginica*. However a 2.4-fold increase as compared to control plants was observed in GR activity in plants treated with both Cd and NaCl indicating a better tolerance to heavy metal in presence of NaCl. Lefevre et al. (2010) reported enhancement in GR activity as major component involved in heavy metal (Cd) tolerance in xero-halophyte *A. halimus*. GR may be involved in the regeneration of reduced glutathione by reduction of oxidized glutathione under salinity stress to maintain redox status of the cells as observed in halophytes. The GR activity gradually decreased in *S. maritima* with increasing salinity and increased with increasing As level. However when salinity and As treatment both were applied simultaneously, there was no significant increase in GR activity as compared to control plants (Panda et al. 2017). It is an important enzyme and plays an important role in maintaining of redox status in ascorbate-glutathione cycle in halophytes under heavy metal stress and endogenous H_2O_2 content through an oxido-reduction cycle (Halliwell-Asada pathway) (Bose et al. 2014; Rangani et al. 2016).

6.3.7 Dehydroascorbate Reductase and Monodehydroascorbate Reductase

Monodehydroascorbate reductase (MDHAR) (EC 1.6.5.4) and dehydroascorbate reductase DHAR (EC 1.8.5.1) are also important enzymes of the ascorbate-glutathione pathway. MDHAR is FAD enzyme that catalyses the reduction of monodehydroascorbate radical (Lunde et al. 2006). With its ability to directly regenerate ASA, MDHAR contributes towards maintaining a reduced pool of ASA (Sharma et al. 2012). MDHAR directly uses NADPH to recycle ascorbate. However MDHAR is an efficient electron acceptor (Noctor and Foyer 1998; Asada 2000), and it can be reduced directly to ascorbate using photosynthetic ETC electrons. This enzyme is mainly located in mitochondria and peroxisomes, and along with APX it is involved in scavenging of hydrogen peroxide (Del-Rio et al. 2002; Mittler 2002). Its isozymes are also found in other cellular organelles like chloroplast, mitochondria, cytosol, peroxisomes and glyoxysomes (Hossain et al. 1984; Jimenez et al. 1997; Sharma et al. 2012; Das and Roychoudhury 2014). DHAR like MDHAR also helps in regeneration of ascorbic acid (AA) pool in plant cells (Das and Roychoudhury 2014). Ascorbic acid (AA) is a major antioxidant in plants for ROS detoxification and photosynthetic functioning. The DHAR function as an important regulator of AA recycling by catalysing the regeneration of ascorbic acid from its oxidized form. The univalent oxidation of ascorbic acid leads to the formation of MDHAR, which is converted to DHA via further oxidation reduction. This DHA is then reduced to AA by the action of DHAR also requiring GSH (Eltayeb et al. 2007). Few studies have been conducted on MDHAR and DHAR response under heavy metal stress in halophytes. The overexpression of DHAR genes enhanced the tolerance to environmental stress in tobacco and *Arabidopsis* (Chen and Gallie 2006; Eltayeb et al. 2007). The increased activity of DHAR under stress conditions may be because of increasing level of AsA. High level of AsA under salinity and As treatment may be one strategy to reduce oxidative damage in *S. maritima* (Panda et al. 2017). In halophyte *K. virginica*, DHAR activities increase to about 2.5-fold in Cd-treated plants; however no significant effect was observed under NaCl alone and a combination of both Cd and NaCl (Han et al. 2013). However a 15% reduction in MDHAR activity was observed with Cd stress as compared to control, and no significant effects were observed with both Cd and NaCl and alone NaCl-treated plants.

6.3.8 Non-enzymatic Antioxidants

The non-enzymatic antioxidants include ascorbic acid, glutathione, tocopherols, carotenoids, flavonoids and proline. These antioxidants provide protection to cellular components from damage either by interrupting cascade of uncontrolled oxidation (Noctor and Foyer 1998) or donating an electron to neutralize free radicals to non-reactive species (Oztetik 2012). Ascorbate and glutathione are two important antioxidants involved in ROS detoxification via ascorbate-glutathione cycle under stress conditions (Foyer and Noctor 2005). They are involved in detoxification of ROS-induced oxidative stress. Glutathione will be discussed in details under sulphur metabolism and proline under osmoprotectants subheadings.

Ascorbic acid is an abundant, low molecular weight, water-soluble antioxidant involved in ROS detoxification under stress conditions. It has the ability to donate electrons in a number of enzymatic and non-enzymatic reactions and thus is involved in ROS scavenging (Smirnoff 2005; Gill and Tuteja 2010). It is located in many plant tissues like meristematic and photosynthetic cells. It plays very important role in many processes like plant growth, differentiation and metabolism. In plant cell AA is mainly found in cytosol, with a significant amount in apoplast, and acts as a first line of defence for ROS detoxification (Barnes et al. 2002). The oxidation of AA involves two steps, first to produce MDHAR which, if not reduced immediately to ascorbate, disproportionate to AA and DHA. Ascorbic acid reacts with free radicals H_2O_2, OH^- and O_2^- to protect membranes from oxidative damage and also regenerate α-tocopherol from tocopheroxyl radical (Shao et al. 2005). Ascorbic acid also preserves the activities of metal-binding enzymes (Zaefyzadeh et al. 2009).

In halophyte *K. virginica*, a significant increase of twofold in AsA level was noticed with Cd+NaCl-treated plants as compared to plants exposed to Cd stress alone. However NaCl treatments resulted in no significant change in ascorbate content as compared to combined treatments (Han et al. 2013). Panda et al. (2017) studied the ascorbate content in *S. maritima* under NaCl, As and combined treatment and reported that the AsA/DHA ratio increased by approximately threefold with salinity treatment of 200 and 600 mM as compared to control plants. With 200 μM As treatment, an 11.8-fold increase in AsA/DHA ratio was observed, but a slight increase was observed with the combined treatment of As (200 μM) and NaCl (200 mM). The increase in ratio is due to either decrease in DHA or increase in AsA content, and the possible reason behind this may be decreased rate of oxidation of AsA and increased rate of its synthesis under stress conditions. The decrease in DHA content under salinity and heavy metal stress may be due to induction in DHAR activity in stress condition or increase in GSH level which acts as electron transport (Foyer and Noctor 2005; Ghosh et al. 2016). In contrast to these results, Demir et al. (2013) reported an increase in DHA levels under combined stress of arsenic and salinity in *Cakile maritima.* The AsA/DHA and GSH/GSSG ratios are very important for maintaining cellular redox status, and changes in these ratios may be considered as first sign of oxidative stress in plants (Foyer and Noctor 2005). The cellular redox homeostasis helps in detoxification of oxidative stress (Foyer and Noctor 2005; Parida and Jha 2010).

Tocopherols are a group of lipophilic antioxidants collectively termed as vitamin E. Tocopherols have four isomers α, β, γ and δ. The α-tocopherol isomer has maximum antioxidative properties and capability to scavenge ROS and lipid free radicals. These characteristics make it an indispensible protector and essential component of plant biomembranes (Hollander-Czytko et al. 2005; Kiffin et al. 2006). Tocopherols are synthesized in organisms with the ability of photosynthesis, and these are present only in green tissues of plants. Tocopherol uses homogentisic acid (HGA) and phytyl diphosphate (PDP) as precursors for its biosynthesis. The main enzymes involved in the biosynthesis of tocopherol are 4-hydroxyphenylpyruvate dioxygenase (HPPD), homogentisate phytyl transferases (VTE2), 2-methyl-6-phytylbenzoquinol methyltransferase (VTE3), tocopherol cyclase (VTE1) and *γ*-tocopherol methyltransferase (VTE4) (Li et al. 2010). The major role of tocopherol is protection of PSII. They can quench excess energy of PSII by reacting with O_2 and thus protect the lipids and other membrane constituents of chloroplast. They serve as a potent free radical scavenger due to ability to inhibit chain propagation step of lipid peroxidation cycle. α-Tocopherol can scavenge free radicals like $RO^{\cdot}$, and ROO present in the membranes convert them into $TOH^{\bullet}$ which interacts with GSH and AA and is subsequently recycled to its reduced form (Igamberdiev et al. 2004). Oxidative stress has been reported to activate the expression of tocopherol biosynthetic genes in higher plants (Wu et al. 2007). Han et al. (2013) reported decrease in levels of α-tocopherol (35%) under Cd (5 μM) treatment in response to Cd-induced oxidative stress in halophytic plant *K. virginica*. Only 50 mM NaCl in nutrient solution slightly increased the α-tocopherol levels as compared to control, but an increase of about 28% was observed with NaCl in Cd-treated plants showing the enhanced protective mechanism in halophytes.

Carotenoids are lipophilic non-enzymatic antioxidant pigments. They can be synthesized under stress conditions and have the ability to scavenge and deactivate ROS (Safafar et al. 2015). These antioxidative pigments are also found in plants as well microorganisms. They further include two types of pigments xanthophylls (contain oxygen) and carotenes (purely hydrocarbons and contain no oxygen). Carotenoids are present in chloroplast membranes. They quench singlet oxygen which is generated when light energy absorbed by chlorophyll is not dissipated through photosynthesis and protect chlorophyll from photooxidative damage. Therefore, a reduction in carotenoids has a serious consequence on chlorophyll pigments. They react with lipid peroxidation products to terminate chain reactions, thus stopping further damage. They inhibit oxidative damage and quench triple sensitizer (3Chl*), excited chlorophyll molecules (Chl*) thus preventing the accumulation of singlet oxygen and protect photosynthetic machinery from further damage (Dar et al. 2017).

da Silva (2010) reported an overall increase in chlorophyll a, chlorophyll b and carotenoid content up to 400 μM Zn treatments, and above it Zn was found toxic for the *H. portulacoides* plants. Bertrand and Poirier (2005) stated that many studies showed decrease in photosynthetic pigment under heavy metal stress, but some other researchers observed an increase in carotenoid content (Mallick and Rai 1999; Mallick 2004). MacFarlane and Burchett (2001) reported a significant decrease in carotenoid content when exposed to Cu (800 μM) treatment in a mangrove *Avicennia marina*. Pb treatment showed no significant effect on carotenoid content, but decline was observed with Zn at 1000 μg/g in the growing medium. Cu and Zn are mobile but show restricted translocation to shoot due to endocasparian strips, while Pb is actively excluded at root, thus having less effects on plant metabolism. Carotenoid contents of *S. maritima* did not vary significantly under arsenic, salinity and combined treatments (Panda et al. 2017). No effects on chlorophyll content under salinity and heavy metal stress may be due to no effect on chlorophyllase activity, thereby protecting chlorophyll degradation (Rangani et al. 2016). Sghaier et al. (2015) studied the *Tamarix gallica* under salinity, As and salinity+arsenic treatment and reported no change in level of photosynthetic pigments, chl a, chl b, chl a/b, total chlorophyll and carotenoids. In contrast salinity-induced decline in carotenoid content was observed in other halophytes like *Arthrocnemum macrostachyum* (Redondo-Gomez et al. 2010); chenopodiaceous halophytes including *Suaeda salsa* (L.), *Kochia scoparia* (L.) and *Beta vulgaris* (L.) (Takagi and Yamada 2013); *Quinoa* (Amjad et al. 2015); and *Panicum turgidum* (Koyro et al. 2013).

Flavonoids are mainly found in plant leaves, floral parts and pollens. They act as important secondary antioxidants by scavenging ROS, locating and neutralizing radicals before cell damage and protecting photosynthetic damage under environmental stress conditions (Fini et al. 2011).

6.4 Sulphur Metabolism and Its Role in Heavy Metal Detoxification

Sulphur (S) is an ubiquitous and essential macronutrient in plants. In higher plants its uptake is mainly in the form of sulphate anions from the soil which through a series of reactions is converted into organic S-containing compounds like the amino acids, cysteine (Cys) and methionine (Met). These organic compounds are essential components of many proteins, lipids, polysaccharides, iron-sulphur cluster, many vitamins (biotin and thiamine), cofactors (CoA and *S*-adenosyl-met), some peptides (glutathione, phytochelatins and metallothioneins), etc. In addition some amount of sulphur can also be taken up in the form of sulphur dioxide (SO_2) and hydrogen sulphide from the air which again through a cascade of reactions gets converted to organic S-containing compounds. Sulphur-containing compounds are involved in many biochemical and physiological processes via regulation of enzymatic activities and redox balance including abiotic stress tolerance mechanism particularly in heavy metal detoxification (Gill and Tuteja 2010). The sulfhydryl group of cysteine residues has high nucleophilicity which makes them react with a number of molecules like free radicals, reactive oxygen species, toxic electrophilic xenobiotics and heavy metals (Leustek et al. 2000; Nocito et al. 2007). These effects indicate a unique role of cysteine in biological systems. Aslund and Beckwith (1999) explained that the two cysteine residues of a polypeptide chain may interact in an oxidation reaction through the formation of a reversible double bond which helps in maintenance of protein structure and regulation of protein activity. This interconversion of two thiol groups in disulphide bond may involve balance of redox cycles. In redox cycles balance transfer of electron is a must during normal and oxidative stress conditions. The sulphur-containing molecules play an important role in heavy metal detoxification in halophytes also. The important sulphur-containing molecules are discussed below.

6.4.1 Glutathione

Glutathione is an important low molecular weight thiol in plant cells. It has been detected in almost all cell organelles like cytosol, endoplasmic reticulum, mitochondria, chloroplast and vacuole (Yadav 2010). It is an important and essential metabolite with multiple functions including defence against salinity- and heavy metal-induced ROS production (Foyer and Noctor 2005), heavy metal sequestration (Cobbett and Goldbrough 2002; Freeman et al. 2004) and xenobiotics detoxification (Dixon et al. 1998). Two principal structural features of glutathione (GSH) are presence of thiol group on cysteine and γ-glutamyl linkage. GSH is the major transport and reduced form of sulphur in plants. It is synthesized by two ATP-dependent reactions by the action of glutamylcysteine synthetase catalysing the formation of peptide bond between carboxyl group of glutamate and amino group of cysteine to yield γ-glutamylcysteine (γ-EC). It is the regulatory step under the high/more GHS requiring conditions (Noctor et al. 1998). The second reaction encompasses glutathione synthetase which catalyses the bond formation between glycine residue and γ-glutamylcysteine (γ-EC) to form GSH. According to Wachter et al. (2005) studies, GSH1 is present in the plastids, and GSH2 is present in both plastids and cytosol in case of *Arabidopsis thaliana* and *Brassica juncea*. Cysteine is proposed to be the rate-limiting factor for glutathione biosynthesis. Cysteine is the final product of sulphur assimilation pathway, and GSH biosynthesis is correlated with S assimilation pathway (Rausch and Wachter 2005). Glutathione plays a very important role in a number of biological processes, and it is the most abundant intracellular thiol and γ-glutamyl compound. Further its physiological significance can be divided into two categories. First one is as an important pool for reduced sulphur and regulation of sulphur uptake by plant roots, and second its cysteine residue helps in chelation and thus in antioxidative defence system and redox control for salt and heavy metal detoxification in halophytes.

The main basic and recognized function of glutathione is when its reduced form is oxidized to its disulphide form (GSSG) during thiol-disulphide interactions and the GSSG is again recycled to GSH by the action of NADH-dependent glutathione reductase enzyme in cell organelles and cytosol where it is present. This recycling is rapid, and the simple cycle represents the basis for confirming its role as a powerful redox buffer (Gill and Tuteja 2011). During oxidative stress GSH gets oxidized first by ROS as a part of antioxidant defence system and prevents excessive oxidation of other sensitive components of cell. GSH can scavenge ROS such as O_2^-, H_2O_2 and OH^- radicals produced as a result of stress (Gill and Tuteja 2011). The features of GSH like its high concentration and its high reduction state make it a favourable antioxidant under stress conditions. Unlike the other antioxidative enzymes and metabolites that scavenge ROS, the oxidized GSSG is rapidly recycled to GSH by GR in cell organelles and cytosol (Halliwell and Foyer 1978; Kataya and Reumann 2010). GSH also protects cell membranes by maintaining zeaxanthin and tocopherol in the reduced state (Gill and Tuteja 2011). This property protects the plant from the deleterious effects of combined salt and heavy metal stress. The thiol group of GSH is responsible for its chemical reactivity and functions. The nucleophilic nature of the thiol group in GSH is important in the formation of mercaptide bond with metals as well as in reacting with some electrophiles (Yadav 2010). These kinds of reactions are catalysed by glutathione *S*-transferase (GST) and have been reported to be required in the process of detoxification of different abiotic stresses (Marrs 1996; Leustek et al. 2000). Additionally, GSH is a substrate for GPX and GST (Gill and Tuteja 2010). The conjugated forms are then transported to the vacuole and protect the plant cells from harmful toxic effects (Klein et al. 2006). However, the consumption of reduced glutathione in xenobiotic or heavy metal stress results in a transient decrease of cytosolic glutathione (GSH) content. This affects the GSH/GSSG redox potential, inducing a redox signal under stress conditions (Nocito et al. 2006). Therefore, GSH-based detoxification process will have an effect on redox potential of cell, and thus maintenance of GSH/GSSG ratio becomes very essential for the survival of plants in heavy metal stress conditions (Gill and Tuteja 2011). Halophytes generally have a high GSH/GSSG ratio and better tolerance to heavy metal stress. Higher GSH content maintains the thiol group containing proteins and enzymes in their native stage under stress conditions and has been reported to increase the salinity and arsenic tolerance potential in halophytic plant *S. maritima* (Vromman et al. 2016). Panda et al. (2017) reported that the ratio of reduced and oxidized glutathione (GSH/GSSG) did not change under salinity, heavy metal (As) and their combined stress and this helped in maintaining cellular redox balance in *S. maritima*. Higher GSH content corresponds to higher tolerance against heavy metal stress-induced oxidative damage (Freeman et al. 2004). It is suggested that production of GSH under stress conditions in halophytic and metal-accumulating plants shared a common mechanism. Increase in GSH content and/or other antioxidative enzymes has been reported in a number of halophytes. Overexpression of *S. brachiata* glutathione transferase in tobacco conferred tolerance up to 300 mM

NaCl (Jha et al. 2011). Similarly, Lokhande et al. (2011) have observed the role of glutathione and ascorbate as antioxidant in balancing cellular redox homeostasis in halophyte *S. portulacastrum* (L.) under salinity stress. Therefore, manipulating GSH biosynthesis by genetic engineering in plants under stress conditions results in increased tolerance to ROS (Sirko et al. 2004). In vitro studies with the biosynthetic enzymes from parsley and tobacco reported a feedback inhibition of γ-glutamylcysteine synthetase (γ-ECS) by reduced glutathione (GSH) (Noctor and Foyer 1998). Exogenously applied GSH had a positive effect on the indices of stress under metal treatments (Cai et al. 2010). Limited information is available regarding transport of GSH-metal complex across the membranes; however, an ATP-binding cassette transporter AtATM3 has been found as GSH-Cd transporter across mitochondrial membrane. This transporter was isolated from the mitochondrial protein of *A. thaliana.* Kim et al. (2006) reported the induction of AtATM3 gene expression in plant roots in response to Cd and Pb stress, indicating the role of ATP-binding cassette transporter in the regulation of cellular GSH levels and thus oxidative metabolism.

Reduced glutathione is a direct precursor for the synthesis of phytochelatins, a Cys-rich peptide involved in heavy metal detoxification (Zenk 1996). Low GSH content has been correlated with Cd sensitivity, and this may be due to less PC synthesis (Xiang et al. 2001).

6.4.2 Phytochelatins (PCs)

PCs have been reported to be present in the plant kingdom including all angiosperms, gymnosperms and bryophytes (Gekeler et al. 1989). These were first isolated from plant cell suspension cultures upon Cd exposure (Grill et al. 1985). Besides Cd, other heavy metals like Cu, Zn, Pb, Ni and Hg have been reported to induce the synthesis of PCs. Generally plants enhance the synthesis of phytochelatins in heavy metal stress conditions (Sruthi et al. 2017). PCs contain sulphur which plays an important role in their synthesis and also in detoxification of heavy metals by forming heavy metal-binding peptides particularly Cd-binding peptides (CdBP) (Cobbett and Goldsbrough 2002). PC synthesis in response to Pb treatments leads to the formation of PC-Pb complex (Piechalak et al. 2002). PC translocation studies in *Arabidopsis* have shown that they can transport from roots to shoots through a long-distance transport mechanism. Studies with xylem and phloem sap from *Brassica napus* have confirmed the transport of PCs. Further it was reported that PCs and Cd are present in high concentrations in the phloem sap as compared to xylem sap, thus indicating that PCs can function as long-distance carriers of Cd (Yadav 2010). Cd mainly forms PC-Cd and GSH-Cd complexes and gets transported (Mendoza-Cozatl et al. 2008). Phytochelatins have a role in heavy metal detoxification and in maintaining ion homeostasis (Zenk 1996; Hirata et al. 2005). Though hyperaccumulation does not use this expensive strategy commonly to cope with high doses of heavy metals, the presence of constitutive and functional PCs are ancestral characters (Petraglia et al. 2014) that may help the plant to minimize damage under conditions of excess metal concentration in non-metallophytes (Tennstedt et al. 2009). Now a lot of database is present in public sector after the cloning of PCS gene. Expressed sequence tag (EST) data supports the view that PCS genes are present in all higher plants. Sequences homologous to PCS have been reported in various monocot and dicot plants. Yadav (2010) also reported sequence data for the presence of PCS genes in ferns and diatoms. The role of phytochelatins in regulation of heavy metal stress in nodulated plant such as *Lotus japonicus* has also been reported (Ramos et al. 2007, 2008).

Phytochelatins have a general structure (γ Glu-Cys)$_n$Gly, where n varies from 2 to 11. These are enzymatically synthesized polypeptides using glutathione as precursor in the presence of enzyme phytochelatin synthase (PCS) and help in metal detoxification by forming complex with metal-Cd complex and transporting it to the vacuole (Sachiko et al. 2009; Gill and Tuteja 2011). The sulfhydryl group of PC forms a complex with heavy metal as reported for arsenic in rice (Tripathi et al. 2012) and xero-halophyte *Atriplex atacamensis* (Vromman et al. 2016). They reported that arsenic is converted to arsenite and binds to SH group of PCs and forms a PC-As complex which then is transported to vacuole where pH range favours the high molecular weight PC-As complexes. However sequestration of the PC-Pb complex to vacuole has not been reported (Yadav 2010). The PCS has been reported to be activated on treatment with heavy metals like Cd (Cobbett and Goldbrough 2002; Thangavel et al. 2007). The halophytic plant black mangrove *Avicennia germinans* exhibits tolerance to polluted environment and is correlated with overexpression of AvPCS coding genes induced by heavy metals Cd and Cu during initial hours of treatment (Gonzalez-Mendoza et al. 2007). This overexpression is transient and is sufficient to trigger an efficient detoxification mechanism against long-term heavy metal stress. Heavy metal-induced oversynthesis of PCs in halophytes contributing towards the tolerance mechanisms may be able to increase glutathione concentration in a better way than glycophytes. The intracellular level of GSH determines the level of PCs that a plant is able to synthesize under stress conditions (Liu et al. 2015). However Panda et al. (2017) observed that a higher GSH content under As treatments did not reflect in higher PC synthesis in *S. maritima* which could be due to As-PC complex formed in roots, lesser transport of As from root to shoot. Phytochelatins are involved in detoxification of a wide range of heavy metal ions like Cd^{2+} and Cu^{2+}. Bankaji et al. (2016) demonstrated that Cd^{2+} and Cu^{2+} stress caused PC accumulation in the halophyte *Atriplex halimus* that can be considered as hyperaccumulating species.

High GSH levels activate PCS which catalyses PC-heavy metal complex. The enzyme PCS become active upon the formation of a thiolate between two GSH molecules and heavy metals (Cd-GS2)/(Zn-GS2). Vatamaniuk et al. (2000) reported that this activation also involves the transfer of γ Glu-Cys moiety to free GSH or already synthesized PC. These PC-heavy metal complexes are transported to vacuole, and this is a more stable form of heavy metals (Mendoza-Cozatl et al. 2005)

Manipulation of PCS by genetic engineering and mutant studies has further confirmed the role of PC in heavy metal tolerance (Yadav 2010). Pomponi et al.

(2006) reported that availability of GSH is directly correlated with overexpression of AtPCS1 genes for Cd tolerance and accumulation. The heavy metals Pb, Cu, Zn and Cd resulted in overexpression of TaPCS1 (a wheat PCS) in shoots of plants when grown in polluted soil (Gisbert et al. 2003; Martinez et al. 2006). However, in some plants increase in PC synthesis was observed without stimulated GSH that leads to GSH reduction and plant found less tolerant to heavy metal contaminants. Zhu et al. (1999) reported an increased tolerance to Cd in overexpressed γ-Glu-Cys synthase gene from *E. coli* in *Brassica napus*. Lee and Kim (2010) reported the expression of *Arabidopsis* PCS in a yeast mutant deficient in PCS resulted in tolerance to Cd but not to Cu. Sachiko et al. (2009) revealed in mutation studies in PC synthase that replacing Cys residue with Ala resulted in less synthesis of PC; furthermore the mutant PCS was sensitive to oxidative conditions. This work emphasized on the importance of Cys-rich region in PCS for antioxidative activity.

6.4.3 Metallothioneins (MTs)

MTs are also cysteine-containing proteins which bind with metals and are found in almost all organism including plants, animals and microorganisms. Based on the location of cysteine residue, plant MTs have been divided into four types (Cobbett and Goldbrough 2002). These proteins were originally identified in animals for their ability to protect against Cd toxicity. Besides metal chelation MTs have been proposed to be involved in other cellular processes also like regulation of cell growth and proliferation, repair of DNA damage and scavenging of reactive oxygen species (Cherian and Kang 2006). MT superfamily is comprised of low molecular weight polypeptides generally less than 10 K Da, high metal content, low aromatic amino acid content and amino acid sequence motifs containing numerous Cys residues with characteristic distribution and spectroscopic expressions typical of metal thiolate clusters (Freisinger 2011). MTs bind to different heavy metals by formation of mercaptide bonds between its cysteine residue and metal. Therefore the arrangement of cysteine residues is important in determining the metal-binding properties of MTs (Cobbett and Goldbrough 2002; Blindauer and Leszczyszyn 2010). On the basis of cysteine amino acids arrangement, the plant metallothioneins have been grouped into four types: MT1, MT2, MT3 and MT4. Pagani et al. (2012) reported the expression of MTs in soya bean. GmT1, GmT2 and GmT3 were ubiquitously expressed and GmT4 synthesis was restricted to seeds. GmT1 is mainly present in roots; GmT2 and GmT3 are predominant in leaves and GmT4 in the seeds. GmT2 and GmT3 were highly responsive to Cd treatments indicating their role in Cd detoxification mechanism. MT Cd binding has been reported in *A. thaliana* (Zimeri et al. 2005) and *Vicia faba* (Lee et al. 2004).

Guo et al. (2008) studied the expression of *Arabidopsis* MTs in the copper-sensitive yeast mutant *D cup1* and found tolerance and accumulation equal to wild-type leaves. This copper tolerance indicates MTs are able to function as Cu chelators. Expression of all four MTs provided increased tolerance to some extent in

Zn-sensitive mutants also; however MT4 which is expressed in the seeds provided higher Zn tolerance and accumulation.

These MTs are also involved in balancing metal homeostasis or tolerance mechanism as they can also bind metals. Studies conducted on *Bruguiera gymnorrhiza* (L.) Lam., a most salt-tolerant mangrove halophyte, showed that the genes coding for MT2 (type −2) were upregulated by metals Zn, Cu and Pb (Huang and Wang 2009). Further (Huang and Wang 2010) reported higher tolerance to Zn, Cu, Pb and Cd in a halophytic mangrove *Avicennia marina* where transgenic *E. coli* LB21 overexpressing a gene coding for the protein GST-AmMT2. Location wise MT2 was mainly present in leaves while MT1 was in roots of plants. *Salicornia brachiata* is an extreme halophyte generally exposed to heavy metals in coastal areas. Chaturvedi et al. (2014) transformed tobacco with *Salicornia brachiata* MT2 gene for its functional validation. SbMt2 was found to be involved in binding and accumulation of Cu and Cd. They also reported that transgenic lines overexpressing SbMT2 genes showed a high ratio under stress conditions thus indicating that SbMT2 plays a role in ionic homeostasis also. Thus it may be hypothesized that overexpression of the genes coding for MT2 in halophytic plants shows positive function in relation to tolerance to heavy metals. However different elements have different impact on MT2 coding genes. Similarly Usha et al. (2009) reported that significant upregulation of PjMT2 in *Prosopis juliflora* with Zn and Cu and Cd treatment did not change the expression. Similarly in *Salicornia brachiata*, SbMT-2 expression was upregulated by Zn and Cu but not affected by Cd metal (Chaturvedi et al. 2012). The sequestering ability of MTs depends on the metal also as observed in *Salicornia brachiata* a fourfold higher Zn sequestration was observed as compared with Cu.

Role of MTs genes in antioxidant defence responses has also been reported by many researchers in the literature (Yang et al. 2009; Wang et al. 2009; Xue et al. 2009; Zhu et al. 2010; Kumar et al. 2013; Chaturvedi et al. 2012, 2014). Chaturvedi et al. (2012) have also observed that SbMT-2 expression from the halophyte may be enhanced by salinity, drought and heat, but a decreasing effect was found with cold stress. Further studies by Chaturvedi et al. (2014) showed that *SbMT2* gene expression in tobacco mitigates the deleterious effect of salt, drought and metal stress. Lower membrane injury, lipid peroxidation, H_2O_2 and proline content and high activity of antioxidative enzymes like SOD, POX and APX transgenic lines indicate the possible role of SbMT2 in ROS scavenging and detoxification mechanism under stress conditions.

6.5 Osmoprotectants

Low molecular weight organic compounds generally called compatible solutes/ osmolytes are water soluble, independent (to metabolic reactions) and non-toxic in nature even at higher cellular concentrations.

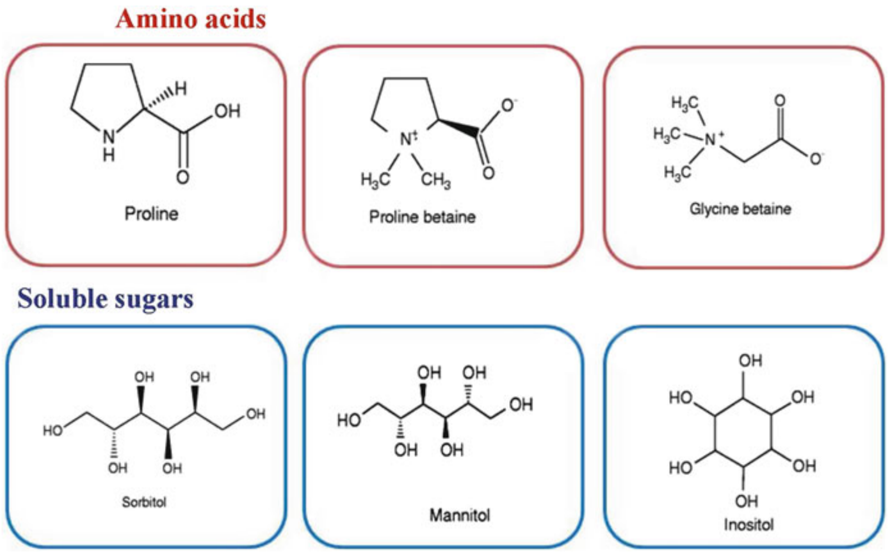

Fig. 6.1 Structures of common osmolytes present in halophytes

Strong resistance of halophytes to heavy metals tightly shows its parallel characteristics of salt resistance. Increase in concentration of osmoprotectants helps halophytes to fight against heavy metals and other abiotic stresses by maintaining water balance through lowering of osmotic potential, thus making all the physiological functions happening normally (Flowers and Colmer 2008). Metal stress creates water stress which in turn causes oxidative damage to cellular structures, and the concentration of osmoprotectants is directly related to heavy metal tolerance, giving clear indication of the role of halophytes in phytoremediation of heavy metals in saline patches. The speed of synthesis of osmolytes is also directly correlated with degree of ion toxicity and thus explains their potential of phytoremediation.

Different osmolytes synthesized by plants have been identified and listed in Fig. 6.1, including different polysaccharides (trehalose, glucose, sucrose, raffinose fructose and fructans); sugar alcohols (polyols) like sorbitol, mannitol, inositol and methylated inositols; amino acids, such as methyl-proline, proline betaine, proline, pipecolic acid and hydroxyproline betaine, glycinebetaine and choline O-sulphate; and tertiary sulphonium compounds, such as dimethylsulphoniopropionate (DMSP) (Rhodes et al. 2002; Ashraf and Foolad 2007).

6.5.1 Proline

In combating oxidative damage, plants face numerous challenges, and to overcome the stress, they explicit different strategies, one of which is the synthesis of osmolytes which provide protection against the damage caused to cellular structures and making the plants survive under stress conditions (Parida and Das 2005). One such osmolyte is proline, for which the precursor is glutamate; the enzyme catalysing the reaction is pyrroline-5-carboxylate synthetase (P5CS) (a key enzyme in proline biosynthesis) to pyrroline-5-carboxylate (P5C) (Szabados and Savoure 2010) which further reduces to proline. Mitochondria are the site of proline catabolism, which is catalysed by the enzyme proline dehydrogenase or proline oxidase (ProDH) to glutamate (Servet et al. 2012). The second precursor for proline biosynthesis is ornithine, which on transamination produces proline via enzyme ornithine-d-aminotransferase (Verbruggen and Hermans 2008).

The action of proline differs at different levels and in different tissues. It is involved in the alleviation of cytoplasmic acidosis and sustaining $NADP^+$/NADPH ratios required for metabolism (Hare and Cress 1997). Proline accumulates under stress conditions and serves as a sink for excess reductants, providing the NAD^+ and $NADP^+$ necessary for maintenance of respiratory and photosynthetic processes.

Commonly proline gets accumulated in cytosol, parallelly with vacuolar Na^+ sequestration. The cell membrane integrity is maintained by the interaction of phospholipids with proline, which in turn also keeps the quaternary structures of proteins intact. Sharma and Dietz (2006) and Lefevre et al. (2009) have observed three major roles of proline under heavy metal stress, viz. metal binding, antioxidant defence and signalling. Chai et al. (2013) observed the mixed effects of NaCl on phytotoxicity caused by Cd stress in relation to proline accumulation. Lefevre et al. (2009) and Saiyood et al. (2012) reported that *Suaeda maritima* showed that resistance to mixture of inorganic pollutants was directly proportional to its capability to add proline and soluble sugars in the roots, stems and leaves with similar finding in *Atriplex halimus*, in response to Cd treatment.

Siripornadulsil et al. (2002) showed the positive relation between the increased proline levels and improved protection against Cd, in microalgae. The possible reason is that proline reduces Cd-induced free radical damage and maintains a stringent reducing environment (higher GSH levels) within the cell. Huang et al. (2010) explained that proline, GSH and PCs-SH play an important role in ameliorating the effect of HM toxicity in two mangroves *Kandelia candel* and *Bruguiera gymnorrhiza* exposed to multiple HMs (Cd^{2+}, Pb^{2+} and Hg^{2+}) by maintaining optimum metabolism (physiological and biochemical). Heavy metal induces both a secondary water stress (Nedjimi and Daoud 2009) and oxidative stress in plants (Verma and Dubey 2001). In addition to its role as an osmolyte for water economy, proline helps to stabilize subcellular structures (e.g. membranes and proteins), scavenge free radicals and buffer cellular redox potential under stress conditions (Ashraf and Orooj 2006). The proline content basically maintains the balance between the cytoplasmic water potential to that of vacuole, where most of the inorganic ions are sequestered (Flowers et al. 1986).

Thomas et al. (1998) reported that in leaves of *M. crystallinum*, a tenfold increase in copper caused 15-fold increase in the proline. However, the magnitude of increase was more when the plants were exposed to salt stress. Proline accumulates in metal-stressed plant cells even when they are turgid, along with their additional role as an antioxidant/chelator (Sharma and Dietz 2006).

From the above discussion, it seems that halophytes can better cope with heavy metal stress than other plants as they have the ability to absorb them from soil and then degrade or reduce them to their organic forms which are non-toxic as referred in Table 6.2.

6.5.2 Glycinebetaine

Glycinebetaine is also one of the compatible solutes found in the cytoplasm in salt-tolerant plants. Choline is the precursor of glycinebetaine synthesis, which is converted to betaine aldehyde and to glycinebetaine through a series of enzymatic reactions of choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH), respectively. The other pathways known are the direct *N*-methylation of glycine, but choline pathway is the main biosynthetic pathway present in all plant species (Ashraf and Foolad 2007; Fitzgerald et al. 2009).

Halophytic plant species shows the triggered synthesis of glycinebetaine on exposure to high concentration of heavy metals and NaCl. The increased concentration of glycinebetaine serves as an intercellular osmoticum, and the increase corresponds to rise of osmotic pressure and helps in maintaining membrane integrity by protection of cellular structures, viz. chloroplasts and photosystem II. Bose et al. (2014) reported superior ability of halophytes to accumulate glycinebetaine. Han et al. (2013) reported that accumulation of glycinebetaine in response to higher amounts of NaCl delays Cd-induced senescence, possibly by the maintenance of maximum quantum yield efficiency, effective quantum yield of photosystem II and electron transport rates. Transgenic plants having transgenes for glycinebetaine or proline have not been accepted as they could not produce the required amount of glycinebetaine or proline that can ameliorate the abiotic stresses. Alternatively Ashraf and Foolad (2007) demonstrated that external application of GB or proline to plants under stress has significant effects. Lefevre et al. (2009) reported oversynthesis of glycinebetaine in leaves of *Atriplex halimus* under Cd stress, whereas in *Kosteletzkya virginica*, copper stress exhibited the same results (Han et al. 2012).

Sesuvium portulacastrum is a well-known metallotolerant halophyte and also accumulates trans-4-hydroxyprolinebetaine and 3,5,4-trihydroxy-6,7-dimethoxyflavone 3-glucoside. In contrast the concentration of glycinebetaine decreased in *Suaeda salsa*, in response to Cd stress with increase in choline (Liu et al. 2008). As betaine is synthesized from choline, the authors suggested that the elevated choline should be related to the depleted glycinebetaine.

Table 6.2 Effect of heavy metal stress on osmoprotectant levels in different halophytes

Halophytes	Heavy metals	Response	Reference
Aeluropus littoralis	Cd, Co, Pb and Ag	Increased proline levels	Rastgoo and Alemzadeh (2011)
Mesembryanthemum crystallinum	Cd	ROS scavenger	Shevyakova et al. (2003)
Zygophyllum fabago	Cd- and Zn-resistant	Increased proline and soluble sugars	Lefèvre et al. (2009)
Suaeda maritima	Inorganic pollutants	Increased proline and soluble sugars	Saiyood et al. (2012)
Atriplex halimus	Cd treatment	Increased proline and soluble sugars	Lefèvre et al. (2009)
		Glycinebetaine	
Kosteletzkya virginica	NaCl and Cu	Quaternary ammonium compounds	Han et al. (2012)
Sesuvium portulacastrum	Metallotolerant	*Trans*-4-hydroxyprolinebetaine and 3,5,4-trihydroxy-6,7-dimethoxyflavone 3-glucoside	Adrian-Romero et al. (1998)
Plantago crassifolia	Salt-tolerant	Proline (Pro) and glycinebetaine (GB)	Pardo-Domènech et al. (2016)
Inula crithmoides	Salt-tolerant	Proline (Pro) and glycinebetaine (GB)	Pardo-Domènech et al. (2016)
Microalgae	Cd	Increased proline	Siripornadulsil et al. (2002)
Kandelia candel and	Cd^{2+}, Pb^{2+} and Hg^{2+})	Proline, GSH and PCs-SH	Huang et al. (2010)
Bruguiera gymnorrhiza	Cd^{2+}, Pb^{2+} and Hg^{2+})	Proline, GSH and PCs-SH	Huang et al. (2010)
Ipomoea pes-caprae	NaCl	Proline	Venkatesan and Chellappan (1998)
Suaeda salsa and *Limonium bicolor*	NaCl	Proline	Liu et al. (2008)
Spartina alterniflora	NaCl	Proline	Gorai et al. (2010)
Sesuvium portulacastrum	NaCl	Proline	Moseki and Buru (2010) and Lokhande et al. (2012)
Juncus roemerianus, *J. maritimus* and *J. acutus*	NaCl	Proline	Boscaiu et al. (2013)
Suaeda altissima	NaCl and HM	Proline	Meychik et al. (2013)
Zygophyllum simplex	NaCl and HM	Proline	Sharma and Ramawat (2014)

6.5.3 Soluble Sugars

In glycophytes osmotic potential is maintained to the tune of 50% by soluble sugars under saline conditions. After understanding the physiological mechanism of salt tolerance in halophytes, it was found that there is significant contribution and higher accumulation of soluble carbohydrates under salinity stress (Kerepesi and Galiba 2000; Parida et al. 2002).

Polyols also play a key role in adapting halophytes to abiotic stress, by compensating the reduced cell water potential, and as oxygen radical scavengers; maintain enzyme activities; and protect membrane structures by their hydroxyl groups, in the case of cellular dehydration (Noiraud et al. 2001). Thus, apart from their established functions as precursors of metabolic compounds, they also act as signalling molecules and major cellular energy source under abiotic stresses (Gupta and Kaur 2005; Hare et al. 1998). Parida and Das (2005) stated that carbohydrates act as osmoprotectants ROS scavengers, maintain osmotic balance and serve as molecules for carbon storage under stress conditions.

Sucrose and trehalose sugars accumulate in plants in response to abiotic stresses (Yuanyuan et al. 2009), acting as osmoprotectants, and membranes stabilization (Lokhande and Suprasanna 2012), along with control of several other important metabolic activities. Sugars help to sustain the growth of sink tissues, controlling the expression of several genes either positively or negatively, involved in photosynthesis, respiration and the synthesis and degradation of starch and sucrose (Hare et al. 1998). Trehalose, a non-reducing disaccharide, is highly soluble but chemically unreactive, making it compatible with cellular metabolism even at high concentrations. Trehalose is present in significant concentrations in several bacteria and fungi but rare in vascular plants (Fernandez et al. 2010; Lunn et al. 2014). Resurrection plants are first to observed for trehalose accumulation upon desiccation.

Chai et al. (2013) reported that NaCl reduced soluble sugar content under moderate Cd stress; the possible reason may be that some soluble sugars were used to synthesize proline by providing carbon skeleton and energy (Manuel and Reigosa 2001). However, the slightly reduced levels of soluble sugar under severe Cd stress may be related to the alleviated osmotic stress with addition of NaCl. Thus, the mechanism of soluble sugar in halophytes in response to NaCl under different Cd stresses may be varied. In the plants Syrian beancaper (*Zygophyllum fabago*) and *Atriplex halimus*, soluble sugars accumulated in the most of the Cd- and Zn-resistant plants, and also they had higher concentration of soluble sugars than the sensitive plants in response to heavy metal stress (Lefevre et al. 2009).

6.6 Conclusions

Halophytes are expected to be more capable to cope with heavy metal stress than glycophytes. One of the main tolerance mechanisms of halophytes involves oxidative metabolism. Halophytes have inherent salinity-tolerant oxidative metabolism which also confers heavy metal tolerance. The coordination of enzymatic and non-enzymatic antioxidative system in halophytes plays a very important role in providing salinity and heavy metal tolerance. Sulphur metabolism also plays an important role in heavy metal tolerance in halophytic plants via the synthesis of glutathione, phytochelatins and metallothioneins. Glutathione, phytochelatins and metallothioneins contribute towards metal detoxification and compartmentalization in halophytes. GSH maintains the redox potential and contributes towards increased HM tolerance in halophytes and is an important antioxidant metabolite. Minor roles of phytochelatins and metallothionein in ROS scavenging have also been proven. The accumulation of osmoprotectants like proline, glycinebetaine and sugars under heavy metal stress in halophytes results in osmotic protection, thus maintaining water status and nutrient uptake. Halophytes can be suitable candidates for phytoremediation/phytostabilization of metal-contaminated areas due to their high tolerance to heavy metals (Fig. 6.2).

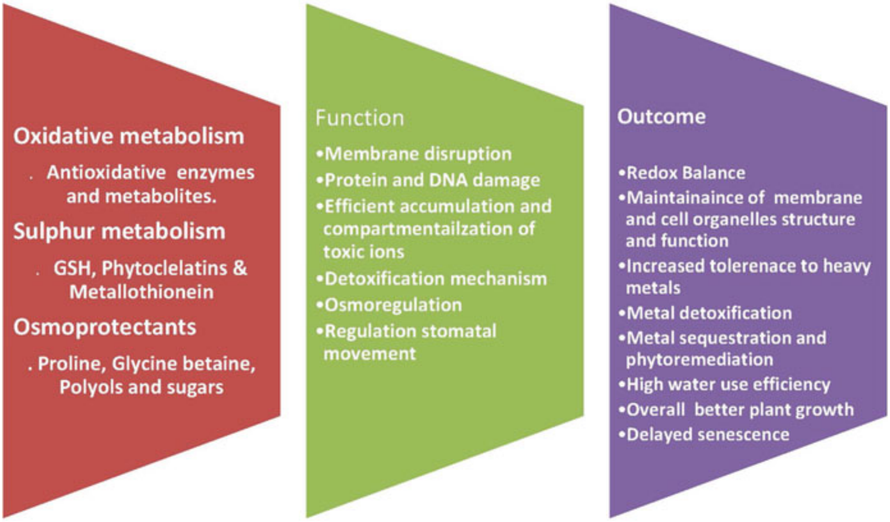

Fig. 6.2 Effects of oxidative metabolism, sulphur metabolism and osmoprotectants on heavy metal tolerance and detoxification mechanism in halophytes

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Chapter 7
Molecular Mechanisms of Osmotic Stress Recovery in Extremophile Plants: What Can We Learn from Proteomics?

Nèjia Farhat and Ahmed Debez

Contents

Abstract During their life cycle, plants are often exposed to phases of high salinity and dehydration stress. Extremophile plants have evolved mechanisms of stress tolerance allowing them to survive or recover from extremely adverse conditions such as water deficit stress and soil salinity. Plant adaptability environmental constraints are linked with deep modifications in proteomic profile, with relevance in abiotic tolerance. Research in extreme drought and high salinity tolerance in resurrection plants and halophytes, respectively, provided some insights into stress tolerance and stress recovery through dynamic changes in protein abundance. Identified proteins under drought and salinity conditions cover a wide range of biological functions: photosynthesis, energy metabolism, protein synthesis, protein folding and degradation and defence response. Proteins related to antioxidant metabolism and scavenging of oxygen radicals were found with higher abundance in halophytes and resurrection plants enabling them to cope with stressful conditions. Comprehensive data from recent proteomics studies confirming the relationship between stress tolerance and specific protein abundance are summarized in this paper.

Keywords Drought · Salinity · Halophytes · Resurrection plants · Recovery · Proteomics

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7.1 Introduction

Plants are frequently subjected to a variety of abiotic stresses which negatively affect plant performance and yield crop. Drought and salinity are major constraints limiting plant growth resulting in a huge restriction of world crop production (Barnabas et al. 2008; Athar and Ashraf 2009). Many studies revealed that plant responses to abiotic stresses through a network of regulatory mechanisms with specific characteristics for various species (Rodziewicz et al. 2014). According to Munns (2002), primary responses to water deficit stress and salinity have been considered typically similar. Indeed, these two constraints share dehydration that reaches, more or less intensely, all plant parts (Chaves et al. 2009). Nevertheless, under long-term salt stress, plants are responding not only to dehydration but also to ion toxicity (Chaves et al. 2009). Both soil salinity and water stress have been considered as transient conditions. Thus, fast and efficient recovery from these stresses may play a crucial role in plant stress adaptation (Chen et al. 2016). Nevertheless, previous investigations focused on plant stress response and ignored to evaluate plant recovery aspects after stress release. Recently, more attention has been devoted to stress release in plants (Perrone et al. 2012; Fang and Xiong 2015), which is considered as a major component of stress tolerance. The active management linking between different adaptive strategies at physiological and metabolic levels that result in dynamic changes in protein abundance can explain the ability of extremophile plants to alleviate and recover from the detrimental effects of a variety of biotic and abiotic stresses (Ghosh and Xu 2014; Kumari et al. 2015). These changes can be best explored using proteomic approach since proteins are the central players of an extensive range of cellular processes (Ghosh and Xu 2014). This powerful tool allows global investigation of plant proteomes at different levels and can be useful to compare and analyse proteome changes under stressful conditions (Fernandez-Garcia et al. 2011). The ability of extremophile plants to preserve healthy tissue and recover following stress relief (salt stress and water shortage) is a key feature for stress tolerance. Several model plants adapted to high salinity (halophytes) or prolonged period of water shortage (resurrection plants) have developed efficient adaptive strategies leading them to resist and continue their growth and development processes (Abreu et al. 2013). Halophytes and resurrection plants are of great importance for proteomic studies to further understanding the plant their tolerance to salt and drought stresses, respectively (Dinakar and Bartels 2013; Griffiths et al. 2014; Kumari et al. 2015). In this paper, we highlight at proteomic scale plant responses to salinity and drought that indicate a capacity for stress recovery and adaptability, resulting in improved stress tolerance.

7.2 Drought Stress

The drought has a major impact on plant growth and crop productivity mainly in arid and semiarid regions throughout the world (Gallé et al. 2007). According to the United Nations Food and Agriculture Organization (FAO), drought covers up to 26%

of the earth's land (Pitman and Lauchli 2002; Rehman et al. 2005). Water is the main constituent of all living organisms and required by all known life forms, as a medium for biochemical activities (Xiong and Zhu 2002; Moradi et al. 2018). Drought is a prolonged period of water scarcity, preventing normal plant growth and leading to extensive damage of crops. Most of higher plants are unable to survive under drought conditions (Dinakar and Bartels 2013). Their relative water content is around 85–100% under actively growing conditions and can withstand only moderate dehydration conditions 59–30%. Below 30% of water content, these plants cannot survive (Höfler et al. 1941). By contrast, a small group of vascular angiosperm plants has evolved unique mechanisms to preserve vital cellular components during severe dehydration and thus can tolerate severe water loss. These plants are known as resurrection plants which were used as model plants for studying desiccation tolerance due to their ability to adjust their water content with the relative humidity in the environment (Dinakar and Bartels 2013). The survival water deficit strategies include the rapid downregulation of growth process and the inhibition of water loss resulting in a quick and efficient photosynthetic capacity re-establishment following a rainfall event (Griffiths et al. 2014). The aptitude of resurrection plants to maintain healthy tissues and to restore plant growth through the strong reactivation of many metabolic pathways is a crucial trait of dehydration tolerance (Griffiths et al. 2014). Since desiccation tolerance is controlled by many mechanisms which can be measured at different levels, a combination between different approaches (physiology, proteomics, metabolomics and genomics) should be informative in order to elucidate mechanisms allowing plant adaptation to drought conditions. For its great importance and impact on drought response and adaption, more attention is paid in this paper on proteomics to examine the impact of drought on plant growth and survival.

7.3 Proteomic Analysis of Resurrection Plants

Here, we focused on specific protein families (proteins associated to photosynthetic process, energetic metabolism, stress and defence, protein folding and degradation, etc.) and protein modification that have been strongly linked and characterized as relevant to allow adaptation to limiting water conditions. In the last decades, proteomic approaches involved in the drought response in plants have been extensively studied. However, there are only few proteomic studies in resurrection plants which are limited to some species. Proteome changes upon drought stress confirm that the abundant proteins in the hydrated tissues are related to photosynthetic function and regulation and carbohydrate metabolism (Dinakar and Bartels 2013; Fig. 7.1). In fact, suppression of the photosynthetic electron transport chain is often observed as a consequence of the excess excitation energy related to the enhanced generation of reactive oxygen species (ROS) (Ghosh and Xu 2014). Different research findings on proteome field revealed that the impairment of photosynthetic process and subsequent recovery are key responses found during drought and after water deficit stress release, respectively (Ingle et al. 2007; Wang et al. 2010; Oliver

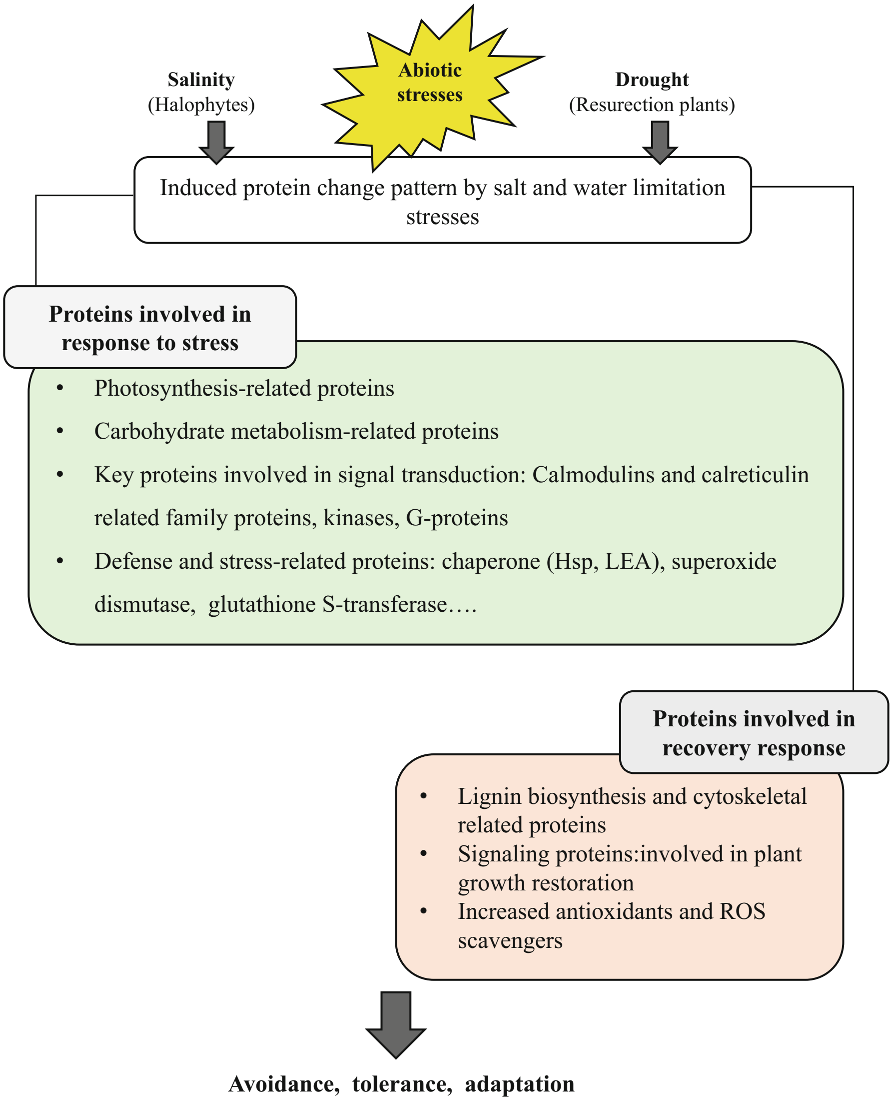

Fig. 7.1 Hypothetical summarizing scheme of proteome change pattern in extremophile plants highlighting the synergism of responses to osmotic stresses (salinity and drought) and during subsequent recovery

et al. 2011). Water scarcity is associated with cell homeostasis and impairment of photosynthetic apparatus (Chaves et al. 2009). The main reason is CO_2 diffusion reduction due to stomata closure (Cornic 2000; Chaves et al. 2009). Proteome changes during dehydration have been elucidated in a relatively drought-tolerant

Populus euphratica by Bogeat-Triboulot et al. (2007). Enhanced abundance of proteins involved in photosynthesis and energy metabolisms such as ATP synthase subunit, ATPase subunit, RuBisCo activase and components of oxygen-evolving complex (OEC) was noticed under water deficit stress conditions. Moreover, an upregulation of proteins related to glycolysis such as GAPDH and PGK was noticed. By contrast, photosynthesis-related proteins (RuBisCo large subunit, chlorophyll a-/b-binding protein and oxygen-evolving complex protein) were downregulated in *Selaginella tamariscina* during dehydration (Wang et al. 2010). Ingle et al. (2007) related photosynthesis impairment in *Xerophyta viscosa* upon drought at 35% relative water content with decreased abundance of photosynthetic proteins such as the two components of luminal oxygen-evolving complex of PSII (PsbO, PsbP), the PSII stability factor HCF136, the α-subunit of the F-ATPase and the transketolase, a Calvin cycle-related enzyme. Similarly, several related proteins to chromatin structure and function, such as the SNF2P protein (an enzyme involved in ATP-dependent chromatin remodelling) in the model resurrection plant *Sporobolus stapfianus*, were found to be enhanced under water deficit stress (Oliver et al. 2011). According to Abreu et al. (2013), such modifications may play an important role on gene expression changes allowing drought adaptation. During dehydration, similar protein profile was shown by Jiang et al. (2007a) in the resurrection plant *Boea hygrometrica,* who related increased abundance of putative ATPase subunits matching a vacuolar H^+-ATPase A subunit to preparation for rewatering. During dehydration, late embryogenesis abundant (LEA) proteins are excessively accumulated in resurrection plants indicating its key role in defence mechanism (Alamillo and Bartels 1996; Ndima et al. 2001). LEA proteins which are known to be synthesized and accumulated in embryo tissue upon desiccation process were identified for the first time in cotton seeds (Baker et al. 1988). It seems that LEA proteins have a great potential to improve crop tolerance to adverse environmental conditions (water deficit stress, salinity and cold). The crucial role of these proteins in cellular protection or mitigation effects of drought stress via ion sequestration and preserving minimum tissue water requirements was well documented (Chakrabortee et al. 2007). Different researches were in accordance to indicate the protective roles ensured by the high accumulation of LEA proteins inresurrection plants during water deficit stress (Michel et al. 1994; Ndima et al. 2001). Phosphorylation of LEA proteins was often described under water limitation, such as in *Zea mays* embryo LEA proteins (Goday et al. 1988) and in *Craterostigma plantagineum* (Röhrig et al. 2006).

Proteome analysis conducted in the resurrection plant *Selaginella tamariscina* revealed downregulation of proteins related to photosynthetic process, energy metabolism, defence- and stress-related proteins and cellular biogenesis under drought conditions (Wang et al. 2010). Antioxidant and energy metabolism-associated proteins were upregulated in *B. hygrometrica* indicating the activation of protective mechanisms in response to dehydration, leading to scavenging ROS, cell wall remodelling proteins, sucrose accumulation, etc. Hence, one can conclude that resurrection plants are able to cope with dehydration through the rapid and efficient accumulation of stress-protective proteins (Dinakar and Bartels 2013).

7.4 Salt Stress

Soil salinity has been considered a major threat affecting crop yield in drylands of the world (Munns 2002). It is estimated that 80 million ha of cultivated lands suffer from salinity problems (Zhang et al. 2012). However, the degree of salt damages depends on the plant age, the duration and the timing of stress (Atteya 2003; Lafitte et al. 2007; Ashraf et al. 2008). Besides, changes in soil salinity can occur in association with many factors: time and space (Epstein and Rains 1987), soil management, water properties, irrigation technique and climate change (de Lacerda et al. 2005). These fluctuations can affect crop adaptability to salt stress, by enhancing or reducing salinity impact on plant responses. The primary salinization of water naturally occurring increase salinity input by evapo-concentration, decrease freshwater input or increase freshwater extraction (Himabindu et al. 2016). By contrast, secondary salinization due to anthropic activities can generate more accented problems (Chaves et al. 2009; Himabindu et al. 2016). For their survival and growth re-establishment during stress period and subsequent recovery, respectively, plants respond by an adjustment in their metabolic pathways (Ghosh and Xu 2014). The mobilization of the metabolic machinery towards plant acclimation and survival occurs via a complex network based on the interaction of physiological, cellular and molecular events developing in the same time and rapidly (Chaves et al. 2009). In high-salt environments, in addition to osmotic stress imposed by water deficit, plants endure ion-specific stress (Blumwald et al. 2000; Shabala and Mackay 2011). Therefore, excessive soil salinity is found to cause dehydration, ion toxicity and nutrient deficiency, along with a suite of metabolic changes, affecting development of salt-sensitive plants and even some tolerant species (Wang et al. 2003; Flowers 2004; Sobhanian et al. 2011). Dehydration caused by salinity is associated with an impairment of photosynthesis, production of reactive oxygen species (ROS), solute accumulation and ion injury (Ashraf and Harris 2004). Understanding plant responses to individual or combined effects of drought and salt stress can play a determinant role in preserving plant productivity and phyto-resources grown under these conditions (Chaves et al. 2009). Adequate management techniques as proteomic approach have become a powerful tool allowing to better understand plant responses to adverse conditions and to improve resource use efficiency by plants (Rodziewicz et al. 2014).

7.5 Proteomic Analysis in Halophytes

Severe osmotic imbalance developed from excessive concentrations of salt leads to harmful modifications at various levels in cellular components (Vinocur and Altman 2005). To counter the adverse effects of salinity, halophytes respond by effective coordination between various adaptive mechanisms responsible for delivering salinity tolerance. To cope with salt stress, plants respond with increase or decrease the abundance of proteins which protects them and avoids the damaging effects of salt stress (Kumari et al. 2015). Hence, more attention has been given to halophytes which play a key role in proteomic research leading to elucidate their salt-adaptive mechanisms with the possibility of cloning genes and transferring the tissue tolerance trait to glycophytes (tobacco, rice, *Arabidopsis*) (Tang et al. 2011). Proteomic studies conducted in several halophytic species such as *Suaeda aegyptiaca* (Askari et al. 2006), *Salicornia europaea* (Fan et al. 2011), *Cakile maritima* (Debez et al. 2012), *Aeluropus littoralis* (Azri et al. 2016), *Thellungiella halophila* (Wang et al. 2013) and *Halogeton glomeratus* (Wang et al. 2015) have identified numerous salt-responsive proteins which fulfil a vast diversity of functions (Fig. 7.1): photosynthesis, carbohydrate and energy metabolism, cell growth and division, protein synthesis and folding, stress and defence, etc. (Zhang et al. 2012).

Photosynthesis-related proteins are differentially changed under saline conditions. RuBisCo a Calvin cycle enzyme, is implicated in the first major stage of carbon fixation process and the competing photorespiration pathway (Spreitzer and Salvucci 2002). Sengupta and Majumder (2009) found that RuBisCo (large subunit and small subunit) was upregulated in *Porteresia coarctata* leaves. However, RuBisCo LSU and RuBisCo SSU activity has slightly reduced in *Aeluropus lagopoides* (Sobhanian et al. 2010). According to Askari et al. (2006), plants need adequate photosynthetic rate to deal with salt stress. Increased CO_2 assimilation was also observed in some halophytes such as *Suaeda aegyptiaca* and *Suaeda salsa* when grown under saline conditions, activating numerous photosynthetic enzymes. The preservation of adequate photosynthetic rate under such conditions in *Suaeda aegyptiaca* was strongly related to enhanced abundance of reaction centre proteins (D1 and D2). Impairment of energy metabolism during salt stress can be related to the high amount of needed energy by plants for their growth and development. This energy is mainly produced through glycolysis process, TCA cycle, ATP synthesis and electron transport chain (ETC) (Chitteti and Peng 2007; Du et al. 2010; Manaa et al. 2011). In a study conducted by Wang et al. (2009), several glycolytic and Krebs cycle enzymes and ATPase isoforms were found to be with higher abundance in *Salicornia europaea* subjected to salt. Other proteins involved in the glycolytic pathways (triosephosphate isomerase, glyceraldehyde-3-phosphate dehydrogenase, PGK and enolase) showed enhanced relative abundance in *Aeluropus lagopoides* (Sobhanian et al. 2010). In addition, an increased accumulation of mitochondrial F1-ATPase beta subunit, ATP synthase CF1 alpha subunit and F1-ATPase, involved in ATP synthesis, has been reported by Wang et al. (2008a) in *Physcomitrella patens* in response to salt stress. According to Zhang et al. (2013), the control of ATP metabolism is an adaptive strategy to deal with high salinity.

Under salt stress, reactive oxygen species (ROS) are abundantly accumulated (Polle 2001), as a result of osmotic stress and nutrient imbalance (Munns and Tester 2008). An excessive generation of ROS may exceed the plant antioxidant defence system, resulting in oxidative stress that may disturb cell homeostasis and, consequently, may be implicated in programmed cell death activation (Dat et al. 2000). An efficient antioxidant defence machinery involving enzymatic and non-enzymatic systems has found to appear at a high level to scavenge ROS and to adapt to high salt levels. According to Xiong and Zhu (2002), the capacity to reduce oxidative damage seems to be an adaptative trait to enhance stress tolerance. Proteomic studies on several salt-responsive species (*Solanum chilense,* canola and *S. europaea*) showed a higher abundance of SOD in response to salt stress (Wang et al. 2009; Zhou et al. 2011), revealing its crucial role in defence response. Increased SOD levels were also noticed in *Tangut nitraria* (Cheng et al. 2015). However, its activity was induced in *Puccinellia tenuiflora* treated with 50 mM NaCl but significantly diminished when exposed to 150 mM NaCl (Yu et al. 2011). *Suaeda aegyptiaca* plants exposed to salt treatment, levels of antioxidant enzymes such as cytosolic isoform of Cu/Zn-SOD, GPX, quinone oxidoreductase, stromal isoform of APX as well as enzyme cyanase involved in degradation of cyanide ions were induced (Askari et al. 2006). Different studies have indicated that the salinity tolerance is strongly related to the antioxidative defence activity (Abogadallah 2010; Gupta and Huang 2014). Moreover, to avoid the risk of protein misfolding or unfolding which may result in non-functional proteins, cells produce proteins with chaperone functions such as chaperones, like heat-shock proteins (HSPs), as well as cytosolic, chloroplastic and mitochondrial chaperonins (Kosová et al. 2011; Kumari et al. 2015). The effect of salinity on HPS70 which are involved in various cellular processes was well discussed by Cheng et al. (2015) and Sobhanian et al. (2010). Changes in proteins involved in signal transduction were also observed under adverse conditions, including salinity (Zhang et al. 2013). These comprise receptors situated in the plasma membrane (PM) or in the cytoplasm, G protein, calcium-sensing proteins and phosphoproteins involving activation of kinase cascade (Ghosh and Xu 2014). Different families of Ca^{2+} signalling-related proteins were identified in plants, such as calmodulin (CaM) and calreticulin (CRT) (Cheng et al. 2009; Li et al. 2010) which were found to be upregulated by salt stress. The key role of calmodulins (CML) in the transduction of stress-response signals is reported in many studies. Increased tolerance to water shortage and salinity conditions was observed in the transgenic *Arabidopsis* expressing rice CML (OsMSR2) (Xu et al. 2011). The calreticulin (CRT), another Ca^{2+-} binding protein, which is involved in calcium signaling in the endoplasmic reticulum (Qiu et al. 2012), is differentially accumulated in response to salt stress (Jiang et al. 2007b; Aghaei et al. 2008). Moreover, increased number of 14-3-3 proteins was often observed in plants exposed to high salinity, such as GF14a and GF14b in rice (Malakshah et al. 2007), 14-3-3-like protein A in wheat (Wang et al. 2008b) and 14-3-3 proteins in sugar beet (Yang et al. 2012). These proteins may play a key role in plant development (Roberts 2003) since they are known as positive regulators of the electrochemical gradient across the plasma membrane (Denison et al. 2011).

7.6 Recovery Aptitude in Extremophile Plants Dictates Survival

Recovery aptitude after salt/water stress may be strongly related to the severity and duration of applied stress. Under continuous drought conditions, yield loss is unavoidable (Chen et al. 2016). In their natural biotopes, crops are exposed to continuous cycles of drought and rehydration (Perrone et al. 2012). After stress release, plants require to resume rapidly their growth. The recovery phase is very complex that linked the readjustment of distinct processes to repair detrimental effects caused by water deficit stress leading to plant growth restoration (Chen et al. 2016) (Fig. 7.1). Generally, plants exposed to moderate stress quickly re-establish after water deficit stress release as compared to plants subjected to acute dehydration. In the latter, only 40–60% of the maximum of photosynthetic process is restored 1 day following stress release, and photosynthesis re-establishment endures few days, without always recovering maximum levels (Grzesiak et al. 2006; Gallé et al. 2007). Rewatering (for 10 days) of *Populus euphratica*, subjected previously to drought stress, was associated with increased abundance of some photosynthetic-related proteins, such as RuBisCo activase and proteins of the water-splitting complex (Bogeat-Triboulot et al. 2007). Hence, as soon as water shortage is relieved, plants start the stress-release cycle that can be distinguished by an active adjustment of proteome profile. For example, increased abundance of actin isoform B was found in different parts of soybean seedlings (leaf, hypocotyl and root) exposed to water deficit stress and following stress release (Mohammadi et al. 2012), indicating that actin may play a critical role in repairing injured membranes. Similarly, accumulation of proteins related to lignin biosynthesis, an important component of plant cell wall, was usually described under drought conditions. Modification in the cell wall is known to maintain cell osmotic balance and protective membrane integrity, which is of great importance to plant drought stress adaptability (Ghosh and Xu 2014). Among these proteins, caffeoyl-CoA 3-O-methyl-transferases and class III plant peroxidases showed enhanced abundance in roots of wild watermelon and maize plants (Yoshimura et al. 2008; Degenhardt and Gimmler 2000), during rewatering conditions.

Contrary to drought stress, few studies are trying to evaluate plant response to recovery phase after salt stress mitigation in the root environment, while the soil salinity has been considered a transient condition (Amzallag 1997; Pardossi et al. 1998). As for water limitation, modification in the cell wall was also observed following recovery from salt stress (Fig. 7.1).

Different cytoskeleton-associated proteins were commonly altered during water deficit stress and rewatering conditions, such as actin (Xu et al. 2010; Cao et al. 2017), profilin (Cao et al. 2017), tubulin (Peng et al. 2009; Pang et al. 2010) and other proteins associated with cytoskeleton dynamics. These alterations were found to be strongly related with other physiological responses, such as morphological response. In fact, the downregulation of profilin in *Amygdalus mira* roots resulted in a significant reduction of filamentous actin number leading to actin disorganization. These modifications were concomitant with the morphological aspect of *Amygdalus mira* roots which became shrivelled and brown (Cao et al. 2017).

7.7 Conclusion

Both salinity and drought are considered among the primary causes of plant loss worldwide. This review provides information of plant responses to salinity and water limitation at a proteomic level leading to elucidate adaptive mechanisms of salinity and drought tolerance in halophytes and resurrection plants. It seems that proteins may play a critical role in making these plants tolerant by minimizing ionic and osmotic effects. We can conclude that generally under abiotic stresses such as salinity and dehydration, proteins and metabolites related to photosynthesis are downregulated in tolerant species. Activation of various defence mechanisms together with upregulation of energy metabolism-related proteins and accumulation of high levels of osmoprotective compounds was often observed in these plants. At the recovery phase, rearrangement of proteome repertoire was found following salinity and drought stress, thus leading to repair injuries caused by drought and salinity. Future investigations on plant recovery aptitude are expected to improve our understanding of plasticity, enabling halophytes and resurrection plants to tolerate abiotic constraints to which they are exposed.

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Chapter 8
Halophytic Microbiome in Ameliorating the Stress

**Ahmad Mahmood, Ryota Kataoka, Oğuz Can Turgay,
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Contents

Abstract Stress environments hinder the crop growth and development, and under ever-increasing food demand circumstances, concerns of food security have asked for exploring options to overcome such stress conditions. High soluble/exchangeable salt stress referred to as salinity stress resulting from environmental characteristics (i.e., climate and soil parent material) and human-induced factors such as fertilization and irrigation poses serious threats to crop production in saline areas on different extents ranging from low to very high, categorically. This stress affects the plant growth through osmotic stress, which ultimately leads to several physiological disruptions including oxidative stress, nutrient imbalance, and water uptake problems. Subsequently, halophytes gained importance for their accumulation capability leading toward the development of phytoremediation techniques when manipulated through anthropogenic activities. The diversity of halophytes in such conditions

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offered a huge genetic pool together with wide options for recultivating such saline areas. The variety of halophytic plants also put forward the promising microorganisms associated with such plants helping in ameliorating the stress through various mechanisms, viz., antioxidant and other stress-related exudates production, 1-aminocyclopropane-1-carboxylate deaminase release, chelating agents production, and expression of stress-related genes along with widely understood enhancement of the plant growth through a multitude of processes. Such organisms including bacteria, fungi, and arbuscular mycorrhiza, epiphytic or endophytic, have been reported to enhance the phytoremediation potential of halophytes. Keeping in view the potential of halophytes and associated microbiome, this chapter will focus on genetic and agronomic potential of halophytes and role of allied microorganisms in enhancing the salinity tolerance and assisted phytoremediation of saline soils.

Keywords Halophytes · Plant growth-promoting bacteria · Plant growth-promoting fungi · Mycorrhiza · Saline soils · Salt marshes

8.1 Introduction

There are many halophyte definitions which deal with EC and NaCl concentrations that plants can tolerate. Practically halophytes are plants that tolerate salt concentrations that do not allow to live other species (Flowers and Colmer 2008). There are approximately 1450 halophytic plant species documented (eHALOPH Database), while we consider a total number of plant species which is approximately 350,000 (The Plant List Database); the percentage of halophytes in total plant species is only 0.4%. Saline habitats have great diversity from tidal marshes and coastal lagunas to inland salt lake shores and salt deserts. Even though great majority of halophytic plants concentrated on few plant families such as Amaranthaceae and Poaceae, the rest of them are dispersed to more than 50 plant families (eHALOPH Database). Since saline habitats and evolutionary history of halophytes are diverse, they have many different adaptation mechanisms. And most of them have more than one adaptation mechanism to be able to survive in saline places. There are many studies conducted to understand their adaptation mechanisms, but most of them concentrated on their morphology, anatomy, physiology, gene regulation, and ecology. Halophyte microbiome interactions as an adaptation mechanism are quite a new subject and got attention in the last decade. However, information about plant growth-promoting microorganisms colonizing in the halophytes and their role in adaptation to saline environments is limited. Still, many reports have been existing that plant growth-promoting microorganisms can assist plants in extreme conditions. The bacteria help the plants by nitrogen fixation, increasing nutrient availability, and production of certain metabolites which are promoting plant growth. The fungi help the plants with the modifications of root architecture, solubilization of certain minerals from decaying organic matter such as phosphorus, and the production of certain metabolites which plants needed to be fit in saline conditions.

Many places around the world are facing with increasing population to feed and decreasing freshwater resources. Saline and sodic soils impact nearly 20% of the all irrigated land surface and 2% of all dryland agricultural land surfaces in the world (FAO 2018). While we consider three-fourth of the earth surface covered with salty water, understanding of halophyte adaptations became more and more important. Halophytes can be used for human benefits directly as a crop or as a gene resource for biotechnology; plant-promoting microbiome that associated with halophytes is a promising resource which can be applied to glycophyte crops to increase salt resistance and yield.

8.2 The Halophytic Microbiome

The interaction among living organisms has a long history, where cases of synergism have gained importance among the beneficial relationships. The microbes being consistently on one side have been successfully fulfilling this synergism with macro-, meso-, and microflora and fauna. The anthropogenic factor led to manipulation of such natural relationships, and consequently, identification and application of such instances came into study and application. Plant-microbe interaction has developed certain shapes including antagonism and synergism, where the latter, besides providing space and food, also utilizes such relationships for coping biotic and abiotic stresses. Same is the case in the halophytes which in combination with epiphytic and endophytic microbes cope the stress more efficiently (Ruppel et al. 2013), serving as ecological stress tolerance along with genetic processes. The microbes in the discussion include fungi, bacteria, and archaea, which have different extent of salinity tolerance and ameliorating the stress. The fungi include epiphytic and endophytic species, along with the endomycorrhiza and ectomycorrhiza, the bacteria, and archaea also categorized as endophytic and epiphytic. Instances of such microbes from extreme environments, and their adaptation to the particular locale (Imhoff 2017; Siliakus et al. 2017), especially isolations from saline habitats indicate that the microbes have promising ability to counter such stress.

Such microbes depending on their ability to grow in the saline environments can be categorized as halotolerant and halophilic. The former can, occasionally, tolerate up to 25% sodium chloride (NaCl), and among the latter, microbes needing salts for their growth: the non-halophiles require less than 1% NaCl, slight halophiles grow in 1–3% NaCl, moderate halophiles grow in 3–15% NaCl, and the extreme halophiles can grow in an environment containing 15–25% NaCl concentrations (Margesin and Schinner 2001; Ventosa et al. 2008). The heterotrophic nature of the microbes contrasting to the autotrophs has enabled the formers with adaptation toward certain environments, as of saline, resulting in an abundance of microbes even in saturated environments. The tolerance and utilization mechanisms discussed later in the chapter bring forward the prospects of such microbes in saline and hypersaline soils.

Wide range of habitats has resulted in halophilic and/or halotolerant microbes, for instance, salt lakes (Hedi et al. 2009), seacoasts (Kumar et al. 2012), arctic terrains

(Yukimura et al. 2009), salt mines (Enache et al. 2014), plants pickled in salt solution (Abou-Elela et al. 2010), soil (Orhan and Gulluce 2015), and endophytic environments (Zhao et al. 2013). Several examples of isolation from habitats mentioned above and application to other crops have shown salinity tolerance, along with enhancing the plant growth. Halophiles are also tolerant to temperature (Kunte et al. 2002), pressure, and dryness (Mesbah and Wiegel 2012), suggesting their biotechnological potential too. Halotolerance and halophilicity show different responses and adapt to such circumstances differently, offering the manipulation of such interactions for enhancing required and ever sought better plant growth.

8.2.1 Plant Growth-Promoting Bacterial Relationships in Saline Habitats

The bacterial interaction with the plants, halophytes particularly, offers the potential of ameliorating the salinity along with enhancing the growth of plants. Different species of bacteria, endophytic and epiphytic isolated from diverse kind of halophytic plants and applied for the amelioration of stress, are summarized in Table 8.1. The diversity of halotolerant bacteria has been reported from rhizosphere soil, and endophytic environment and genera like *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, and *Pseudomonas* have been reported as enhancing salt stress tolerance in diverse kind of plants (Paul and Lade 2014). The isolations of endophytic bacteria from *Medicago truncatula*, followed by sequencing analysis, revealed similarities of the isolates with reported halotolerant and halophilic bacteria (Yaish et al. 2016). The study further documented the alteration of the bacterial community due to salinity and PGP mechanisms. Another instance showed the effect of salinity on the metabolism of rhizobacteria (Szymańska et al. 2016), suggesting the hinderance in physiology, thus leading the bacteria toward tolerance and utilization of salts. Such circumstances lead toward the biochemical and genetic adaptation of bacterial communities toward adverse environments (van der Meer 2003), such as salinity. Similarly, the plants that struggle growing in saline areas lead toward recruitment of bacteria, already adapted to such environments, helping the plants grow well.

The bacteria help the plants thrive in extreme environments through plant growth promotion by nitrogen fixation, increasing nutrient availability, and production of certain metabolites, as well as coping the stress through ACC deaminase, activation of defense mechanisms like cell wall restructuring, and release of exopolysaccharides (Rampelotto 2010). Additionally, the problem of nutrient fixation within the soil, phosphate as an example when applied in the saline soils, is quickly immobilized, and bacteria capable of solubilization can help increase availability leading toward better plant growth (Goldstein 2009). The plant growth-promoting bacteria (PGPB) further categorized as endophytes (PGPE) and rhizobacteria (PGPR) show similar mechanisms for stress tolerance. The endophytic

Table 8.1 Halophyte-associated bacteria showing plant growth-promoting traits

Species	Associated halophyte	Habitat	Mechanisms shown	References
Bacillus sp.	*Arthrocnemum macrostachyum*	Endophyte		Navarro-Torre et al. (2017)
Bacillus sp. and *Arthrobacter pascens*	*Atriplex leucoclada*, *Haloxylon salicornicum*, *Lespedeza bicolor*, *Suaeda fruticosa*, and *Salicornia virginica*	Rhizosphere	Phosphate solubilization, bacteriocin, osmolytes, and siderophore production, increase in antioxidant enzyme activity	Ullah and Bano (2015)
Bacillus endophyticus, *Bacillus tequilensis*, *Planococcus rifietoensis*, *Variovorax paradoxus*, and *Arthrobacter agilis*	*Salicornia europaea*	Endophyte		Zhao et al. (2016)
Bacillus licheniformis	*Suaeda fruticosa*	Rhizosphere	Indole acetic acid, ammonia production, phosphate solubilization	Goswami et al. (2014)
Arthrobacter sp. and *Bacillus* sp.	*Salsola grandis*	Rhizosphere	Siderophore and indole acetic acid production	Kataoka et al. (2017)
Brachybacterium saurashtrense	*Salicornia brachiata*	Rhizosphere		Jha et al. (2012)
Pseudomonas sp.				
Bacillus subtilis	*Puccinellia tenuiflora*	Commercially available		Niu et al. (2016)
Enterobacter sp.	*Psoralea corylifolia*	Rhizosphere and endophyte	Indole acetic acid production	Sorty et al. (2016)
Halomonas sp.	*Salicornia* sp.	Rhizosphere	Ammonia and indole-3-acetic acid production, phosphate solubilization	Mapelli et al. (2013)
Variovorax paradoxus	*Suaeda physophora*	Rhizosphere	1-aminocyclopropane-1-carboxylate (ACC) deaminase activity	Zhou et al. (2017)
Micrococcus yunnanensis	*Nitraria tangutorum*			
Planococcus rifietoensis	*Kalidium capsicum*			

bacteria being facultative, and spending part of their life in the soil, also depict the potential of horizontal gene transfer, and other gene sharing strategies, thus enabling the widespread bacteria with stress tolerance.

Microbes when exposed to high salts environment show loss of turgidity and dehydration of cytoplasm due to water potential difference (Paul and Lade 2014). They cope such circumstances by maintaining the salt concentration inside the cells initially through uptake of (potassium ions) K^+ (Whatmore et al. 1990). Rhizospheric bacteria have also been reported to make turgid biofilms by certain polymers (Xiang et al. 2008) protecting themselves from salinity (Wijman et al. 2007), release of polysaccharides which also help in sheath formation around the roots and in the soil (Chen et al. 2009), and osmolytes production, viz., amino acids, betaines, ectoines, polyols, and sugars including their derivatives for coping various kinds of stresses (Lamosa et al. 1998). The structural changes in the cell membrane through changes in proteins, glucans, and polysaccharides (Paul and Lade 2014), fatty acid composition, and acyl chains (Klein et al. 1999) have also been observed. The osmoregulation showed by bacteria includes the accumulation of compatible solutes, which protect against desiccation and other stress factors (Fernandez-Aunión et al. 2010). Chen et al. (2016a) postulated that bacteria could overcome the high salt stress through storage of sodium ions (Na^+) within the vacuoles, removing Na^+ from the roots, buildup of soluble sugars, improving the antioxidant level, and regulation of stress-related genes in maize. The physical biofilm formation by *Bacillus amyloliquefaciens* also limits effects of salinity on barley, thus proposing amelioration of stress with the help of bacteria (Kasim et al. 2016). Similarly, endophytic bacteria have also been reported producing trehalose-6-phosphate synthase as an example of osmoprotectants (Suárez et al. 2008), ammonium (Jha et al. 2012), volatile compounds, and exopolysaccharides (Vurukonda et al. 2016). The reports of efficient colonization by PGPR even under increased salinity propose the salinity amelioration by plant-associated bacteria.

Certain bacteria, for instance, *Pseudomonas fluorescens*, produced alanine, aspartic acid, glutamate, glycine, and threonine within the cell (Paul and Nair 2008). The same genus has also been observed releasing exopolysaccharides which by retaining water and controlling the carbon sources flux enhance the survival of the microbes under stress conditions (Sandhya et al. 2009). Similarly, the release of oleic acid and cyclopropane fatty acids in the lipid membrane by *Lactococcus lactis* has been reported in osmotic stress (Guillot et al. 2000). Similar to physiological adaptation, genetic adaptations, varied proteomics, and gene regulation have also been reported in bacteria induced by salt stress (Diby et al. 2005; Paul et al. 2006).

8.2.2 *Plant Growth-Promoting Fungal Relationships in Saline Habitats*

The plant growth-promoting fungi (PGPF) have long been known for beneficial effects on plant growth (Hyakumachi 1994) including several genera where *Aspergillus*, *Fusarium*, *Penicillium*, *Phoma*, *Piriformospora*, *Rhizoctonia*, and *Trichoderma* have been reported widely (Hossain et al. 2017). Similar to PGPR, PGPF also enhances the plant growth and helps confer different biotic and abiotic stresses. The mechanisms for plant growth include the modifications of root architecture, solubilization of certain minerals from decaying organic matter, and the production of certain metabolites (Hyakumachi 1994; Meera et al. 1994), whereas the mechanisms of stress suppression include production of antibiotics, enzymes, mycoparasitism, competitions, and the induced systemic resistance (ISR) (Benítez et al. 2004; Khan et al. 2008, 2012). The fungal cells can also melanize their cell walls against abiotic stresses, thus reducing the loss of compatible solutes (Plemenitaš et al. 2008). Similarly, the cell membrane adaptability under the stress circumstances, through regulation of sterol in response to fatty acid modifying enzymes, is another mechanism of salinity tolerance in fungi (Gostinčar et al. 2009; Turk et al. 2004).

The PGPF can also be categorized as halotolerant and halophilic, as they have the ability to adapt to external osmolarity (Ruppel et al. 2013). The report of obligate sodium requirement by fungus *Thraustochytrium aureum* has been published, which cannot be replaced by potassium (Garrill et al. 1992). The fungal associations with plants as affected by environmental and host factors have been studied, where the fungal community was found correlated with the level of salinity (Maciá-Vicente et al. 2012). Fungi have been isolated from vast saline environments like seawater, saline soils, and salt marshes. The isolation of fungus from salterns (Gunde-Cimerman et al. 2000) indicates the potential of fungal survival even in saturated environments.

The resilience of higher fungi to extreme environments is due to their capability of producing osmotic substances, and it was observed that the *Penicillium* spp. and *Aspergillus* spp. could tolerate NaCl concentration as high as 20% or more (Tresner and Hayes 1971). The buildup of certain compatible solutes, for instance, betaine, glycerol, and proline, in their intracellular spaces induces resistance to high salt concentration (Ruppel et al. 2013; Blomberg and Adler 1992). Fungi including soil fungi as well as endophytic fungi can interact with many plant species and can promote plant growth, besides conferring abiotic and biotic stress. *Trichoderma* spp. well known as biological control agent have been isolated as PGPF (Table 8.2). Four types of mechanisms such as ACC deaminase, auxin, and gibberellin production, phosphate solubilization, and ISR for biocontrol in *Trichoderma* spp. have been reported (Viterbo et al. 2010; Contreras-Cornejo et al. 2009; Altomare et al. 1999). At the same time, some *Trichoderma* spp. significantly contributes to the adaptation of plant to salinity stress. Similarly, plant growth promotion and plant resistance were induced against nematodes in wheat by *Trichoderma longibrachiatum* T6

Table 8.2 Halophyte-associated fungi showing plant growth-promoting traits

Species	Salinity tolerance	Habitat/isolated from	Mechanisms shown	References
Trichoderma longibrachiatum T6	150 mM	Rhizosphere		Zhang et al. (2016)
Trichoderma virens Gv. 29-8 *Trichoderma atroviride* IMI 206040 (formerly *Trichoderma harzianum*)	–	Rhizosphere	Auxin	Contreras-Cornejo et al. (2009)
Trichoderma harzianum Rifai 1295-22	–	Rhizosphere	P solubilization	Altomare et al. (1999)
Trichoderma harzianum T-203	–	Rhizosphere	Improvement of plant nutritional level	Yedidia et al. (2001)
Trichoderma asperellum T203	–	Rhizosphere	ACC	Viterbo et al. (2010)
Penicillium simplicissimum GP17-2	–	Rhizosphere of *Zoysia* grass (*Zoysia tenuifolia*)	Systemic resistance	Hossain et al. (2007)
Penicillium oxalicum	–	Rhizosphere soil of pearl millet		Murali and Amruthesh (2015)
Aspergillus ustus	–	Axenic tissue of potato cultures	IAA-related indoles and gas	Angel et al. (2011)
Aspergillus fumigatus sp. LH02	140 mM	Endophytic fungi from root of soybean	Gibberellins	Khan et al. (2011)
Piriformospora indica	300 mM	Endophytic fungi	Auxin and others	Waller et al. (2005)
Fusarium equiseti strains GF18-3, GF19-1	–	Rhizosphere		Saldajeno and Hyakumachi (2011)

along with countering the salinity stress on seedling growth (Zhang et al. 2016). The same group discussed that the enhancement of antioxidant defense system and gene expression might have led to salinity tolerance by the plants. In another example, *Trichoderma harzianum* T83 was isolated and observed promoting the growth of *Suaeda salsa* L., a halophytic species. The fertilizer containing *T. harzianum* T83 effectively promoted the growth of *S. salsa* in soil affected by salinity, besides enhancing the quality of saline coastal soil (Chen et al. 2016b). They also investigated and found that the quantity of amino acids, Ca^{2+}, K^{+}, organic acids, proline, and soluble sugars was higher in *S. salsa* when inoculated with *T. harzianum* T83, and the strain also promoted root vigor and enzyme activities such as peroxidase and superoxide dismutase and reduced the malondialdehyde concentration (Chen et al. 2016b). Similarly, there are some reports of the *Penicillium* spp. and *Aspergillus* spp.

having PGP ability under salt conditions. Their mechanisms are similar to those of *Trichoderma* spp.; however, some reports showed that they were not living in rhizosphere but inside the plant as an endophytic fungus. Khan et al. (2011) showed that endophytic *Penicillium funiculosum* LHL06 helped in countering the salinity stress in soybean along with reprogramming of the plants for improved growth and biosynthesis of isoflavone. The gibberellin production in *Penicillium* strains and the influence of salt stress on the gibberellin production have been reviewed (Leitão and Enguita 2015). Endophytes are attractive potential for the resource that confers plant resistance against abiotic and biotic stress through plant growth-promoting effect. In addition to endophytic *Penicillium* spp., *Aspergillus* spp., *Fusarium* spp., and *Piriformospora indica* stimulated plant growth, and some of them confer enhanced tolerance to salinity and resistance against biotic stresses (Khan et al. 2011; Bilal et al. 2018; Waller et al. 2005). There are still few reports of PGPF under salinity condition, and the future research should be conducted to clear the mechanisms responsible for the growth-promoting effect and investigate the isolates having an ability of plant growth promotion under salinity conditions.

8.2.3 Arbuscular Mycorrhizal Relationships in Saline Terrestrial Habitats

The fungi are chemoorganotrophic; most are aerobic or fermentative organisms referred to molds, mildews, rusts, smuts, yeasts, and mushrooms. They constitute a major portion of soil biota and dominant agents in organic matter decomposition and form important symbiotic relationships with algae, insects, and higher plants as well. Mycorrhizal fungi are the most abundant nonpathogenic and mutualistic symbioses on earth. It is a well-known phenomenon that almost 90% of terrestrial plants are associated with root-colonizing fungi, establishing an intimate and permanent mutualistic symbiosis, called “mycorrhiza.” In 1885, Bernhard Frank recognized these special structures in the roots for the first time and also noticed its physiological role in the soil (Frank 1888). This symbiotic life form has been referred to as “vesicular-arbuscular mycorrhiza” for many years and then replaced by “arbuscular mycorrhiza,” since not all endomycorrhizas of this type develop vesicles, but all form arbuscules (Strack et al. 2003).

The major mycorrhizal associations are “ericoid mycorrhizas” (EM), “ectomycorrhizas” (ECM), and “arbuscular mycorrhizas” (AM). Ericaceous plants are characteristic of acidic or peaty soils and harbor numerous symbiotic fungi, including EM characterized by the fine intracellular coils occupying rhizodermal and/or cortex cells of ericaceous hair roots (Vohnik and Albrechtová 2011). EM extend only a few millimeters from the roots but have been indicated to possess active chitinase and phosphatase to degrade resistant organic components such as lignin, chitin, and cellulose, in these acidic soil environments (Paul and Clark 1996).

ECM contains septate fungal cells infecting the roots of trees and shrubs of temperate regions. The plants such as pine, fir, spruce, hemlock, oak, and birch are almost exclusively ECM. Additionally, the eucalypts, casuarinas, and acacias in the tropics are also ECM. The mycelia of ECM have been proved to participate in water and nutrient absorption. Similar to EM, ECM is closely associated with the decomposition processes in the forest litter and synthesizes a range of enzymes, i.e., phosphatase cellulose and protease, but does not appear to degrade lignin (Paul and Clark 1996).

Exhibiting no discernible root or outside structural change, the endotrophic AM is the most common mycorrhizal symbiosis occurring in the world ecosystems. There is a vast amount of literature emphasizing the fact that 80% of all world plants are colonized by AM fungi. Major plant families such as Brassicaceae, Caryophyllaceae, Chenopodiaceae, and, among the monocots, all families other than Poaceae (grasses) are generally accepted as non-AM due to poor colonization with only a few roots carrying intraradical hyphae (Bothe 2012). However, many crop plants are strongly AM positive, and AM has been reported to be found in many different ecosystems such as deserts (Corkidi and Rincön 1997; Dalpé et al. 2000; Titus et al. 2002), tropical rainforests (Brundrett et al. 1999; Guadarrama and Álvarez-Sánchez 1999; Siqueira and Saggin-Júnior 2001; Zhao et al. 2001; Gaur and Adholeya 2002), aquatic environments (Khan 1993), and strong saline (Carvalho et al. 2001; Sengupta and Chaudhuri 2002) and alkaline soils (Landwehr et al. 2002) as well as from ecosystems with salty marshes (Hildebrandt et al. 2001; Kim and Weber 1985; Hoefnagels et al. 1993; Sengupta and Chaudhuri 1990; Carvalho et al. 2001; Aliasgharzadeh et al. 2001) and halophytes (Ho 1987; Mason 1928; Kahn 1974; Hoefnagels et al. 1993; Brown and Bledsoe 1996; Bothe 2012).

Such diversity in the literature can also explain the reasons for a tremendous number of research efforts aiming at understanding the functional roles of this ancient and widespread symbiotic empire living in the plant root zone. As the most important microbial symbioses for the majority of plants, the benefits serviced to the plant-soil interface by AM fungi can be lined up as (i) regulatory effects on plant water potential under drought (Augé 2001; Füzy et al. 2008; Barzana et al. 2012) and salinity stress (Evelin et al. 2009; Porras-Soriano et al. 2010; Porcel et al. 2012); (ii) supplying plants with phosphate and other nutrients (Smith and Read 1997; Strack et al. 2003; Jeffries et al. 2003); (iii) improvement of water-stable soil aggregation (Andrade et al. 1998; Miller and Jastrow 2000) especially through binding of soil particles by means of a stable hydrophobic glycoprotein, glomalin produced by AM fungi (Wright and Upadhyaya 1998, 1999); (iv) acting as bioprotectants against pathogens (Bødker et al. 1998; Slezack et al. 2000); (v) facilitating the survival of their host plants growing on metal-contaminated land by enhancing their nutrient acquisition and, protecting them from the metal toxicity, absorbing metals (Jeffries et al. 2003; Leung et al. 2013); and (vi) the degradation of organic pollutants (Joner and Leyval 2003).

Despite all these efforts, there are still many challenges to be addressed for AM fungi, especially regarding their contribution to the sustainable maintenance of plant health over challenging climate and soil environments. In this sense, the symbiotic interactions between salt-tolerant plants, i.e., halophytes and AM fungi, have received an increasing attention because the mechanisms of salt and drought stress alleviation by AM fungi exist (Hildebrandt et al. 2001; Ruiz-Lozano and Azcón 2000; Scheloske et al. 2004; Füzy et al. 2008; Aroca et al. 2009; Ruiz-Lozano et al.

2012). Stocker (1928) defined halophytes as plants resistant to higher salinity levels at least during a period of their life that the majority of plants will not survive. Salt marshes worldwide are the common habitats with remarkably similar halophytic diversity and zonal distribution depending on the salt level in soils (Chapman 1960; Walter 1968).

The aim of this section of the chapter, therefore, is to compile the evidence and knowledge concerning AM fungi-halophytic plant symbiosis which existed mainly in salt marsh environments. The main driving factor attracting researchers to explore such connections can be referred to enhancing the potential for implementation of mycorrhizal biotechnology in agricultural plant production under stress conditions, i.e., drought, salinity, and alkalinity, through understanding physiological and molecular mechanisms within mycorrhizal and non-mycorrhizal halophytes.

Salt marshes are usually characterized as the lands influenced by tidal flooding with seawater that leads to partial or total submergence of vegetation, high salinity, and anoxia in the soil. These conditions create an anaerobic and chemically reduced plant rhizosphere causing oxygen deficiency and phytotoxin accumulation (Armstrong et al. 1991). Eventually, plant life, species diversity, and distribution pattern are largely affected by salt and oxygen and concentrations depending on flooding conditions and hot seasons affecting salt movement in soil (Armstrong et al. 1985; Pennings and Callaway 1992). This is the reason for decreasing soil salinity, soil moisture, and anaerobiosis from the lower to the higher zone of a salt marsh, forming a zonated pattern in the vegetation, and may explain complex biochemical, morphological, and physiological adaptations of salt marsh plants to waterlogging and salinity (Naidoo et al. 1992). The rhizosphere microorganisms, especially AM fungi, are therefore believed to enhance the ecological adaptation of these plants, including pioneer plant colonizers, to salt marsh environments (Sengupta and Chaudhuri 1990; Khan and Belik 1995).

Briefly, AMF symbiosis under salt stress was often found to result in enhanced nutrient uptake and production of osmoregulators, higher K^+/Na^+ ratios, and Na compartmentalization within plant tissues and also improved photosynthesis or water use efficiency (Evelin et al. 2009; Porcel et al. 2012). On the other hand, the literature on associations between AM fungi and salt marsh halophytes is somewhat controversial. For example, AM fungi have been indicated to improve plant tolerance to salinity under stressful environments (Jindal et al. 1993; Ruiz-Lozano et al. 1996), whereas some other findings pointed out to suppression of mycorrhizal infection by high soil salinity (Pfeiffer and Bloss 1988; Juniper and Abbott 1993) and soil inundation (Harley and Smith 1983). In between these contrary views, Miller (1999) showed that waterlogging only partially inhibits AM colonization of wetland grasses. Looking at these findings, it can be assumed that the halophyte-AM fungi symbiosis depends on the level of salinity and water content and halophytes that are living in extremely saline and flooded conditions are not colonized by arbuscular mycorrhizal (AM) fungi (Peat and Fitter 1993).

However, distribution of AM fungi in salt marsh ecosystems has been found to be related not only to fluctuating water regimes and saline-soil chemistry but also to host plant species. It was a long time ago that colonization of halophytes by AM fungi had been proved by Mason (1928), subsequently followed by some other researchers (Kahn 1974; Hoefnagels et al. 1993; Brown and Bledsoe 1996). Boullard (1959) indicated that the degree of mycorrhizal colonization within the rhizosphere of the salt aster (*Aster tripolium*) was considerably high and relevant to the amount of carbohydrate supplied by the plant. Rozema et al. (1986) found that there was a substantial degree of variation in AM fungal infections among about 20 salt marsh halophytes. Their field observations indicated that some of the species (*Aster tripolium*, *Limonium vulgare*, *Festuca rubra ssp. litoralis*, *Salicornia brachystachya*, *S. dolichostachya*, *Plantago maritima*, *Glaux maritima*, *Puccinellia maritima*) had a high or intermediate degree of AM infection, whereas other species (*Atriplex hastata*, *Juncus gerardii*, *J. maritimus*, *Spartina anglica*, *Cochlearia anglica*, *Spergularia maritima*, and *Triglochin maritima*) exhibited a very low mycorrhization or even no mycorrhizal hyphae in their root segments. More recently, Carvalho et al. (2001) contended that distribution of AM fungi in the salt marsh is more dependent on host plant species than on environmental stresses and salt marsh halophytes were shown to have different mycorrhization levels. For instance, several halophytes are strongly AMF positive, whereas many halophyte families such as Caryophyllaceae, Plumbaginaceae, or Cyperaceae are known to be non-mycorrhizal (Bothe 2012). On the other hand, the dominant salt marsh grass, such as *Puccinellia spp.*, has a variable structure of AM colonization with many specimens lacking a positive sign of AMF colonization (Hildebrandt et al. 2001; Landwehr et al. 2002). Bothe (2012) stated *A. tripolium* as the best mycorrhizal halophytes as all samples of this plant collected from many different field sites over the years were strongly AM fungi positive with almost all roots showing intraradical hyphae, arbuscules, and vesicles. This can be attributed to well-developed aerenchyma in this species (Rozem et al. 1986). In their greenhouse experiments, Scheloske et al. (2004) indicated that non-colonized *A. tripolium* plants had large aerenchyma, which is typical for plants of often flooded areas, while AMF-colonized *A. tripolium* had much smaller aerenchyma and distinctly more parenchyma cells. Due to its high degree of mycorrhizal colonization, *A. tripolium* was applied as a model plant in many cases for understanding the connections between AMF-plant symbiosis and salt tolerance mechanisms (Carvalho et al. 2001, 2003; Neto et al. 2006). However, mycorrhizal status of *Spartina anglica*, *Juncus gerardii*, and *J. maritimus* are difficult to explain since they have high root porosities but have no mycorrhizal infection (Rozem et al. 1986), which is in accordance with other observations on Juncaceae (Mason 1928; Fries 1944). Boullard (1964) mentioned that the lack of AM fungal infection in *Triglochin maritima* could possibly be due to the resistance of fungal infection, based on the presence of the toxic cyanogenic glucosides and sulfurous substances.

Thanks to advances in methodology and technology achieved over the last two decades, the ecology and diversity of AM fungi have gained new insights into the species that are present within the rhizosphere of halophytes. The PCR-RFLP analysis performed on the AM fungi spores isolated from diverse alkaline soil environments (dominated by NaCl, Na_2CO_3, Na_2SO_4, or $CaSO_4$) in Central Europe indicated that 80% of all spores from the different sites belonged to one single

PCR-pattern which closely matched that of *Glomus geosporum* BEG11 (Landwehr et al. 2002). The preponderance of *G. geosporum* in salt marshes was also confirmed by some other authors in Portugal (Carvalho et al. 2001) and Poland (Grzybowska 2004) or Germany (Bothe 2012) as well. Based on these important findings, *G. geosporum* has been considered to have a specific role in conferring salt tolerance to halophytes, and many experiments over the years were conducted concerning the effects of *G. geosporum* on the growth of various plants in the greenhouse conditions (Bothe 2012). Although some of the results were encouraging, plants inoculated with *G. geosporum* did not gain a consistent resistance against to salt stress over the control trials (Füzy et al. 2008).

However, there are many works in the literature reporting positive results on the alleviation of salt stress of crops by AMF, i.e., Cantrell and Linderman (2001), Feng et al. (2002), Giri and Mukerji (2004), Sharifi et al. (2006), Zuccarini and Okurowska (2008), Porras-Soriano et al. (2010), Wu et al. (2010), and Evelin et al. (2012), which has been extensively reviewed by other authors Evelin et al. (2009), Ruiz-Lozano et al. (2012), and Porcel et al. (2012). Bothe (2012) attributes the high number of experimental results with positive outcomes in the literature to the low publication potential of investigations with failure. Another inconvenience can be changing salt tolerance of *Glomus* isolates differing from saline and nonpolluted soils (Ruiz-Lozano and Azcón 2000). Therefore, such experiments are not easy to perform and mimic natural field conditions.

Consequently, increasing scientific and public attention worldwide on sustainable land management have pointed out to sustainable use of saline-alkaline soil resources through the approaches such as breeding of salt-tolerant plants, engineering plants using different genes, and leaching of excessive salts or desalinizing seawater for irrigation purposes (Evelin et al. 2009). However, most of these approaches are laborious and costly for developing countries (Cantrell and Linderman 2001), and unfortunately, only a few genetic traits of salt tolerance have been explored so far (Schubert et al. 2009). Therefore, an increasing number of investigations have been recently carried to elucidate the role of AM fungi in the alleviation of salinity stress in halophytes (Evelin et al. 2009; Porcel et al. 2012). However, although AM fungi seem to alleviate the salt stress of plants, the results published so far do not appear to be convincing enough.

8.3 Mechanisms of Salinity Tolerance and Utilization

The halophytic microbiome confers salinity tolerance to plants through various mechanisms, indirectly by promoting the plant growth, modifications of root system, and enhancing the supply of certain essential nutrients (Hashem et al. 2016) and directly by influencing the defense system of the plants, through promoting the enzymatic and nonenzymatic defense systems (Ahmad et al. 2015; Wu et al. 2014) in case of AMF, 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Cheng et al. 2007; Mayak et al. 2004), diverse proteins production, accumulation of osmolytes, regulation of genes, and ion transporters, and finally through production of exopolysaccharides (Etesami and Beattie 2018) and buildup of solutes, glycerol being the most common (Zajc et al. 2014), accumulation of Na^+ within the cell (Prista et al. 2005), cell wall melanization (Gunde-Cimerman and Zalar 2014), and reducing the membrane fluidity (Gostinčar et al. 2011), in case of fungi.

The salinity besides affecting the growth and production of plants also limits the activity of microbes (Szymańska et al. 2014). Such problems also cause the biochemical and genetic adaptation toward saline habitats. Archaea adapt to saline environments through the accumulation of salts within the cytoplasm by the function of intracellular enzymes, whereas bacteria being superior in metabolism adapt to such kind of environments by organic solute accumulation (Margesin and Schinner 2001). Generally, the microbes adapt to such habitats through two major strategies, namely, "high salt in," in which the stability and activation of proteins are aimed, and "low salt, organic solutes in" in which significant production and accumulation of organic solutes occur (Ma et al. 2010), like *Halobacillus* recognized as chlorine-dependent species that shows the adaptation toward different levels of salinity through releasing glutamate and glutamine in case of lower and medium salinities and proline and ectoine at higher saline environments (Saum and Müller 2008a, b). These osmoregulators also protect enzymatic structures, leading toward stress tolerance (Lamosa et al. 2000). The mechanisms include salt avoidance through cell membrane modifications, removing the salts out of the cells, and adjustments of the cellular environment by the accumulation of osmolytes, and certain proteins, including enzymes regulations (Ruppel et al. 2013). Finally, the induced systemic tolerance (IST) has also been put forward which is induced by physical and chemical changes with the help of plant growth-promoting microorganisms. The term IST introduced by Yang et al. (2009) encompasses various mechanisms of salinity tolerance showed by microbes. The *Bacillus amyloliquefaciens* induced salt tolerance in *Arabidopsis* has been reported, which also led toward an increase in plant biomass (Liu et al. 2017).

8.4 Prospects

The isolation from halophytes and application to the non-halophytic plants has potential benefits, and a growing interest has been shown toward utilization of halophyte-associated microbiome (He et al. 2018; Navarro-Torre et al. 2017; Yuan et al. 2016). The evolution of salinity tolerance by the halophyte-associated bacteria, either endophytic or epiphytic, can enhance the plant tolerance to the level of salinity, thus enhancing the plant growth even in saline environments eradicating the threat of poor growth (Dimkpa et al. 2009). Widespread saline land and the threat of salinization offer the use of halophilic microbes for remediation and reclamation of soils. Secondly, the new insights suggesting the heavy metal phytoremediation through halophytes assisted by associated microorganisms have shown promising results, as many soils are co-contaminated by salts and heavy metals (Lutts and

Lefèvre 2015). The potential of plant growth promotion by halophytic microbes can be successfully manipulated, leading toward better plant growth even in heavy metal-polluted soils (Dodd and Pérez-Alfocea 2012). Furthermore, the biotechnological options using halophiles and halotolerant microbes can be explored for novel genes and pathways.

8.5 Application of Microbes

Application of such microorganisms to the plants has been practiced through various mechanisms including seed coating, covering, and inoculation, soil application, root dipping, foliar application, and biopriming, each showing potential merits and demerits (Mahmood et al. 2016). For saline environments, the bacterial survival being an issue, broth culture has been applied for inoculation (Ali et al. 2017). Considering the saline environments, the emergence and initial growth of the plants are limited by higher levels of salts, thus asking for either transplantation of hardened plant nursery or efficient osmoregulation assisted by applied halophytic microbiome, allowing plants to withstand salinity, with lesser or no effects on the plant growth.

8.6 Conclusion

The halophytic microbial associations with plants help the latter not only in salinity tolerance but also in amelioration of the stress besides the supplementary functions. The microorganisms, with variations among the functions, help the plants through enhancing the stress-related characteristics in direct mechanisms, improved nutrient availability, and production of certain metabolites in indirect mechanisms, consequently leading toward better plant growth and survival in saline habitats. This relationship can thus be modified and manipulated for the desired plant growth, where besides bioaugmentation, stimulation of local microbes can be carried out through nutrient management. The microbial aspect integrated with phytoremediation can be more sustainable and economical when compared with other saline soils reclamation strategies. The bio-phytoremediation also offers output from least utilized marginal lands, as feed, if not food.

So far, the literature has revealed that there are certain communications between halophytic plants and diverse endophytic and epiphytic bacteria and fungi in which stress suppression mechanisms are directly or indirectly designed to facilitate the survival of these mysterious plants through harsh environmental periods and conditions in nature. Understanding of these connections is crucial not only for pure-science purposes but also for putting this knowledge into the practice under degraded soil environments, where we might have to grow agricultural plants in the future.

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Chapter 9
Economic Utilization and Potential of Halophytes

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Contents

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Abstract Agricultural land is continuously becoming less available for cultivation due to increasing population and unfavourable environmental conditions including climate changes. Salinity, worldwide, is one of the biggest problems for agriculture leading to significant yield losses especially in dry lands. The best solution for proper use of these lands would be by using salt-tolerant crops or crops with phytoremediation properties. Since the phytoremediation potential of salt-tolerant crops is negligible, thus, cultivation of halophytes serves as replacement for crop plants to desalinize the saline or alkaline areas. Halophytes constitute most of natural flora of the saline soils, with maximum survival and productivity. Therefore, there is an urgent need to explore halophytes, which will give an insight into the mechanisms adopted by halophytes for survival and productivity on saline areas. Also, saline agriculture can be made feasible by exploring halophytic growth attributes. In addition, halophytes can serve as alternate crops in waste lands while making them suitable for traditional crops over a period of time. Thus, the importance of halophytes in growing over saline areas not only brings out ecological recovery of saline soils but also produces huge biomass as a biofuel for renewable energy source and ultimately leading of CO_2 sequestration. Hence, the phytoremediation property of halophytes can be tremendously cashed in a more economic way with minimum inputs. In coastal areas, mangroves support the living system w.r.t. agriculture, aquaculture and wild life and also stabilize the coastal saline lands. Mangroves are also providing commercial products in form of wood with multi-uses in coastal areas. In the present review, a brief compilation of the potential and special adaptive biology of halophytic plants under salinity stress is done with the remediation mechanism of these hyperaccumulators plants.

Keywords Halophytes · Phytoremediation · Economic utilization · Adaptive biology · Hyperaccumulation

9.1 Introduction

To overcome the increasing demand of food, fibre and energy, there is excessive irrigation of agricultural land (Brown et al. 2014), and soil salinity increases continuously due to overirrigation of cultivable land with less water use efficiency and poor drainage (Ventura et al. 2015). Total area of agricultural land is continuously decreasing for cultivation of regular crops. Approximately 45 Mha irrigated land is affected by salinity representing more than 20% of total land (Munns and Tester 2008). The salinization of agricultural land is so fast that by the twenty-first century, it may reduce approximately 50% of productive lands (Mahajan and Tuteja 2005). Approximately, 11% of irrigated area across world has already been affected by salinization (FAO 2012). The salt-affected areas are alarmingly increasing in the developing and challenged countries including 1 Mha in Bangladesh (Hossain 2010), 6.73 Mha in India (Sharma and Singh 2015) and 3–6 Mha in Pakistan

(Qureshi et al. 2008), which is very harmful for agricultural production in changing environmental scenario. Increased soil salinity adversely affects seed germination, photosynthesis, respiration, transpiration, membrane injuries and other metabolic activities (Hasanuzzaman et al. 2012) in plants. Agronomic practices alone are not sufficient as corrective measures for saline soils but in addition, use of salt-tolerant crop varieties is also required. The introduction of halophytes with phytoremediation property is more economic and eco-friendly technology for proper use of waste and salty soils. Several studies have been carried out by many researchers during the last decade in which plants with property of removing salts from degraded soils (Ashraf et al. 2010; Devi et al. 2016). Halophytes (salt-loving) are the plants which complete their growth under high saline environments (Stuart et al. 2012), occuring wildly throughout the world. A criterion for the development of halophytic crops covering large fields is to make plants capable to tolerate higher levels of salinity, even equal to seawater saline levels (approx. 500 mM NaCl) (Yensen 2006). Since, halophytes being adapted to environments with salinity levels of 200 mM of NaCl (approx. 20 dS m^{-1}) (Flowers and Colmer 2008), such plants are found abundantly in coastal saline, arid and semi-arid soils, having more evaporation than precipitation (Manousaki and Kalogerakis 2011). Such plant species constitute approximately 1% of total world's flora. Some halophytes can grow better under saline conditions with increased productivity under increasing salinity levels, such halophytes are termed as euhalophytes. The possible adaptive features of such euhalophytes might include balance of redox ions, salt inclusion, osmoregulation, ion homeostasis, ROS defence system, succulence and/or salt excretions which help to cope with saline environments (Hasanuzzaman et al. 2014).

So, the halophytic plants growing well in the highly saline soil can replace traditional crops and are also being used as potential source for food, fuel, fodder, fibre, medicine, etc. (Lokhande and Suprasanna 2012). At the same time, halophytic plant species can be harvested (above ground portion of the plant) which possess desalination property and restore the saline soils with removal of salts. These possible strategies using halophytes can bring the waste and marginal lands in proper cultivation making the unused agricultural soils more productive, thus imparting a new way for enhanced and sustainable crop productivity.

The major concern for agriculture sector is to increase the food production 50–70% (Millar and Roots 2012) to fulfil the increasing demand of food for the projected population of 9.3 billion by 2050 (Ruan et al. 2010). This target is difficult to achieve through the presently cultivable land. Most of the agricultural crops are highly sensitive to salt stress and mainly sodium chloride. A significant reduction in yield (19%) at lowest level of soil salinity EC 2 dS m^{-1} has been reported in beans (*Phaseolus vulgaris*) (Maas 1990), 14% in peppers (*Capsicum annum*), 12% in corn (*Zea mays*) and 12% in potatoes (*Solanum tuberosum*). Although plant breeders are making efforts to develop salt-tolerant crops, it is a difficult and complex task, salinity tolerance being a multigenetic trait (Flowers et al. 2010) and therefore very few salt-tolerant lines of crop plants. For the last decade, the concept of saline agriculture has emerged to evaluate halophytes, majorly for fodder production, under saline areas or with saline irrigation (Ruan et al. 2010).

This chapter summarizes the adaptation and suitability of halophytic plants to improve the farming systems in degraded lands.

9.1.1 History of Halophytes: Success Stories

In the 1950s the aspect of halophytic crop production began, and efforts have been undertaken internationally during the 1970s designated as the “Biosaline Concept” for food and fuels. Boyko (1966) first reported the property of halophytic plants to desalinate soil and water. Later on, halophytes were found as plants that cover a bulk of natural flora of the saline lands with excellent biomass and completing their life cycle on the saline milieu. These observations explored the idea for halophytes as potential salt-tolerant crops (Glenn et al. 1999). Halophytes could not be defined precisely for hundreds of years (Flowers and Colmer 2008), until an open description of “naturally salt-loving plants” was modified, and halophytes were again defined as plants having growth benefits with some substantial amounts of inbuilt salts in the growth media (Shabala and Mackay 2011). This definition was again modified to plants having the capability to complete their life cycle with higher levels of salt, 200 mM NaCl. The optimum concentration of salts for monocot halophytes is approximately 50 mM NaCl, and for dicots, the threshold level is 100–200 mM NaCl (Flowers and Colmer 2008). No significant yield reduction was noticed in *Suaeda maritima* when irrigated with seawater (Greenway and Munns 1980) which is normally beyond the tolerance limit of all cultivated conventional crops. This specific tolerance limit makes halophytes well suitable for “saline agriculture” and is beneficial for a wider community including farmers (Riadh et al. 2010). Twenty-six halophytic species have been characterized as salt-tolerant in Australia alone. Illustrations were made by comparing the effects of salinity. Wheat in general is a salt-sensitive crop; even lowest levels of NaCl strongly suppress its growth and yield. Cuin et al. (2009) noticed a 70% reduction in shoot dry weight at 150 mM NaCl treatment, whereas the grain yield of stressed plants was as low as 6% of the control. Quinoa, a seed crop (family Chenopodiaceae), is highly rich in nutritional values, being cultivated since 7000 years in Andean region of South America. Quinoa plants take benefit of sodium in the growth media at as high as 100–200 mM NaCl and hence behave as a true halophyte. Few quinoa varieties have been reported to grow even in sea water having salinity level of 40 dS m^{-1} (Koyro and Eisa 2008). Quinoa is maximum yielding at salinity levels than wheat. In the USA, the average quinoa grain yield was recorded 1.3–1.9 t ha^{-1}, while in Denmark grain yield was 2–3 t ha^{-1} (Jacobsen et al. 2010). Quinoa also finds commercial use in bakery and confectionary including salads and soups. In view of above results, quinoa can be explored for saline agriculture as an alternate to cereals.

Halophytes are best suited for desalinization and reclamation of saline soil (Flowers et al. 2010), e.g. dry matter of *Atriplex nummularia* (old man salt bush) accumulated 20–40% NaCl in biomass yield of 20–30 t ha^{-1} $year^{-1}$ (Manousaki and

Kalogerakis 2011). *Suaeda fruticosa* (seablite) can extract 2.5 t of salt ha^{-1} year^{-1} in a single harvest when irrigated with saline water (Ghnaya et al. 2005).

Different criteria have been laid out to define halophytes by different scientists. Few definitions are listed below:

1. Plants which are capable of normal growth in saline habitats and also grow out well in normal soils having tolerance for salt concentrations more than 0.5% at any growth stage (Stocker 1928).
2. Plants specifically prefer to grow on saline soils are halophytes (Dansereau 1957).
3. Plants occupying saline soils with solutions of at least 3.3 bar equivalent to 70 mM salts (Greenway and Munns 1980).

9.1.2 Classification of Halophytes

I. Halophytes can also be classified on their habitat.

- (i) Obligate: These halophytes grow only in saline environment with appropriate plant growth and development, e.g. Chenopodiaceae family.
- (ii) Facultative: These halophytes can establish and survive on salt-affected soils, but their threshold performance is achieved only in minimal salty or no-salt conditions. Such plants belong to majorly Poaceae and Cyperaceae families but include some Brassicaceae along with many dicotyledons, e.g. *Aster tripolium*, *Glaux maritima* and *Plantago maritima*.
- (iii) Habitat-indifferent halophytes. Plants which are indifferent for their original habitat but can adapt very well to salt-affected soils.

II. Classification of plants of saline habitats (euhalophytes):

- (i) Salt-requiring halophytes:
  - (a) Obligatory halophytes: Plants depend on salts for their growth and survival, e.g. *Salicornia* sp. and various bacteria and algae.
  - (b) Preferential halophytes: Plants whose growth and development improve in the presence of salts, e.g. *Aster* sp., *Nitaria* sp. and *Suaeda* sp.
  - (c) Salt-enduring: Plants enduring a high protoplasmic salt content, e.g. *Suaeda monoica*.
- (ii) Salt-resistant halophytes:
  - (a) Salt-excluding halophytes: Plants accumulating salts in specific hairs, e.g. *Atriplex* sp. Plants secreting salts from their shoot, e.g. *Aeluropus* sp., *Limonium* sp. and *Tamarix* sp.
  - (b) Salt-evading halophytes: Plant evading salt uptake, e.g. *Rhizophora* sp. Plant evading salt transport into the leaves, e.g. *Prosopisfoxia*

III. Vegetation flora of salt basin in northwest India has been classified into five categories by Sen and Rajpurohit (1978) as below:
   (i) True halophytes: Plants growing in saline soil, i.e. *Aeluropus lagopoides*, *Suaeda fruticosa*, *Salsola baryosma*, *Cressa cretica*, *Zygophyllum simplex* and *Haloxylon recurvum*.
   (ii) Facultative halophytes: These could be defined as plants growing in saline as well as in nonsaline soils. These further have two habitats: (a) mainly saline but can grow in nonsaline areas, e.g. *Trianthema triquetra*, *Launaea nudicaulis*, *Tamarix dioica*, *Eragrostis ciliaris*, *E. pilosa*, *Salvadora persica* and *Cleome brachycarpa*, and (b) preferably no-salts but can grow in saline areas, e.g. *Pulicaria wightiana*, *Euphorbia granulate* and *Indigofera cordifolia*.
   (iii) Transitional halophytes: The type of plants growing only at the transitional margin of saline and nonsaline areas, e.g. *Sporobolus helvolus*, *S. marginatus* and *Haloxylon salicornicum*.
   (iv) Marshy halophytes: Plants growing in waterlogged areas of salt basins, e.g. *Scirpus roylei*, *S. tuberosus*, *Mariscus squarrosus* and *Tamarix troupii*.
   (v) True glycophytes: Plants growing in nonsaline soil, e.g. *Dactyloctenium sindicum*, *D. aegyptium*, *Cenchrus setigerus*, *C. biflorus*, *Citrullus colocynthis*, *Cucumis callosus* and *Solanum surattense*.

Later, Rajpurohit (1980) classified them into three groups:

(i) *True halophytes* growing to their optimum only on saline soil (above 0.5% NaCl level)
(ii) *Facultative halophytes* growing very well on saline (at 0.5% NaCl level) soil as well as on nonsaline soil and behave as halophytes or glycophytes, respectively
(iii) *Glycophytes* growing only in nonsaline habitat for their optimal growth

9.1.3 Non-halophytes/Glycophytes

Glycophytes are the salt-sensitive plants, and their leaves cannot tolerate high levels of salt and are often not much affected by lethal salt concentrations in their natural habitats. Mostly plants can survive at very low levels of salts, but many plants cannot tolerate highly saline soils or water. The dominating salts in saline areas are mostly sodium chloride, releasing sodium and chloride ions in water, and the growth of glycophytes is retarded by these ions. Such plants can survive only in fresh water containing less than 125 parts per million of soluble salts. This tolerance behaviour between halophytes and glycophytes in their contrasting adaptive strategies is significant.

Keeping this adaptive potential of halophytes, these can be explored for the following perspectives (Glenn et al. 1999):

(i) How the halophytes survive and maintain productivity on saline water can be explored for development of tolerant varieties in conventional crops (Zhu et al. 1997).
(ii) Saline agriculture can be understood more through halophytes growing in natural agronomic settings.
(iii) Halophytes can be developed as new model plants (Choukr-Allah et al. 1996).

9.2 Physiology of Halophytes

Salinity causes certain structural changes in halophytes. They have thicker leaves, smaller and fewer stomata, larger cells and presence of well-developed water-storing tissues. Many halophytes show highest degree of succulence (e.g. *Salicornia*) which occurs due to the development of larger cells on the spongy mesophyll and presence of multilayer palisade tissue. On the other hand, salt-secreting halophytes which do not accumulate more salts are generally non-succulent. The possible cellular mechanism of salt tolerance in halophytes, e.g. plants belonging to Chenopodiaceae, is their capacity to survive under high external salt concentrations through osmotic adjustment. As Na^+ and Cl^- ions are harmful, still their concentration in the cytoplasm is maintained lower than in the vacuole. This adjustment of low toxicity is mainly maintained by the osmolytes proline and glycine betaine.

The primary importance of the physiology of halophytes in salt tolerance is to transport and regulation of Na^+ and Cl^- ions. Although halophytes are tolerant to salinity, it has been observed that at germination stage they are less tolerant as compared to later growth stages. Under natural conditions, seeds of halophytes may remain dormant till the onset of rains. The root growth of halophytes is not affected by the presence of salts. The roots of plants such as *Suaeda monoica* and *Atriplex halimus* can reach up to 5 m depth. The roots of some of the halophytes (*Prosopis farcta* and *Alhagi*) have been reported to reach the depth up to 20 m. Differences in ionic concentration in halophytes and glycophytes: Plants can survive at high external concentration of salt as well as high internal concentrations particularly in the leaves. The glycophytes are the plants of nonsaline environments, normally having high K^+/Na^+ ratio in their leaves, whereas halophytes, the plants of saline environments, in which K^+/Na^+ ratio tends to be lower and the overall ion concentration higher.

9.3 Mechanisms Adopted by Halophytes

Salinity is not always harmful for all plants. Lots of studies have been done on distribution, exploitation and physiology of salt tolerance of halophytes (Koca et al. 2007; da Silva et al. 2008). Salts taken up by halophytes do not directly control plant growth by affecting turgor, photosynthesis or the activity of one or another enzyme;

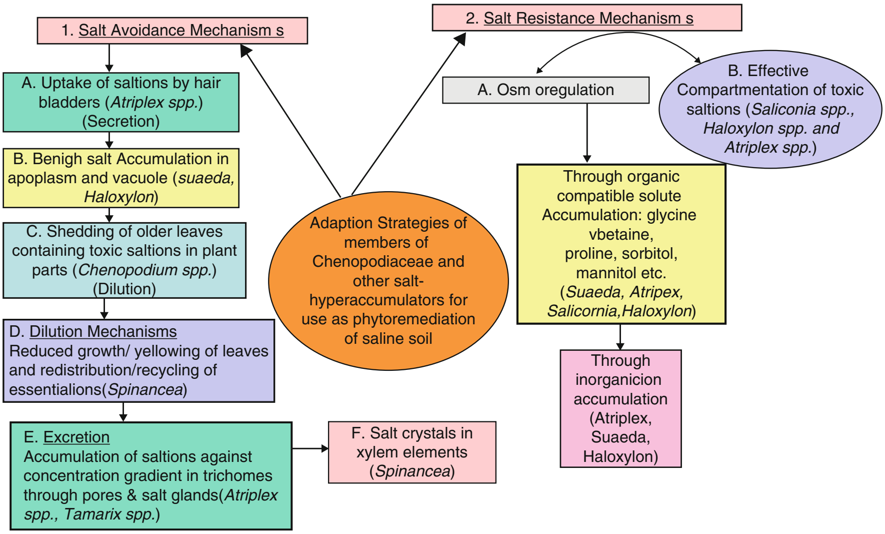

Fig. 9.1 Mechanism of salt avoidance and tolerance in halophytic plants

rather it is the build-up of salts in old leaves which brings about harmful effects. The senescence of older leaves affects the supply of assimilates or hormones to the growing organs and thus affects growth (Munns et al. 1995). Halophytes have also adopted by developing these basic mechanisms of osmotic adjustment: accumulation of inorganic salts, mainly NaCl in the vacuole, and accumulation of organic solutes in the cytoplasm. Large vacuoles of halophytes may have a modified lipid composition to prevent leakage of Na^+ back to the cytoplasm (Glenn et al. 1999), e.g. *Suaeda maritima*, a potential halophyte, occupies 77% of the mesophyll cells of vacuoles (Hajibagheri et al. 1984) which make it capable of accumulating higher concentration of salt as much as 500 mM. Based on different adaptive strategies, the level of total salt accumulation in the shoot is mostly species specific. Cumulatively several adaptive mechanisms (Fig. 9.1) have been reported in relation to salt tolerance in halophytes including ion compartmentalization, osmolyte production, germination responses, osmotic adaptation, succulence, selective transport and uptake of ions, enzyme responses, salt excretion and genetic control (Koyro et al. 2011).

9.3.1 Strategies for Adaptation of Plants to Salt Stress/Salt Avoidance Mechanism

9.3.1.1 Exclusion

In these plants the root system possesses an ultrafiltration mechanism for harmful ions. Radial transport of ion is restricted. Ions are transported from soil solution to the xylem from where they are transported along with transpiration stream in to the shoot. Here involves the radial transport of ions between the soil and xylem. So the plant having adaptation restricts the radial ion transport from soil solution to xylem. However, some of the ions get transported via symplastic pathway by avoiding the casparian strip. The plants which adapt to this exclusion mechanism are able to exclude ions in the meristematic region of shoot, leaves which are actively expanding and actively photosynthesizing tissue. They maintain low Na^+/K^+ ratio, and this facilitates protein synthesis and other metabolic reactions (Passive process), e.g. mangrove plants (100% salt exclusion), *Rhizophora mucronata*, *Ceriops candolleana*, *Bruguiera gymnorrhiza* and *Kandelia candel*.

9.3.1.2 Excretion

Ions are actively secreted (active process). But Na^+ is passively absorbed to the membrane because of high concentration in soil solution and the plant to maintain low Na^+/K^+ ratio, secretes Na^+ back outside into the soil solution. There are certain plants like *Tamarix* and *Atriplex* that develop salt glands in their leaves in which they accumulate large quantity of salts which are injurious to plant. Subsequently, this salt gets crystallized and becomes non-harmful to the plant, e.g. *Avicennia officinalis*, *Avicennia alba*, *Avicennia marina*, *Aegiceros corniculatum* and *Acanthus ilicifolius*.

9.3.1.3 Dilution

The salt accumulated in the plant cells get diluted by more water uptake. Besides this, dilution can also be achieved by rapid growth of tissue. Plants maintain high volume/surface area ratio. It occurs in many succulents in case of ice plant (succulent). They have high volume/surface area ratio and rapid growth.

9.3.1.4 Compartmentation of Ions

It includes spatial arrangement of toxic ions, e.g. Na^+ and Cl^- are generally compartmentalized in the vacuole and/or in less sensitive tissues to avoid their toxic effect. However, when plants are growing in high salt concentrations, an adequate sequestration of ions in the vacuole can become a limiting factor, especially in the case of glycophytes. In this scenario, plants can accumulate excessive amount of Na^+ in the cytosol which negatively affects many aspects of cellular physiology. These ions can be compartmentalized either at organ level where high salts accumulate only in roots compared to shoots especially leaves or at cellular level where salts accumulate in vacuoles than cytoplasm thus protecting enzymes without toxic ion accumulation in the cytosol.

9.3.2 Salt Tolerance Mechanism

Halophytes belong to Chenopodiaceae family with the particular character of taking up sodium and chloride at high rates under saline conditions and thereafter accumulation of these ions in the leaves. While moderately salt-resistant non-halophytic plants own their salt resistance to avoidance, many halophytes have a superior mechanism for growth in a saline habitat, i.e. salt tolerance by ion accumulation and thereby osmoregulation. However, many glycophytes also have ability of osmotic adjustment where organic solutes are involved in imparting tolerance.

The process of maintenance of cell turgor by a sufficient increase in cell solutes to compensate for the external osmotic stress is called osmoregulation, osmotic compensation or osmotic adjustment. Marschner (1995) indicated that synthesis of organic solutes is energy dependent, while Flowers et al. (1977) proposed that accumulation of ions in the vacuole provides solutes for osmotic adjustment. The contribution of inorganic and organic solutes for osmoregulation has important implications for energy balance; thus, it becomes necessary to take into account both the factors including the degree of osmotic adjustment and the type of solutes contributing to the osmotic adjustment in order to achieve a better understanding of the physiological differences among plants with different salt tolerance.

Osmoregulation with inorganic solutes: In most plants, especially the obligate halophytes, osmoregulation in response to severe salt stress is provided mainly due to accumulation of inorganic ions, particularly in the leaf cells. The mechanism of osmotic adjustment depends mainly upon the following processes: (a) membrane permeability; (b) transport kinetics, energetic and selectivity; and (c) negative feedback controls. Different ions have different uptake rates and thus determine the ionic balance. Contribution of chloride is more than sulphate to osmotic adjustment because of fast absorption. When salinity is created by mainly of monovalent cation and divalent anions, cation uptake rates exceed those of anion. This leads to accumulation of organic acids and hence ionic balance is developed. The metabolic assimilation of nitrate and sulphate also creates imbalance in inorganic cations and anions.

The euhalophytes adapt to saline conditions through accumulation of higher concentration of NaCl. These plants have adapted various mechanisms to withstand the high conc. of salt, e.g. increasing succulence, compartmentation, secreting salts from the tissues or various combinations of these mechanisms. However, in several other halophytes, osmoregulation is due to active K^+ uptake. In general the Gramineae, Linaceae and Cyperaceae take up less Na^+ than any other group of higher plants, because they prefer K^+. Osmoregulation with inorganic solutes is not uncommon in glycophytes. In case of tomato, one variety exhibited higher salt tolerance due to accumulation of Na^+ and Cl^- in their leaves, while other variety excluded these ions. Osmoregulation with organic solutes: Maintenance of equilibrium between vacuole (high salt conc.) and cytoplasm (synthesis of compatible organic solutes) has great significance imparting tolerance to halophytes in saline environments. This compartmentation introduces the term "compatible solutes" that are stored in the cytoplasm of cells at low external water potentials. These solutes are not harmful for metabolic functions than the inorganic ions and have been accumulated at high salinity in many species, e.g. glycine betaine, proline, sucrose and organic acids such as malate and oxalate.

Role of organic solutes in the cytoplasm has been proposed by Greenways and Munns (1980) as follows: (a) maintenance of osmotic balance between the cytoplasm and vacuole and (b) a protective effect on enzymes in the cytoplasm. Protective roles of a number of solutes have been established under extreme conditions. Sucrose protected isolated chloroplasts against injury and desiccation and proline increased the solubility of proteins. Osmotic adjustment in the cytoplasm is accomplished mainly by compatible solutes which do not interfere with enzymes and their metabolism. These “compatible solutes” mainly include organic compounds such as the nitrogenous compounds glycine betaine and proline and, in some plants, sugar alcohols, such as sorbitol. In addition, potassium is also maintained in the cytoplasm at a concentration on the order of 4000 mg/L (100 mM). Glycine betaine (500 mM) is a compatible cytoplasmic solute which has been reported to alleviate the toxic effects of 200 mM NaCl on malic enzyme in barley.

In contrast to glycine betaine, proline is highly labile and rapidly disappears after the withdrawal of stress and thus acts as a source of nitrogen and energy. The rate of degradation of glycine betaine in plant tissue is slow in contrast to proline. The difference in the rapidity of accumulation and metabolic liability of proline and glycine betaine suggests that proline accumulation could be major response to a transient stress and glycine betaine to a longer possible stress, usually involving salt accumulation. Thus, unlike proline, glycine betaine is unlikely to represent a potential store of energy and nitrogen.

9.4 Molecular Basis of Halophytic Salinity Response

With the advent of modern biology techniques, novel and exciting insights have been obtained into the molecular basis of the halophytic response. Under the control of non-specific promoter such as 35 CaMV, overexpression of different halophytic genes has been observed to improve salt stress tolerance in various glycophytic recipients. Most of halophytic genes involve genes for salt overly sensitive (SOS) system-related cation/proton antiporters of vacuolar (NHX) and plasma membranes (NHX/SOS1); vacuolar H+ pyrophosphatases (V-H^+PPase); energy-related pumps, such as plasma membrane and vacuolar H^+ATPase potassium transporters; reactive oxygen species scavengers; and different proteins that are involved in signal transduction as displayed in Fig. 9.2.

Our understanding in salinity tolerance comes predominantly from recent work on *Arabidopsis thaliana* where it has been conclusively proved that Na^+ transporter along with the Na^+/H^+ exchangers and a sodium transporter are involved across cell membranes and tonoplast. Horie and Schroeder (2004) have reviewed the components of salt signalling pathway regulating these genes, and SOS2 and SOS3 have been activated in the response to Na^+. Despite this progress, it is opined (Vera-

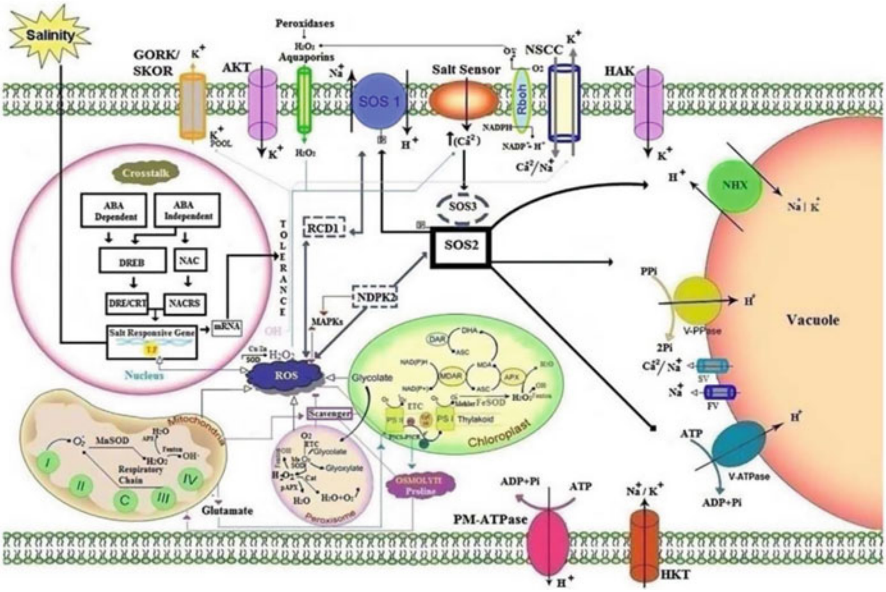

Fig. 9.2 Schematic representation of salt tolerance mechanism in halophytic cell. (Adopted from Himabindu et al. 2016)

Estrella et al. 2005) that certain novel type of responses of halophytes may be ignored in glycophytic system like *Arabidopsis*. Thus, it is held that halophytes may have developed unique mechanisms or regulatory pathways primarily responding to stress, different than of glycophytes. This school of thought has taken workers back to using of ice plant (*Mesembryanthemum crystallinum*) and some other halophytes like *Salicornia bigelovii* and *Atriplex gmelinii* to further explore halophytic salt tolerance (Hamada et al. 2001). But unlike *Arabidopsis*, these plants are not suitable for use as genetic models. A large EST database has been generated in ice plant along with a mutant collection (Chusman and Bohnert 2000). However, the technique to readily transform this plant is yet to be developed.

During the last decade, several groups have initiated the use of *Thellungiella halophila* commonly known as salt cress, as a close *Arabidopsis* relative another halophytic model (Amtamann et al. 2005). Salt cress is not only salt-tolerant, but it also is near to ideal genetic model system with genome size of approximately double than *Arabidopsis*; sharing on average 92% sequence identity with *Arabidopsis*, *T. halophila* can be analysed in shortest span due to its short life cycle (Bressan et al. 2001). Vera-Estrella et al. (2005) observed that in salt cress old leaves are the site of Na^+ accumulation occurred in, followed by young leaves under salt stress. The H^+ transport and hydrolytic activity of salt cress tonoplast and plasma membrane H^+-ATPases increased in leaves and roots with salt treatment. Na^+/H^+ exchange rate of tonoplast was greatly stimulated by NaCl in salt cress leaves and roots. An increased expression of *SOS1* was seen in plasma membrane of salt-treated salt cress roots, but the levels of AHA3 and HKT1 were normal. NHX1 was only seen in root plasma membrane fractions with salt-induced upregulation of protein expression. The expression of vacuolar H^+-translocating ATPase subunits was normal with no significant changes in expression of subunits VHA-A or VHA-B in salt-treated plants. However, an increased expression of VHA-E was seen in leaf tissue. Thus, there is a systematic control of Na^+ distribution and storage in cress plants with delimitation of ionic balance across both the tonoplast and plasma membrane.

Lv et al. (2012) found that another euhalophyte *Salicornia europaea* can survive in saline conditions of more than 1000 mM NaCl. To explore the mechanism of this plant, experiments were conducted at different NaCl concentrations, and various parameters like plant growth, Na^+ accumulation and distribution at organ, tissue and subcellular levels were monitored. It was found that this euhalophyte maintains an optimal growth up to 200–400 mM with better photosynthetic rate; shoots accumulated more Na^+ than roots of *S. europaea*. Probably Na^+ ion themselves act as osmoprotectant to maintain cell turgor and thus enhanced photosynthetic competence and plant growth. SEM-X-ray and TEM-X-ray microanalyses clearly depicted compartmentation of Na^+ predominantly in the cell vacuoles of shoot endodermis tissues. Also, the increased transcript levels of *SeNHX1*, *SeVHA-A* and *SeVP1* may impart an important role in Na^+ sequestration into the vacuoles in saline conditions. Hence, the salt tolerance of *S. europaea* might be due to a multiple sodium compartmentalization mechanism.

This compartmentation of toxic sodium ions has great significance for halophytes in a saline environment. Vacuolar membrane, i.e. tonoplast, has better transport mechanisms to maintain steep solute gradients, but the tonoplast of glycophytes is lacking such efficient transport mechanisms and therefore may not cope to maintain the required solute gradients for osmotic adjustment. So, salt-accumulating halophytes maintain turgor by the process of osmotic adjustment, which is necessary for continued growth.

9.5 Phytoremediation

Phytoremediation is a nondestructive clean-up process of using plants as decontaminants for soil and water. Plants also have the capability to degrade organic pollutants and remove or stabilize metal contaminants. Various techniques are used by plants for this purpose (Fig. 9.3).

Phytoremediation is a sub-technique used for decontamination with the following mechanisms (Salt et al. 1998):

(i) Phytoextraction: It is also called phytoaccumulation. Here, plants are used at waste sites to accumulate pollutants (metals) which are converted into the harvestable form of metals in plant parts. This leads to decontamination of soils.

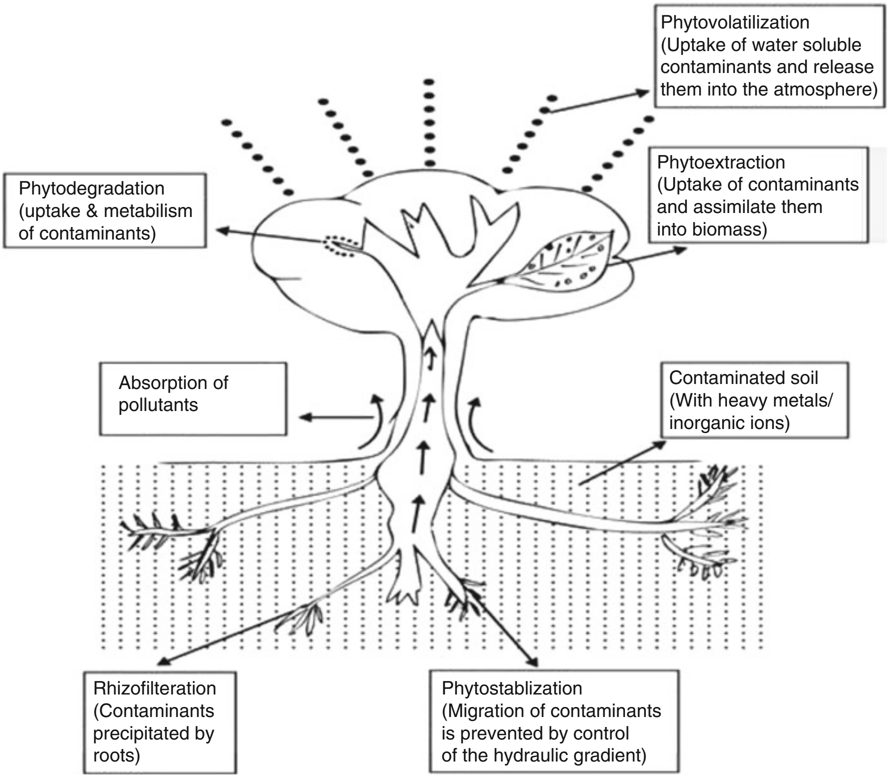

Fig. 9.3 Overview of phytoremediation

(ii) Photodegradation: Plant metabolic activities directly degrade organic pollutants.
(iii) Phytostabilization: Plants stabilize the pollutant in soil by preventing erosion, leaching or runoff and by converting pollutant to less bioavailable forms (e.g. via precipitation in the rhizosphere).
(iv) Phytovolatilization: Plants uptake some pollutants which evaporate in volatile form and thus use of plants to remove pollutants from air.
(v) Rhizofiltration: It is the use of roots or whole plant (phytofiltration). Hyperaccumulating plants absorb the pollutants from polluted effluents, i.e. metals or toxic salt ions.

Phytoremediation can be achieved using vascular plants, algae and fungi to remove or breakdown through microorganisms in the rhizosphere (McCutchen and Schnoor 2003). Phytoremediation is also economic than conventional methods for best waste management practices. Various metals, metalloids, nonmetals, surfactants, radionuclides, salts, nutrients, xenobiotic organic chemicals (compounds that

Table 9.1 Some case studies involving halophytic plants in salinity remediation through hyperaccumulation

Hyperaccumulator plant(s) used; site and nature of studies	Quantification of remediation	References
Suaeda fruticosa, Pakistan	Accumulation (Na^+ and other salts) of 9.06% salt on a fresh weight basis	Chaudhri et al. (1964)
Suaeda maritima, Pakistan	Could remove 504 kg of NaCl from saline land from 1 ha in 4 month time	Ravindran et al. (2007)
Juncus rigidus and *Juncus acutus*, Egypt	EC of the soil decreased from 33 to 22 dS m^{-1} in single growth period	Zahran and Abdel (1982)
Suaeda Salsa, Northern Egypt	Produces 20 tons dry weight ha^{-1} containing 3–4 tons of salt	Ke-Fu (1991)
Portulaca oleracea	Highest salt uptake (497 kg ha^{-1}) with biomass production of 3948 Kg ha^{-1}	Hamidov et al. (2007)
Apocynum lancifolium, *Chenopodium album*; Girlan, Khirezm Region, northwest Uzbekistan	*Chenopodium album* produced 3.25 t ha^{-1} $year^{-1}$ dry biomass removing 569.6 kg ha^{-1} salt ions from 0.3 m of the soil profile amounting to 1.47% of the soil salts	Hamidov et al. (2007)
Sesuvium portulacastrum	Accumulation of 30% of Na^+ content in shoot over the 170 d	Rabhi et al. (2008)
Suaeda fruticosa, *Suaeda nudiflora*, *Salsola baryosma*, *Haloxylon recurvum* and *Atriplex lentiformis* grown in salinity microplots at CCS HAU, Hisar	These plants were found to be best salt hyperaccumulators and also had high biomass. These plants had the potential of desalinization of saline soils from 16 to 2 dSm^{-1} in 4.9–6.1 years	Datta and Angrish (2006) and Devi et al. (2008, 2016)
Wild-growing *Tecticornia indica* and *Suaeda nudiflora*; Soliman sublake, north-east Tunisia	Both perennial plants exhibited high productivities and Na^+ accumulation, i.e. *T. indica* 7.4 t dry weight ha^{-1} and Na^+ 0.7 t ha^{-1} and *S. nudiflora* 0.75 t ha^{-1} and 0.22 t ha^{-1}, respectively	Ouni et al. (2013)
Urochondra setulosa, *Suaeda nudiflora*, *Sporobolus marginatus*, *Aleuropus lagopoides*, sodic, saline and saline-sodic microplots, Karnal, India	Soil pH_s and EC_e reduced considerably in sodic and saline treatments. In saline-sodic soils, EC_e reduced from 10 to 6; 15 to 7.2; 20 to 9.2 dS m^{-1} and pH reduced from 9 to 8.27, 8.33, 8.35, respectively	Kumar et al. (2016)

are foreign to living organisms), sewage and air pollutants are differentiate hazardous wastes that can be removed through phytoremediation.

Several investigations of the halophytic plants for desalinization of saline soils by accumulating high salt concentration in their above ground biomass. Some relevant reports are tabulated (Table 9.1).

9.5.1 Advantages and Limitations

Advantages

- Since tree and grasses are also utilized as fodder, timber and fuel, hence phytoremediation through them is beneficial.
- It is economic and can be installed both in situ and ex situ.
- The physiology of halophytes is easy to understand.
- This technique is environment friendly, feasible and easily acceptable by general public.
- Phytomining also brings in the reuse of valuable metals.
- Phytoremediation is as mush feasible and viable just as the agriculture.
- It leaves no destructive effect on the environment.
- They avoid excavation and hence no risk of spreading the contaminants.

Limitations

- Since phytoremediation is brought about mainly by roots, thus it is limited up to the spreading of the roots.
- It is a time-consuming process.
- Mainly hyperaccumulator plants are used.
- Sometimes few contaminants can be toxic to the plant.
- During autumn season, the contaminants may get recycled through the food chain or may release into environment.
- The higher solubility or leaching of the contaminants may bring out environmental damage.

9.6 Potential Use of Halophytes Under Salinity

During the last half of the twentieth century, the potential use of halophytes as crops was explored much (Rozema et al. 2013). On the basis of research on saline agriculture, database of halophytes with economic benefits has been developed during the 1960s in Israel (Aronson 1989). After that various halophytic species have been studied by various workers for the re-greening and vegetation of salt-affected lands as well as for improving industrially polluted lands (Cambrolle et al. 2008; Lewis and Devereux 2009). Halophytes have also been explored as floricultural crops (Cassaniti et al. 2013) and as biofilters for aquaculture wastes (Buhmann and Papenbrock 2013).

Worldwide, salt-affected lands are continuously increasing with changing climate conditions, and thus there is an urgent need to develop highly salt-tolerant crops in present scenario of the adverse climatic conditions. Halophytes are the best option under such environments since they produce satisfactory yield under salty condition. Halophytes have also been tested as vegetable, forage and oilseed crops in agronomic field trials.

9.6.1 Halophytes as Fodder

The best fodder quality includes high palatability, digestibility and appropriate nutritional value, i.e. high protein and low fibre, ash and oxalate contents. Salt accumulation reduces the nutritional value and feeding quality of most plants. Mixed plantation of halophytic grasses and shrubs have been proposed by Norman et al. (2013) to get the benefits of using halophytes in managing toxic effects of salts. Few halophytic plants are excellent fodder source for animal feeding in saline areas. Grasses have also been used in combination with other chenopods apart from *Atriplex* species. The most productive species yields 10–20 t ha^{-1} of biomass on seawater irrigation, equivalent to conventional crops.

Livestock such as sheep, camels and cattle survive well on certain halophytic feeds. The basic criteria for halophytes to be used as forage include biomass production along with nutritive value of feed (Norman et al. 2013). The nutritional ingredients of traditional domestic animal diets can be replaced with halophytes (forage seed products) with some exceptional high salt content and anti-nutritional compounds in some species. Anti-methanogenic properties of fodder of *Pennisetum clandestinum* (kikuyu grass) help in reducing greenhouse gas (GHG) production in ruminant livestock by reducing methane gas production in grazing sheep and cattle (Muscolo et al. 2013). The halophytic grasses *Leptochloa fusca*, *Spartina patens* and *S. virginicus* are used for forage production in Egypt. In India also, many halophytic species are used as forage for cattle, camel and goats including *C. dactylon*, *Aeluropus lagopoides*, *Terminalia catappa* and *Brachiaria mutica* (Dagar 2005).

The plant species with approximately 10–20 t DM ha^{-1} of biomass are considered as most productive halophytes in saline irrigated conditions, and such plants are equivalent to conventional forage species under normal conditions. For better animal health and productivity, the best use of halophytes is in combination with a grain supplement (ICBA 2007; Norman et al. 2013).

9.6.2 Halophytes as Energy Crops of Biofuel

Since there is no competition of conventional agriculture crops with halophytes, hence these could potentially involve in the cropping system as natural resources for soil, water and energy. Irrigation with treated sewage and brackish water yields between 26 and 52 t ha^{-1} year^{-1} in salt cedar (*Tamarix* spp.) which is comparable with traditional cash crops (Eshel et al. 2010). Cropping these salt-tolerant halophytes as energy crops on poor agricultural land will certainly help to conquer the issues of less available land for food production (Qadir et al. 2008).

Halophytes can also be used as a source of biofuel and fuel wood. The world's biofuel reserves are substantially being depleted day by day and will exhaust soon (Shafiee and Topal 2009), and hence bioethanol could be potentially replaced as an alternate renewable energy source (Demirbas et al. 2011; Abideen et al. 2012). For the last decade, bioethanol is rapidly taken as a substitute for gasoline (Del Campo et al. 2006). In developing countries, salt-tolerant plants are already in use for cooking and heating (Ladeiro 2012). The lignocellulosic biomass of halophytes consisting of lignin, hemicellulose and cellulose produces eco-friendly biomass, subsidizing the food versus fuel production debate, and hence represents a sustainable resource.

The growing of halophytic plants solves the dual purpose, i.e. firstly, it somehow counteracts the dependency on fossil fuels and secondly reduces the global warming through greenhouse gases. In the coastal zone of China, species like *Tamarix chinensis*, *Phragmites australis*, *Miscanthus* spp. and *Spartina alterniflora* are being used as biofuel crops, whereas in the coastal region of Pakistan, *Halopyrum mucronatum*, *Desmostachya bipinnata*, *Phragmites karka*, *Typhadom ingensis* and *P. turgidum* are being used. The grass spp. *Panicum virgatum* produces comparable yields of ethanol as corn (Zea mays) which is popularly used ethanol production. *Prosopis* and *Tamarix* sp. are excellent source of fuel wood.

9.6.3 Halophytes as Human Food

Halophytes are being used for human consumption for decades, e.g. a perennial salt grass *Distichlis palmeri* is being consumed as a food crop by the native South Americans and also the indigenous Cocopah people living along the lower Río Colorado in Mexico. Yensen (2006) reported that in various parts of the world, this species is used in bakery for making biscuits and bread due to more fibres than wheat. It produces grains of high nutritive value (1.25 t ha^{-1}) even under flooded and sea water salinities (Pearlsteina et al. 2012). Another spp., quinoa (*Chenopodium quinoa*) tolerating salinity up to 40 dS m^{-1}, is also consumed as an exotic food being staple foods of native South Americans (Adolf et al. 2013). The nutritive value of gluten-free quinoa grain is much higher than traditional cereals (Vega-Gálvez et al. 2010). Seeds are enriched with lysine (an essential amino acid), iron, magnesium, vitamin E, copper and phosphorus (James 2009). The grain yield potential of up to 5.2 t ha^{-1} has been reported under temperate environments in Argentina (Gómez et al. 2011). Likewise, pearl millet (*Pennisetum typhoides*) can also tolerate salinity greater than 30 dSm^{-1} and can serve as a food crop yielding up to 1.6 t ha^{-1} (Jaradat 2003), while consuming as food, halophyte leaves taste similar to available salad leaves.

(i) In Delaware (USA), the yield of *Atriplex triangularis* was 21.2 t ha^{-1} under sea water irrigation, and people in the Netherlands, Belgium and Portugal consume its leaves due to its taste similar to spinach leaves (Leith et al. 2000).
(ii) *Salicornia bigelovii* is an alternative source of omega-3 polyunsaturated fatty acids and hence grown profusely for fresh produce markets in the USA and Europe (Zerai et al. 2010; Ventura et al. 2011). It also contains antioxidant-carotene, ranging 4.7–15.9 mg/100 g fresh weight in the leaves (Lu et al. 2010).
(iii) In many parts of the world, perennial wall rocket (*Diplotaxis tenuifolia*) is also consumed as a leafy vegetable (de Vos et al. 2013).

(iv) In Columbia, many mangrove species are being used as food, e.g. *Avicennia marina* and *A. germinans* (Leith et al. 2000).
(v) In different regions of India, the seedlings of *Chenopodium album* and *Amaranthus* spp. are consumed as salads and vegetables, whereas *Capparis decidua* raw fruits are used for pickles (Rameshkumar and Eswaran 2013).

9.6.4 Halophytes as Oilseeds and Protein Sources

Certain halophytic plant spp. are rich in oils and proteins, e.g. *Salicornia bigelovii*, seed contains 28% oil and 31% protein, and this quantity is comparable to soybean yield and seed quality. Other known halophytic sources of oil and protein include *Suaeda aralocaspica* (Wang et al. 2012), *Suaeda moquinii* (Weber et al. 2007), *Salvadora persica* (Reddy et al. 2008), *Batis maritima* (Marcone 2003), *Suaeda salsa*, *Descurainia sophia* and *Chenopodium glaucum* (Yajun et al. 2003). Significant higher concentrations of salt are present in the shoot biomass particularly in the leaves, and seeds are relatively salt-free (Jaradat 2003). *S. bigelovii* is highly rich in oil and protein content, and trials are being conducted across the world, e.g. the Middle East (Jaradat 2005; Abdal 2009), Mexico (Grattan et al. 2008) and Africa (Zerai et al. 2010).

(i) *S. bigelovii* seed has 30% oil and 35% protein content (Ho and Cummins 2009) and having properties similar to safflower oil (Zerai et al. 2010).
(ii) Seeds of *Suaeda fruticosa* having 74% unsaturated fatty acid are being used as a source of edible oil (Weber et al. 2007).
(iii) *S. persica* tolerates the salinity from 25 to 65 dSm^{-1}; but seed yield decreased approx. 50% with higher salinity of 55–65 dSm^{-1} (Rao et al. 2004). *S. persica* seeds are rich in lauric (C12) and myristic (C14) acid commonly used in the cosmetic and pharmaceutical industries (Reddy et al. 2008).

9.6.5 Halophytes as Medicinal Plants and Other Commercial Products

Halophytes have their medicinal properties as well, e.g. *Ipomoea pes-caprae* sp. is used for various diseases like fatigue, strain, arthritis, rheumatism and menorrhagia (Rameshkumar and Eswaran 2013). The medicinal value of *Ipomoea* sp. is due to many active secondary metabolites with analgesic, antimicrobial and anticoagulant properties (Meira et al. 2012). *T. catappa* leaf has some antibacterial activity for being used as a cardiac stimulant, treating dermatosis and hepatitis in India (Chanda et al. 2011) and for liver diseases in Taiwan. The polyol-rich food of *T. catappa* is known to have disease-preventing functions (Agarie et al. (2009). *Mesembryanthemum crystallinum* has anti-carcinogenic, anti-inflammatory and anti-ageing properties (Mandloi et al. 2013). Commercially, halophytes also have industrial uses where

Parthenium argentatum (guayule) is used as natural rubber source growing under salinity up to 7.5 dSm^{-1} (Hoffman et al. 1988) and *Suaeda monoica*, a succulent chenopod, is used profusely in the paper industry.

In India, breeding work for salt resistance is carried out at ICAR-Central Soil Salinity Research Institute (CSSRI), Karnal and its various regional stations. In India, two types of approaches are followed for salt tolerance breeding:

(i) Improving yield level of salt-tolerant cultivars: Traditional cultivars of salt-affected areas are improved for their productivity without affecting their salt tolerance ability.
(ii) Transfer of salt-tolerant genes to high-yielding cultivars. Salt-tolerant genes from locally adapted (salt-tolerant) cultivars are transferred to high-yielding cultivars through hybridization and selections.

9.7 Conclusion and Future Projections

Salinity is a worldwide problem for agricultural lands and thus reducing the available lands for crop production. This leads to a need for natural means to correct the defective saline soils and development of highly productive land-use systems to fulfil the challenges of global food security. Also, the adaptability of crops to saline conditions needs to be improved. The precise understanding of physiological/biochemical mechanisms in halophytes under different environmental conditions is very limited, and hence, the need to pinpoint the physiological and molecular indicators to reveal the underlying mechanisms of these processes is required. The need to expand agricultural production for fulfilling food demand of increasing population of over nine billion people by 2050 requires an urgent action. One of the most appropriate solutions may be to make a "depositary" of plant species cultivated in harsh saline environments which can be differentially used for human or animal use. For this remedy, halophytes are can be successfully incorporated into farming systems with significant potential to meet this challenge. This will bring a new opportunity for the farmers to adopt new practices. However, this change will not be immediate, and slowly with time the use of halophytes in saline agriculture to move from the laboratory and small field trials to large-scale commercial production will bring a bright future. So in this chapter, we have briefly reviewed the present status of halophytes with their all explored potentials and further with their economic, commercial and agricultural capacities for improvement of saline soils.

It is evident from the literature also that halophytic species (Chenopodiaceae) have the capacity to desalinize the saline soils efficiently. Halophytic grasses are economically viable plants with that they not only are a source of fodder for animals but do serve as source of fuel wood, grain and vegetables. These also stabilize consistently ever eroding saline lands. The production of bio-salt or vegetable salt from these salt-hyperaccumulator plants can be another possible feasibility in near future. Natural

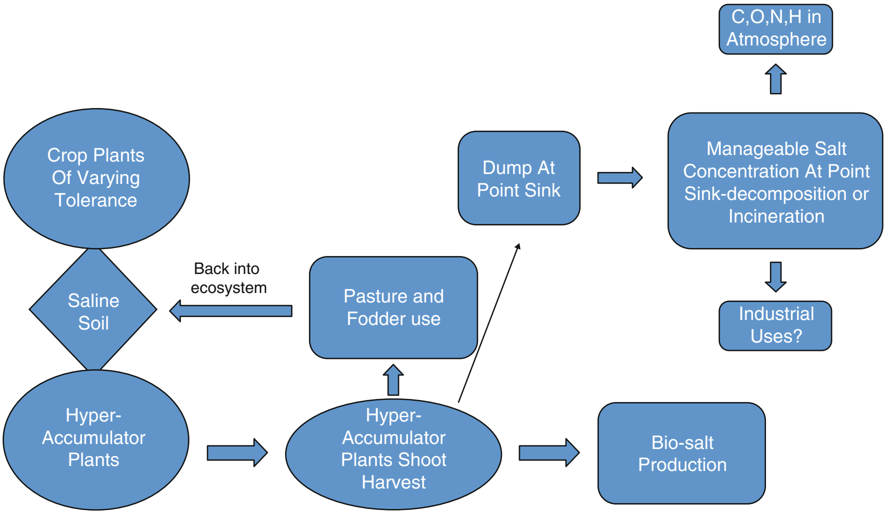

Fig. 9.4 Complementary use of hyperaccumulator plants and crop systems

sun's energy is used by the plants to remove salt ions from soil. Core of hyperaccumulation technologies include transpiration of salts through uptake and sequestration of salt ions into the vacuole. Various saline parks could be raised where co-cultivation of these salt hyperaccumulators along with other commercial crops could be undertaken for soil salinity amelioration on an ongoing basis. Further, the harvesting of these hyperaccumulator plants should be at a sink point. Another most effective utilization of these harvestings from these hyperaccumulator plants could be towards bio-salt production, which shall facilitate natural cycling of the salt Fig. 9.4.

The potential of halophytes for phytoremediation in saline soils has been explored by many researchers stating that some of halophytic plant species were able to remove the toxic salts from the saline soils very effectively. With increasing salinization, the phenomenon of phytoremediation can become a new eco-friendly technology for remediation of saline soils. With developing era of "Omics", identification of novel salt-tolerant genes from halophytes with high biomass yield can pave a way for generation of transgenic plants and improving the tolerance potential of crop plants leading to sustainable crop production.

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Chapter 10
Halophytes: Prospective Plants for Future

Ganesh Chandrakant Nikalje, Shelke Deepak Bhaskar, Kushi Yadav, and Suprasanna Penna

Contents

Abstract Halophytes are the flowering plants native to saline habitats. These habitats contain high salt, heavy metals and other toxic anthropogenic agents. To complete their life cycle in such harsh conditions, halophytes have developed different strategies like development of succulence, compartmentalization of toxic ions, synthesis of osmolytes, increase in activity of antioxidants and synthesis of compatible solutes. Halophytes have significant applied interests towards various agricultural and non-agricultural purposes besides for maintenance of ecological

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balance. Important bioactive metabolites can be derived from halophytic plant species for commercial value. In addition, halophytes can be utilized as alternative plants as they could be cultivated for food, fodder/forage, fuel and medicinal crops on saline lands with the help of salty water irrigation. Apart from tolerance, halophytes can be utilized for environmental cleanup. Many halophytes are hyper accumulators of different heavy metals and salt. In this chapter, we discussed prospective use of halophytes for their economic importance as well their potential implications for environmental cleanup.

Keywords Halophytes · Salinity · Economic importance · Environmental cleanup

10.1 Introduction

To feed increasing population, there is urgent need to increase food production by more than 70% (World Bank 2008). However, with increase in the total area of salt-affected land (~831 million hectares), the productivity of agricultural land is dwindling. With this pace, it is estimated that by middle of twenty-first century, about 50% lands under cultivation will be lost (Gupta and Huang 2014). This global issue can be solved with the help of multidisciplinary approaches. It may include development of tolerant crops (which can tolerate different biotic and abiotic stresses, grow on nutrient deficient soil and give maximum yield), reclamation of degraded saline soil and/or domestication of wild plants with desired characters. In this context, domestication of halophytes is a viable option as these group of flowering plants are endowed with ability to survive under high salinity. Many conventional crops cannot survive under low (40 mM NaCl) salinity, while halophytes can grow and complete their life cycle under high (200 mM or more NaCl) salinity (Flowers and Colmer 2008). The strong pressure of selection also makes them to acquire adaptive features under high salinity. This includes some special anatomical features (salt hairs, salt glands, etc.), physiological and biochemical alterations and changes in metabolic profile. These implications make halophytes suitable candidate to study salt stress adaptation mechanism in plants. Some halophytes like *Quinoa* and *Salicornia* contains high nutritive values. *Quinoa* contains 4.4g proteins, 21.3g carbohydrates, 0.9g sugar and 2.8g fibres per 100 g seeds, while *Salicornia* is used as vegetable which contains 5% Vitamnin A, 4% Vitamin C and 4% iron. Most of the halophytes contain polyphenols which can be utilized in food, pharmaceutical, cosmetics and medicinal industries (Hasanuzzaman et al. 2014). Along with such value addition, halophytes play a major role in environmental protection. Halophytes like *Sesuvium*, *Medicago*, *Cackile*, *Salicornia* and *Atriplex* were well studied for their application in phytodesalination, phytoremediation, sand dune fixation, phytostabilization (Table 10.1; Fig. 10.1), etc. In this article, we highlighted the prospective economic importance of halophytes and their diverse roles in sustainable agriculture and environmental protection.

Table 10.1 Diverse applications of halophytes

Halophytic species	Stress tolerance	Active principles	General uses	Medicinal uses	Environmental protection	References
Arthrocnemum sp.	NaCl, Cd	Gallic acid, 3-hydroxy-4′-methoxyflavone, cyaniding, chrysoeriol, quercetin, catechol, syringic acid, luteolin	Fodder	Anticancer activity	Phytoremediation of Cd	Redondo-Gómez et al. (2010) and Boulaaba et al. (2013)
Cakile maritima	NaCl, Cd	Ascorbic acid, flavonoids, coumarins, alkaloids, triterpenes, sterols and sulphur glycosides	–	Preventive role against cardiovascular diseases	Phytoremediation of Cd	Ben Amor et al. (2006) and Radwan et al. (2008)
Chenopodium quinoa	NaCl	20-hydroxyecdysone, flavonoid glycosides, acacetin, kaempferol, quercetin, quercetin glucuronide, ferulic acid, oleanolic acid, hederagenin, phytolaccagenic acid	Cooking and baking, animal feed, green fodder and pellets	Controls fasting blood glucose in obese and hyperglycemic, response to stress	–	Gomez-Caravaca et al. 2012 and Graf et al. 2014
Mesembryanthemum crystallinum	NaCl, Cu, Zn	Procyanidins and propelargonidins	Salad green or vegetable	Cardioprotective, anticancer, antibacterial and antiviral activities	Phytoremediation of Cu and Zn	Herppich et al. (2008) and Falleh et al. (2011)
Salicornia sp.	NaCl, Pb	Fibres, polyphenols and flavonoids	Salad greens, vegetable, fodder	Immunomodulatory, lipid-lowering, antiproliferative,	Phytoremediation of Pb	Patel (2016) and Ventura et al. (2011)

(continued)

Table 10.1 (continued)

Halophytic species	Stress tolerance	Active principles	General uses	Medicinal uses	Environmental protection	References
				osteoprotective and hypoglycemic		
Sarcocornia ambigua	NaCl, Pb, Zn, Cu and Fe	Galangin, kaempferol, quercetin, isoquercetin, p-coumaric acid, vanillic acid, caffeic acid, ferulic acid, syringic acid	Salads	Antioxidant activity	Phytoremediation of Pb, Zn, Cu and Fe	Bertin et al. (2016) and Gago et al. (2011)
Sesuvium portulacastrum	NaCl, Cd, As, Ni, Cs, Pb	Dihydrostigmasterol, benzoic acid, 3,4,5-trihydroxy-(gallic acid), capsaicin, epicatechin, ecdysones, flavonoids, ecdysterone, adenosine, 2′-O-methyladenosine and L-tryptophan	Vegetable, fodder	Antioxidant, antimicrobial, anti-HIV activity	Phytoremediation of As, Cd, Pb, Ni, Cs; phytodesalination, dye degradation	Nikalje et al. (2017b)
Thellungiella sp.	NaCl, phenanthrene	Phytoalexins: wasalexin A, biswasalexin A1 and biswasalexin A2	–	Antifungal activity	Phytoremediation of phenanthrene	Pedras et al. (2009) and Shiri et al. (2016)

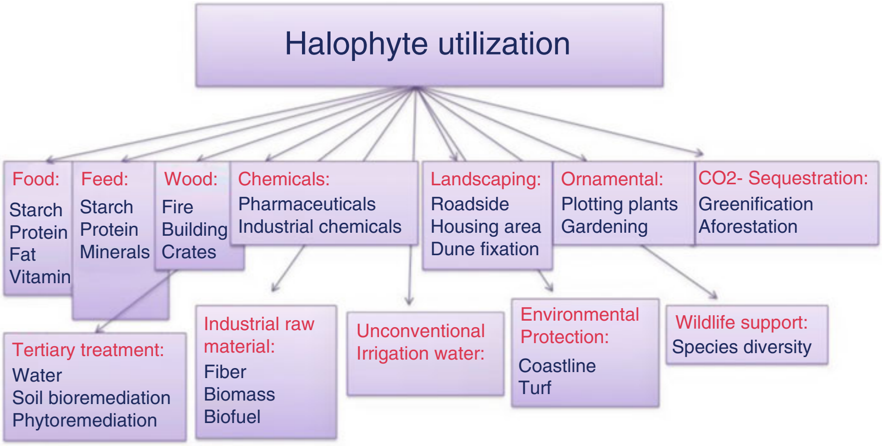

Fig. 10.1 Utilization of halophytes for economic benefits and environmental cleanup

10.2 Economic Values of Halophytes

Enormous conventional and non conventional efforts are being taken to improve salt tolerance in crops, but these efforts have resulted in only few productive salt-tolerant varieties (Roy et al. 2014). Most of the work has been limited to the laboratory level with few studies at green house or field level. In this regard, domestication of naturally salt tolerant, halophytes can provide a better option to mitigate adequate food production. Halophytes can be irrigated with brackish/saline water or can be cultivated in salt-affected agricultural lands for food, fuel, fibres, fodder, medicines and other value added products (Glenn et al. 1999; Nikalje et al. 2017b). Halophytes can be utilized as alternative crops to conventional crops, and good quality water can be diverted to other highly productive cash crops like rice, sugarcane, wheat, etc. This will solve problem of water non-availability (Koyro et al. 2011). Therefore, different halophytes need to be studied for their economic potential for agricultural, industrial and/or ecological purpose. In the following subsections, economic benefits of halophytes are described.

10.2.1 Food

Halophytes acquire their niche in saline soils, which are rich in different salts and micro- and macronutrients. It makes nutritional profiles of halophytes adequate for human consumption (Barreira et al. 2017). In addition, they contain polyunsaturated fatty acids, phenolic compounds, different vitamins and essential nutrients like manganese (Barreira et al. 2017). Halophytes such as *Aster tripolium*, *Crithmum* *maritimum*, *Salicornia* sp. and *Portulaca oleracea* are consumed as vegetable in culinary purposes (Tardio et al. 2006). In addition, they synthesize important metabolites like amino acids, sugars, antioxidants, quaternary ammonium compounds and polyols (Muchate et al. 2016). These compounds have primary role in reactive oxygen species scavenging, as osmolytes for ion homeostasis and protection from oxidation (Nikalje et al. 2017a). The osmolytes have nutritive value and health-promoting benefits and protective role against diseases (Buhmann and Papenbrock 2013). The ability of halophytes to grow in saline and brackish water has been utilized to conserve water resources for human consumption. Promotion of halophytes for sustainable biosaline agriculture is an emerging need due to their increasing market demand and high nutritional value, for e.g. Quinoa (Panta et al. 2016; Nikalje et al. 2017b). In European markets, halophyte products have high demand. The vegetables and salad crops (*Salicornia* and *Aster*) are being sold in markets at relatively high price (Boer 2006). *Salicornia* is a non-seasonal plant and can be cultivated throughout the year for vegetables (Boer 2006). Along with them *Beta maritima*, *Crambe maritima* and *Salsola soda* are new potential vegetables. In South America, Quinoa has long history of cultivation. It has more than 2500 accessions and tolerant to salinity, drought, frost and wind. It is rich in essential amino acids, fatty acids, minerals and vitamins, which gained interest to consider this plant in global food security programme (Adolf et al. 2013). Bolivia is the major producer of Quinoa; it produces 0.5 t ha^{-1} grain yield, but under optimized conditions of cultivation, it is expected that it may increase up to 3–5 t ha^{-1} (Adolf et al. 2013).

10.2.2 Fodder/Forage

The fodder crop must have high biomass, digestibility and palatability for animals. They contain high proteins, low oxalate, fibre and ash content (El Shaer 2004). Khan et al. (2009) systematically screened different halophytes and reported two halophytes, namely, *Desmostachya bipinnata* and *Panicum turgidum* as potential candidates for fodder production. They also developed mass scale fodder production on salinized land by saltwater irrigation and patented. This system has produced 50–60,000 kg/ha/year fodder (equivalent to maize) on saline soil (Khan et al. 2009). Halophytes irrigated with salt water, if provided with leaching conditions and optimum salinity, can give higher yield as compared to conventional crops and water use efficiency. The conventional forage crops like maize can be replaced with halophytic plants, but due to relatively high salt content and anti-nutritional properties, there are some restrictions in using them. The high palatability and good nutritional value (high protein and low fibre content) shows potential of halophytes as fodder (El Shaer 2004). The salt content of halophytes can be nullified by using mixture of forage plants for feeding. For example, *A. nummularia* was mixed with other herbaceous species, and annual grasses (with low salt content) can be a good fodder for animals (Barrett-Lennard and Setter 2010). According to Aronson (1985), there are about 95 halophytes with potential of forage or fodder. Among them some species of *Atriplex* contain 1.26–2.09 kg m^{-2} dry matter and 15.5–39.5% fibre and 10.2–19.5% crude protein. Trees like *Aegiceras corniculata*, *Rhizophora mucronata*, *Avicennia marina* and *Ceriops tagal* are used for camel and cattle feed. In arid and semiarid regions, *Salvadora*, *Acacia*, *Prosopis* and *Ziziphus* are incorporated in traditional fodder. *Salicornia*, *Chenopodium*, *Atriplex*, *Suaeda*, *Salsola* and *Kochia* are shrubs, while *Chloris virgata*, *C. gayana*, *Echinochloa turnerana*, *E. colonum*, *Aeluropus lagopoides*, *Sporobolus marginatus*, *Dactyloctenium sindicum*, *Puccinellia distans* and *S. marginatus* are grass species popularly used as animal feeds and fodder.

10.2.3 Edible Oil

The demand for edible or vegetable oil is increasing with time which is responsible for rapid growth of oil extraction industries (Weber et al. 2007). Cotton, mustard, rape and canola are the major domestic sources of edible oil. However, all of them are sensitive to high salinity, and their yield significantly reduces biomass production and oil content under influence of salt stress. Weber et al. (2007) analyzed six halophytes (*Alhagi maurorum*, *Arthrocnemum indicum*, *Cressa cretica*, *Haloxylon stocksii*, *Suaeda fruticosa* and *Halopyrum mucronatum*) for their edible oil-producing ability. The results revealed that except *A. maurorum*, all the halophytes possess about 65–74% unsaturated fatty acids, and all of them have 22–25% edible oil. A report on halophytes of Great Basin desert of North America revealed 85–90% unsaturated fractions of individual fatty acids and total lipids (Weber et al. 2001). The edible seed oil of halophytic origin is said to have comparable oil quality with that of conventional edible oils like olive, canola, etc. (Declercq and Daun 1998). The interesting point to consider is that under the influence of salt, halophytes like *D. sophia* contain high amount of linolenic acid as compared to non-saline conditions (Yajun et al. 2003). Similarly, there are several examples of halophytes which can grow in highly saline areas and produce high amount of edible oil, for example, *Zygophyllum album*, *Kosteletzkya virginica*, *Chenopodium glaucum*, *Crithmum maritimum* and *Salicornia bigelovii* (He et al. 2003; Yajun et al. 2003). Weber et al. (2007) reported that the unsaturated fatty acids (USFA) from *S. fruticosa*, *S. stocksii*, *C. cretica*, *A. maurorum* and *A. macrostachyum* appeared to be best from health prospective. Moreover, seeds of *Salvadora persica* and *S. oleoides* possess 40–50% fats and lauric acid which can be used in preparation of soap and candles. This oil of halophytes has potential to replace/substitute coconut oil (Weber et al. 2007).

10.2.4 Biofuel

The sources of petroleum are exhausting rapidly, and by middle of this century, 50% of it will be depleted (Debez et al. 2017). In addition, reduction in arable land due to increase in soil salinization and depletion of fresh water resources are posing threat to crop production (Sharma et al. 2016). Production of biofuels can be mitigated by plant feedstock if we succeed to identify alternate species other than conventional crops, which can grow in salinized and poor soils. It is convenient to use food crops like maize, soybean or sugarcane and non-food crops like *Panicum virgatum* for bioethanol production, but these crops are of good quality soil and fresh water irrigation. This created competition for resource allocation between bioenergy production and food production, which is under criticism. In this sense, halophytes can be a potential candidate because there are multiple examples of halophyte, which contain high amount of seed oils (Debez et al.). Halophytes like *Desmostachya bipinnata*, *Halopyrum mucronatum*, *Panicum turgidum*, *Phragmites karka* and *Typha domingensis* have potential as bioethanol-producing crops (Abideen et al. 2011). They have high growth rate and can produce high-quality lignocellulosic biomass containing 26–37% cellulose, 24–38% hemicellulose and <10% lignin required for ethanol production. Halophytes like *Euphorbia tirucalli* and *Tamarix* sp. can produce high biomass even under extreme desert conditions (Eshel et al. 2011). The *T. jordanis* contains high cellulose and low hemicelluloses and phenol content which is a desirable condition for ethanol production (Santi et al. 2014).

10.2.5 Medicines

During stress adaptation (both biotic and abiotic), halophytes synthesize several antioxidants and secondary metabolites. *Arthrocnemum macrostachyum* produces alkaloids, flavonoids, phenols and tannins for stress management. However, these compounds have strong antioxidant activities and can be utilized in medicines (Custodio et al. 2012). Some halophytes like *Sesuvium* produce 20-hydroxyecdysone (20E), an insect-moulting hormone which protects the plant from different biotic factors. This 20E is also used in sericulture industry to enhance moulting process of silkworms (Nikalje et al. 2017b). There are several examples, to show that halophytes are rich source of secondary metabolites and novel bioactive compounds that are essential to uplift of pharmaceutical industries and improve socioeconomic status of local peoples. Ethnobotanical studies on coastal halophytes revealed 50 halophytes with several medicinal properties (Qasim et al. 2010). *Cressa cretica* is used in traditional medicine of the skin, stomach, leprosy, asthma and urine-related problems (Shahani and Memon 1988). Halophytes are reported as effective against several diseases. For example, *Achillea millefolium*, *Portulaca quadrifida* and *Solanum surattense* for cold, flu and cough; *Salsola imbricate* and *Zygophyllum propinquum* for vermifuge; *Juncus rigidus* and *Zaleya pentandra* for stomach ailments; and *Solanum surattense* and *Artemisia scoparia* for pain relieving, etc. The saponins isolated from *Acanthus ilicifolius* and alkaloid from *Atriplex vesicaria* possess antileukemic and bactericidal activity (Kokpol et al. 1984). *Ipomoea pes-caprae* exhibits anti-inflammatory activity, and in Thailand it is used as a traditional medicinal plant for the treatment of various types of inflammation including jellyfish sting and dermatitis. For skin disorder, the fruits of the large glabrous shrub *Lumnitzera racemosa* are curative according to the folk medicines. Characterized from the leaves of the plant, there are 3 of the 11 hydrolysable tannins, and chemicals characterized from the Chinese tallow *Sapium sebiferum* possess hypertensive activity.

10.2.6 Ornamentals and Landscaping

The floriculture and landscaping industries have high demand in market, and their success is dependent on new and attractive plants (Zaccai 2002). The conventional ornamental plants require high-quality water, nutrient supply and extensive care to maintain their proper growth and external appearance (Shillo et al. 2002). In some studies, attempts were made to irrigate ornamentals with low-quality brackish water, but the plants show reduced quality of flowers and adverse effect on growth (reviewed by Cassaniti et al. 2013). In this sense, utilization of salt-affected soil for ornamental and landscaping by halophytic plants is a viable solution. Some halophytes that accumulate high amount of salt may contain anti-nutritional compounds and hence not suitable for food/fodder purpose. However, these can possess unique morphology and beautiful flowers like *Aster tripolium*. About 13 families with 42 species with ornamental potential recorded from Mediterranean region (Cassaniti and Romano 2011). The subspecies of *Aster tripolium*, *Pannonicus*, is unsuitable for consumption because of its bitter test. It has distinct and attractive morphology, which makes it suitable for cultivation as flowering pots and cut flowers (Sagi and Erdei 2002). A facultative halophyte, *Sesuvium portulacastrum*, is a salt-, drought-, heavy metal-, toxic dyes-tolerant plant and recommended for biosaline agriculture (Nikalje et al. 2017b). It has conspicuous, attractive, tiny flowers; its colour varies from pink, purple and rarely white (Lokhande et al. 2013) dependant on locality. It blooms throughout the year and has the potential to utilize in landscaping as ornamental plant. The *Crithmum maritimum* possess 30-cm-long, umbrella-like inflorescence which can be utilized in rock gardens (Ben Hamed et al. 2005). Its flowers and succulent leaves both have aesthetic value. Like wise, *Mesembryanthemum crystallinum* (ornamental ground cover), *Inula crithmoides* (yellow flowers) and *Salicornia* (ornamental) are potential candidates for landscaping and floriculture (Jessop 1986; Zurayk and Baalbaki 1996).

10.3 Environmental Cleanup Potential of Halophytes

10.3.1 Phytoremediation

Halophytes are characterized by their ability to survive and complete their life cycle in highly saline soils. Such saline soils are rich in toxic sodium and chloride ions. The adaptation mechanism of halophytes may not be exclusive to these two ions only. The habitat of halophytes is often contaminated with other toxic metal ions. Therefore, halophytes must have developed strategies to combat with toxic metals like arsenic, cadmium, chromium, lead, zinc, copper, manganese, etc. Halophytes like *Sesuvium*, *Atriplex* and *Salicornia* have shown their ability to accumulate such heavy metals (Nikalje and Suprasanna 2018). These characteristics make some halophytes suitable candidates for phytoremediation of toxic compounds. Some of the metal hyper-accumulating halophytes include, *Avicennia alba* (250 mg ml^{-1} Pb), *Rhizophora mucronata* (500 mg ml^{-1} Zn) and *Kandelia candel* (400 mg kg^{-1} Cu and Zn) which show high metal tolerance (Chiu et al. 1995). All these halophytes have their own strategy to combat with toxic metal ions. Halophytes like *Avicennia* sp. tend to restrict metal ions in roots (Peters et al. 1997), while Sesuvium portulacastrum sequester metal ions in vacuoles or leaves (Nikalje and Suprasanna 2018). Therefore, depending on the adaptation mechanism, potential candidate for phytoremediation can be utilized.

10.3.2 Phytodesalination

Halophytes are said to be wonders of saline soil because they live in such condition where other plants cannot survive. The toxic salt ions are inimical to plant growth and development, but halophytes cleverly utilize these ions (especially Na^+) as cheap source of osmolytes and get benefited. Three strategies of salt adaptation have been proposed: the first is salt exclusion where halophytes like *Rhizophora* sp. exclude excessive salt ions from roots; second is salt excretions where halophytes readily absorb salt ions from root zone and excrete from leaves with the help of specialized salt glands, e.g. *Avicennia*; and the third one is salt accumulation, in this halophyte rapidly absorbs salt ions and sequesters them in to vacuole, e.g. *Sesuvium portulacastrum.* Based on severity of the salt-affected soil, for stabilization, salt excluders can be utilized, and salt accumulators will be helpful for reclamation. Apart from these properties, halophyte having high salt tolerance and high biomass production high nutritional properties and value-added products will be desirable (Nikalje et al. 2017b). Halophytes like *Sesuvium portulacastrum* (474 kg ha^{-1} NaCl; Ravindran et al. 2007), *S. maritima* (504 kg ha^{-1} NaCl; Ravindran et al. 2007) and *Portulaca oleracea* (3948 kg ha^{-1} Na, Hamidovet et al. 2007) are the representative examples of potential candidates for desalination. However, still utilization of halophytes for amelioration of saline soil is at primitive stage. There is need to screen more halophytes and their cultivation in saline and degraded soils for reclamation purpose.

10.3.3 Other Economic Benefits

Halophytes grows in tidal, coastal swamps and are referred as mangrove plants. They provide forest products like charcoal, firewood, timber, honey and fishery products. Halophytes like *Avicennia* are a good source of cheap and nutritive fodder for animals (Vannucci 2004). In addition, these plant extracts have medicinal value. Kathiresan (2000) has reported that extract of *Bruguiera* leaves is used to reduce blood pressure and *Excoecaria agallocha* to cure leprosy, epilepsy, etc. (Table 10.1). It also provides seeds for fishery industries. In West Bengal, Sundarban mangroves yield 540 millions of seeds of *Penaeus monodon* (Chaudhuri and Choudhury 1994). These plants have role in protection of coastal region from UV-B radiation, sea level rise, coastal erosion, fury of cyclones, wave action and greenhouse effect (Kathiresan 2012).

10.4 Conclusion and Future Prospects

Among various abiotic stresses, increasing soil salinity is the major threat to agricultural production. To overcome these issues, different biotechnological tools are applied to make tolerant and high-yielding crop varieties. The transgenic lines developed using biotechnology approaches are yet to occupy market place to mitigate the increasing food demand. For the past few decades, a novel concept of "Biosaline Agriculture" has been emerging. In this, different halophytes (salt-tolerant plants) are cultivated using saline/brackish water irrigation as substitute for conventional crop plants. In this way, three major issues can be solved: First, saline/brackish water will be used for biosaline agriculture, and good quality water could be diverted to human consumption and irrigation of high-yielding glycophytic crops. Second, the halophyte can be used as food (vegetable, edible oil), fodder/forage, biofuel, medicines, ornamentals and landscaping. Third, the nonedible halophytes can be utilized in environmental cleanup such as phytoremediation of toxic metals, textile dyes, etc.; phytodesalination of salt-affected soils; and ecological balance. Having natural tolerance to different biotic and abiotic stresses, halophytes can survive and flourish in adverse conditions without yield penalty. These multipurpose plants need to be screened for their products and potential use in environmental cleanup. Domestication of these plants with multiple uses may be prioritized to become an alternative to conventional crops. In the years to come, bio-saline agriculture will surely hold a great promise to supplement sustainable agriculture practices.

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Chapter 11
Sustainable Use of Halophytic Taxa as Food and Fodder: An Important Genetic Resource in Southwest Asia

Münir Öztürk, Volkan Altay, and Aykut Güvensen

Contents

Abstract Halophytes have a great potential in their use as cash crops for fodder, medicine, and other aspects. These saline habitat plants flourish on soils with high salt concentration and can be substituted for conventional crops. A total of 728 taxa of halophytes have been recorded from Southwest Asia. These belong to 68 families. The majority are from the families Chenopodiaceae, Poaceae, Leguminosae (Papiliondeae), Asteraceae, and Cyperaceae. Chenopodiaceae has the largest number of species and genera. It is exceeded by Poaceae which has more genera but fewer species. Halophytes in this region constitute about half the number of halophyte taxa (and families) recorded for the world. A total of 115 halophyte taxa are evaluated as food here together with a total of 331 as fodder. Especially in the Arabian Gulf countries, *Aerva javanica*, *Aizoon canariense*, *Blepharis ciliaris*, *Cleome brachycarpa*, *Convolvulus glomeratus*, *Haloxylon salicornicum*, *Leptadenia pyrotechnica*, *Lycium shawii*, *Senna italica*, *Tecomella undulata*, and *Zaleya pentandra* halophyte taxa are good fodder for camels, cattle, goat, and sheep.

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In the Mediterranean part of Southwest Asia, more than 20 taxa are used as animal feed. These are mainly the taxa like *Aellenia*, *Aeluropus*, *Halocnemum*, *Haloxylon*, *Salsola*, *Sarcocornia*, and *Suaeda*. In Iraq, Iran, Afghanistan, and Pakistan, the number of halophytes used as animal feed exceeds 100 taxa. The use of halophytes for food purposes in Southwest Asia is as follows: Mediterranean countries use over 10 taxa, Arabian Gulf countries use over 10 taxa, and Iraq, Iran, Afghanistan, and Pakistan use over 40 taxa.

Keywords Halophytes · Food plants · Fodder plants · Southwest Asia

11.1 Introduction

According to Hasanuzzaman et al. (2014), the total area of salt-affected soils is reported to lie around 831 million hectares in the world including 397 million hectares of saline and 434 million hectares of saline or sodic soils. The pollution, degrading environmental conditions, increasing natural calamities, and global climate change are reported to be the main cause for the decrease in agricultural lands (Hasanuzzaman et al. 2013a, b, 2014). Salt is affecting approximately 50 million hectares of irrigated land. This accounts for a 20% of the total land. Every year nearly 1.5 million ha of land is taken out of production due to high salinity problems (Pitman and Lauchli 2002; Munns and Tester 2008). If this situation continues like that, nearly 50% of the cultivable lands will be lost by the middle of the twenty-first century (Mahajan and Tuteja 2005).

Halophytes are the plants able to survive and reproduce in environments where salt concentrations exceed 200 mM of NaCl ($\sim$20 dSm^{-1}) (Flowers and Colmer 2008). These plants constitute nearly 1% of the global floral diversity. These plants are capable of completing their life cycle under highly saline conditions (Stuart et al. 2012). Generally, different halophyte taxa grow in different saline regions in the world. These could be coastal saline habitats, on mangrove forest soils, wetlands, marshy areas, arid and semiarid regions, and agricultural fields (Hasanuzzaman et al. 2014).

Many halophytes have been investigated as potential crops under the sea or brackish water irrigation. Their growth on such soils includes a wide range of applications like desalination, heavy metal extraction in order to improve the soil characteristics, biomass production, food, fuel, fodder, and fiber (Debez et al. 2011; Lokhande and Suprasanna 2012; Hasanuzzaman et al. 2014). A direct halophyte plant consumption by humans is limited. However, the seeds of many halophytes have been recorded as new sources of grains or vegetable oils (Hinman 1984; Debez et al. 2011). The plants able to thrive in highly saline habitats can be used to produce materials with high economical value for being salt-tolerant. These are the essential oils, flavors, fragrances, gums, resins, oils, pharmaceuticals, and fibers (Galvani 2007; Ksouri et al. 2007; Debez et al. 2011). They are marketed for use for ornamentation because of their foliage or flowers (Messedi et al. 2004; Slama et al. 2006; Debez et al. 2011). Salt-tolerant species can be grown on land and water unsuitable for conventional crops to produce fuelwood as well as building materials (Debez et al. 2011). The use of such precious strategies can prove helpful in the reclamation of unused and marginal lands, which can be brought under cultivation, opening a new door for sustainable crop production (Hasanuzzaman et al. 2014). In this chapter, we are focusing on the potential human food and animal fodder taxa of halophytes in Southwest Asia.

11.2 General Account of Halophyte Diversity

This region is mostly arid with gravel and sandy desert areas, lying at the edges of a large tectonic plate. A total of 728 taxa of halophytes have been reported from SW Asia (Ghazanfar et al. 2014). From the data available, Turkey has the maximum number of halophytes (±420 taxa), followed by Pakistan (±410 taxa), Iran (±365 taxa), Jordan (±263 taxa), and Saudi Arabia (±250 taxa) (Table 11.1). In Southwest Asia, this group of ecologically valuable taxa is recorded as being about 50% of halophyte taxa (and families) recorded for the world (Aronson 1989; Ghazanfar et al. 2014). Chenopodiaceae, Poaceae, Leguminosae-Papiliondeae, Asteraceae, and Cyperaceae are the dominating families rich in halophytic taxa. The largest number of taxa is found in the Chenopodiaceae, which is exceeded by Poaceae with more genera but fewer species. These findings are in accordance with those recorded for the global halophyte taxa (Flowers et al. 1986; Ghazanfar et al. 2014).

Table 11.1 Number of halophytic taxa in Southwest Asian countries

Country	Total vascular flora	Number of halophytic taxa
Turkey	11,000	420
Iran	7300	365
Pakistan	6000	410
Afghanistan	5000	96
Syria	3500	110
Iraq	3220	135
Yemen	2838	120
Palestine	2700	300
Lebanon	2606	107
Jordan	2521	263
Saudi Arabia	2281	250
Oman	1211	120
United Arab Emirates	650	70
Kuwait	407	80
Qatar	270	70
Bahrain	250	97

11.3 Data Analysis

A total of 16 countries included in Southwest Asian region have been selected as the study area for this investigation. The floristic data published by Batanouny (1993), Batanouny (1994), Le Houérou (1993), Khan (2003), Akhani (2006), Moghaddam and Koocheki (2003), Abbas (2006), Güvensen et al. (2006), Khan and Qaiser (2006), Weber et al. (2007), Yensen (2008), Khan and Ansari (2008), Al-Oudat and Qadir (2011), Cassaniti and Romano (2011), Ghazanfar et al. (2014), Qasem (2015), Breckle (2016), El Shaer and Attia-Ismail (2016), Ghazanfar and McDaniel (2016), Phondani et al. (2016), Öztürk et al. (2008a, b), Öztürk et al. (2014), Öztürk et al. (2016), and Öztürk et al. (2017) has been evaluated in this chapter, together with other published records on halophyte diversity. The halophyte taxa whose status or name has changed, or have become synonyms, or have been included under new combinations, have been corrected following the "Ghazanfar et al. (2014)." The existing potential of food and fodder halophyte taxa has been evaluated taking into account the floristic structure of the study area. The economic potential of the floristic data published for food and fodder halophyte taxa with potential alternative use too has been followed.

11.4 Halophytes Used as Human Food

Many wild halophytes are a rich source of nutrients and bioactive compounds with a taste similar to conventional salad crops (Petropoulos et al. 2018). These are at the same time recorded as being important mediators in various health problems (Trichopoulou et al. 2000). The lifestyle of present-day humans is creating a market niche for commercial cultivation of various halophytes, because some are handpicked as wild greens and some of these show seasonality, and therefore their availability all through the year is not in a position to meet the demands of consumers (Petropoulos et al. 2015, 2016, 2018). According to Petropoulos et al. (2018), the wild-growing halophytes in the Mediterranean Basin are a valuable genetic source with great adaptation to extreme conditions like salinity of soil and irrigation waters. These could serve as a source of alternative cash crops in a saline agriculture regime. Diversified and higher contents of bioactive compounds in some render them as very promising candidates for the food industry. These could be evaluated for designing and producing novel food products with functional and health-beneficial features like beverages, leafy salads, microencapsulated oils, food additives, antimicrobial agents, and many others (Petropoulos et al. 2018). However, there is a need for a multistep approach for implementation before such products can be produced commercially. All this includes an evaluation of various ecotypes of the candidate species for selecting the ones with most promising properties; an integration of selected genotypes in breeding programs for an improvement of selected features like enhanced bioactivity and content of bioactive compounds, improved agronomic features, and decreased content of possible antinutrients; evaluation of cultivation practices to find most suitable practical guides; assessment of the content of bioactive compounds under the conditions of commercial cultivation; clinical and model trials to know about the mechanisms of health effects together with the recommended consumption on a daily basis, for avoiding possible toxicity effects; designing and marketing of novel halophyte food products; a look-into the alternative approaches for healthy diets and well-being together with the increase of consumer awareness; the legislation regarding consumers safety issues and genetic conservation of the halophyte species is very important (Petropoulos et al. 2018).

A total of 115 halophytic taxa with potential food value have been recorded from Southwest Asia (Appendix I). The only species with halophytic ancestors among the conventional crops are beets (*Beta vulgaris*) and the date palm (*Phoenix dactylifera*). These can be irrigated with brackish water. The seed-bearing species used as food are *Salvadora oleoides*, *S. persica*, *Trianthema portulacastrum*, *Oxystelma esculentum*, and *Zizyphus nummularia*. The young leaves and shoots of *Salicornia bigelovii*, *Halosarcia indica*, *Sesuvium portulacastrum*, *Chenopodium album*, *Atriplex hortensis*, *Triglochin maritima*, *Arundo donax*, *Rumex vesicarius*, *Apium graveolens*, *Portulaca oleracea*, and *Suaeda maritima* are used as vegetables, salads, and pickles in several countries of this region. *Suaeda fruticosa* and *Haloxylon stocksii* are used to prepare a kind of baking soda, which is used in the preparation of food. According to Khan (2003) and Khan and Qaiser (2006), some of the species used as salad are the radicles of *Rhizophora mucronata*, *Zizyphus nummularia*, and *Ceriops tagal* and tender leaves of *Thespesia populneoides* and *Hibiscus tiliaceus*. The seeds of halophytes like *Suaeda fruticosa*, *Arthrocnemum macrostachyum*, *Salicornia bigelovii*, *Halosarcia indica*, *Halogeton glomeratus*, *Bassia scoparia*, and *Haloxylon stocksii* are reported to possess sufficient quantity of high-quality edible oil with unsaturation ranging from 70% to 80% (Weber et al. 2001; Weber et al. 2007). The data published by Khan (2003) and Khan and Qaiser (2006) reports that the seeds of *Salvadora oleoides* and *S. persica* contain 40–50% fat. They stress that these plants are a good source of lauric acid. The purified fat can be used for soap- and candlemaking and is a potential substitute for coconut oil.

11.5 Halophyte Taxa with a Potential as Fodder Plants

In arid and semiarid regions for millennia, halophytes and salt-tolerant plants have been used as sources of food (Le Houérou 1993; Glenn et al. 1999; El Shaer 1999, 2010; El Shaer et al. 2005). According to El Shaer (2010), a large number of halophytes, as well as salt-tolerant taxa, have been evaluated as fodder especially under drought conditions as well as fill the gap in feeding animals during fodder shortage resulting from adverse seasonal conditions. The value of certain some halophytic shrubs, legumes, and grasses has been used in pasture improvement programs as well as in many salt-affected regions at the global level (Glenn et al. 1999; ICBA 2006; El Shaer 2010). In arid as well as semiarid areas, many of the fodder plants come from several salt marsh taxa. According to Salerian et al. (1987), Malcolm (1993), and El Shaer (2010), farmers have always been making money from saline wastelands. Extension of halophytes and other salt-tolerant plants into farming practices depends on their compatibility with current land use system. It depends on the provision of enough incentive to encourage pasture and forage crop production as well as on the acceptance by farmers (El Shaer 2010).

In both arid and semiarid regions, the halophytes together with other salt-tolerant plants have been a major part of the feeding program of sheep, goats, camels, and some wildlife animals (Squires and Ayoub 1994; El Shaer 1997a, b, 2010). Shortage of fodder is a common feature in such regions, and it is the main constraint to improve livestock productivity. Tremendous efforts have been spent to find alternative resources of fodder from saline habitats (El Shaer 2006). In particular, the halophytic forage species will have better cash value if their forage qualities such as high palatability and digestibility and good nutritional value in particular high protein and less fiber, ash, and oxalate contents are significantly improved (El Shaer 2006). Generally, the majority of halophyte species contain enough quantity of crude protein, as well as essential nutrients which cover the nutritional requirements of animals (Arieli et al. 1989; El Shaer 1981, 2006). As the plants grow and reach maturity, fibrous materials and ash contents increase, whereas the gross energy and protein contents decrease (Kandil and El Shaer 1988; El Shaer 2006). It has also been reported that during wet seasons, several halophytes are nutritious and can sustain the maintenance requirements of animals, but in summer and autumn when the conditions are dry, the halophytes are poor and need to be supplemented with other ingredients, particularly with higher energy values (Atiq-ur-Rehman 2002; El Shaer 1997a, b, 2006). Although some halophytes are deficient in sulfur and phosphorus, sufficient amounts of major minerals are found in salt marsh plants, which do not produce any harmful effect even when such minerals are found in high concentrations in some of these (El Shaer 1981, 2006; Gihad and El Shaer 1994).

As individual fodder source, the halophytic taxa are not much valuable. The reason being that extended feeding periods produce adverse effects on browsing animals. Different factors are responsible for fodder consumption by different animals because of the variations in the palatability and acceptability of halophytes (Gihad and El Shaer 1994; El Shaer 2006). Some halophyte plants can be given to the animals directly, and some can be left for direct grazing as fresh fodder consumption. Some of the latter are highly or moderately palatable and nutritious, for example, *Atriplex* spp., *Nitraria retusa*, and *Suaeda fruticosa*. These taxa are generally overgrazed and decrease in the cover due to high grazing pressure (El Shaer 1981, 2006). Mixing halophytes as forage with other fodders rich in protein or energy can improve nutritional value to a great extent (El Shaer 2006). As against this many halophyte plants are unpalatable but do produce large biomass all through the year. In arid areas, there is a need for utilization of such plants, particularly during the dry seasons or during long-lasting droughts when other sources of fodder are lacking. Some secondary metabolites or so-called anti-nutritional factors like tannins, alkaloids, saponins, and nitrites hinder the use of some halophytes as these affect negatively (El Shaer 2006). Utilization of such halophytes has been evaluated following different approaches through different processing treatments to improve their palatability and nutritive values (El Shaer and Kandil 1990; El Shaer et al. 1991; El Shaer 2006). One of these approaches is chopping which dramatically improves the palatability of succulent taxa and allows efficient utilization of whole shrubs. Similarly, haymaking, haylage, or ensiling processes of some halophytes also improve their fodder consumption value (El Shaer 2006).

Animal protein is one of the major requirements for human beings. This makes it very important to evaluate all kinds of available pastures, including those which mainly are present in climatically unfavorable regions. Animals generally have to consume the only available fodder source, the halophytes, in such areas (Attia-Ismail et al. 2009; Attia-Ismail 2016). In both the arid and semiarid regions, a deficiency of fodder sources is one of the basic problems to improve the productivity of animals (Attia-Ismail 2016). The desert grazing sheep, camels, and goats require fodder plants with improved nutritional values particularly during the long-lasting dry seasons; this will increase the average annual animal production by more than 25% (Attia-Ismail 2016). Attempts are made to use the marginal sources, for example, saline soils and underground water for producing unconventional fodder ingredients (Attia-Ismail 2016).

The report published by Batanouny (1993) has revealed that the halophytes cover huge areas of rangelands in Algeria, Egypt, Gulf countries, Iran, Iraq, Jordan, Libya, Morocco, Pakistan, Saudi Arabia, Sudan, Syria, Tunisia, and Yemen. The rangelands in these countries are used throughout the year by sheep, goat, and camels, and the species generally consumed are *Atriplex halimus*, *A. mollis*, *A. portulacoides*, *A. glauca*, *A. nummularia*, *Suaeda fruticosa*, *S. brevifolia*, *S. mollis*, *Salicornia arabica*, *Limoniastrum monopetalum*, *Limoniastrum guyonianum*, *Traganum nudatum*, *Salsola vermiculata* var. *villosa*, *Salsola sieberi*, *S. tetrandra*, *Arthrocnemum indicum*, *Salicornia fruticosa*, *Inula crithmoides*, *Halocnemum strobilaceum*, *Tamarix* spp., and *Nitraria retusa*. Fairly good palatability has been recorded for some nonshrubby perennial halophytes such as *Nitraria retusa*, *Suaeda fruticosa*, *Spergularia media*, *S. marginata*, *Hedysarum carnosurn*, *Puccinellia* spp., and *Spartina patens*. Some like *Aster tripolium*, *Heliotropium curassavicum*, *Suaeda maritima*, *Juncus* spp., *Schoenus nigricans*, *Cyperus* spp., *Scirpus* spp., *Phragmites* spp., *Typha* spp., *Arundo plinii*, *A. donax*, *Saccharum ravennae*, and *Ruppia* spp. are almost unpalatable. Out of these, a majority are hygrohalophytes (Batanouny 1993). Very low palatability has been reported in the majority of annual halophytes as they produce little phytomass, e.g., *Hordeum maritimum*, *Polypogon*, *Sphenopus*, *Lepturus*, *Pholiurus*, *Psilurus*, *Eremopyrum*, *Frankenia*, *Aizoon*, *Mesembryanthemum*, *Cressa*, *Zygophyllum*, *Tetradiclis*, *Halopeplis*, *Halogeton*, *Schanginia*, *Suaeda*, *Salsola*, and *Salicornia* (El Shaer and Attia-Ismail 2016). However, any evaluation of halophytes depends on their performance both in the biological as well as its economic input (El Shaer and Attia-Ismail 2016). For an indigenous animal production, shortage of fodder is the main constraint, which therefore needs to be increased. In both arid and semiarid regions, it is a common characteristic accepted as the main constraint to improve livestock productivity (El Shaer and Attia-Ismail 2016). Main income for the people raising animal herds is based on the natural vegetation for rearing sheep, goats, and other herbivores. Although unpalatable halophytes are widely distributed in the world, the halophytic plants like *Atriplex* spp., *Nitraria retusa*, and *Salsola* spp. are considered extremely valuable as a source of fodder during drought periods (El Shaer and Attia-Ismail 2016). Most of the countries in the arid and semiarid regions import large quantities of fodder to fill the nutritional gap of animals. This puts a heavy burden on the farmers as well as the governments. It decreases the net profits from animal investments because of the high costs of imported fodder. Therefore, intensive efforts should be directed to find alternative resources from halophytes as fodder (El Shaer and Attia-Ismail 2016).

The foliage of species like *Avicennia marina*, *Aegiceras corniculata*, *Ceriops tagal*, and *Rhizophora mucronata* are evaluated as camel and cattle feed. Similarly the species of *Acacia*, *Prosopis*, *Salvadora*, and *Zizyphus* trees are well known as a traditional fodder of arid regions. Several species of *Alhagi*, *Salicornia*, *Chenopodium*, *Atriplex*, *Salsola*, *Suaeda*, and *Kochia* are well-known common fodder shrubs. The species like *Leptochloa fusca*, *Aeluropus lagopoides*, *Dactyloctenium sindicum*, *Cynodon dactylon*, *Paspalum vaginatum*, *Sporobolus marginatus*, *Chloris gayana*, *C. virgata*, *Echinochloa turnerana*, *E. colona*, and *Puccinellia distans* are common grass species flourishing on saline and alkaline areas and used as forages (Khan 2003; Khan and Qaiser 2006).

A total of 331 fodder halophyte taxa are distributed in the region (Appendix II). The constraints of using halophytes and other salt-tolerant plants as potential feed resource for animals have been studied at length by El Shaer (2010). The benefits outlined by him are the yield of halophytes and salt-tolerant forages as edible biomass in saline lands where non-halophytic species cannot grow varies from low to high; several halophytes are a potential source of nitrogen and major minerals for sheep and goats fed on low-quality diets; therefore energy supplementation with diets containing halophytes proves effective to overcome nutrient deficiencies in animals; the lignins, oxalates, and nitrates can prove limiting as anti-nutritive factors in the animal diets in particular while utilizing some halophytes and salt-tolerant forages in livestock feeding mainly as sole diets, appropriate mixing of different halophytic taxa, based on their complementary roles, can dilute the negative effects of the anti-nutritive factors cited here and therefore improve animal performance; and finally a wide range of halophytes and salt-tolerant grasses can prove as promising fodder resources for small ruminants raised around the saline areas or in arid and semiarid regions.

11.6 Conclusions

Halophytes are a small but diverse group of plants distributed as natural flora of saline habitats. These remarkable plants have a potential to revolutionize the future by fulfilling the human needs especially those related to food, fodder, fuel, and medicines (Hameed and Khan 2011). The cultivation and conservation of such natural resources can prove helpful in the sustainable maintenance and utilization of halophytic plant wealth. These can be evaluated to develop many small industries with small grants from the government, thereby uplifting the socioeconomic status of the poor. Both government and private sectors should invest in this venture to make halophytes as a resource for future (Hameed and Khan 2011). Sustainable use of our marginal lands and water resources for food-feed crops and forage legumes can prove fruitful for improving our global food security, reduce poverty, resilience against climate change, and enhance ecosystem health in crop-livestock systems (Qureshi 2017). Moreover, a good choice for salinity control and remediation is adoption of halophytes together with salt-tolerant plant taxa, which can have significant effect on the economic development of dry saline regions lying a waste. In addition to this, agroforestry can solve drainage problems. It will also create good environmental conditions for the desert and semidesert areas (Qureshi 2017).

The feasibility of cultivating salt-tolerant plants successfully in saline ecosystems offers unexpected opportunities for everyone including the farmers to identify the most appropriate cash crop halophyte. Their combinations can prove highly beneficial in optimizing the input/output ratios (Debez et al. 2011). In many cases the salt-affected soils and groundwaters cross national boundaries. There is a need for cooperation and coordination at regional and interboundry level. It is very important to elaborate and apply effective salinity strategies. For this purpose there is need to involve politicians, institutions, farmers, water user associations, and all beneficiaries in such applications, so that everybody is familiar with his role (Yensen 2006). In short, we must strive hard to change the general opinion of the farming communities and policy makers related to the questionability of evaluating the salt-affected soils (Debez et al. 2011).

Appendices

Appendix I: Halophytes from Southwest Asia with Potential Human Food Value

Sl. no.	Taxa
1	*Aizoon canariense*
2	*Alhagi graecorum*
3	*Allium trifoliatum*
4	*Amaranthus retroflexus*
5	*Amaranthus viridis*
6	*Apium graveolens*
7	*Arthrocnemum macrostachyum*
8	*Arundo donax*
9	*Asparagus persicus*
10	*Aster tripolium*

(continued)

Sl. no.	Taxa
11	*Atriplex canescens*
12	*Atriplex dimorphostegia*
13	*Atriplex griffithii*
14	*Atriplex halimus*
15	*Atriplex hortensis*
16	*Atriplex leucoclada*
17	*Atriplex littoralis*
18	*Atriplex portulacoides*
19	*Atriplex rosea*
20	*Atriplex sagittata*
21	*Avicennia marina*
22	*Bassia scoparia*
23	*Beta vulgaris* ssp. *maritima*
24	*Bolboschoenus maritimus* ssp. *maritimus*
25	*Bruguiera gymnorrhiza*
26	*Cakile maritima*
27	*Capparis spinosa*
28	*Ceriops tagal*
29	*Chenopodium album*
30	*Chenopodium foliosum*
31	*Chenopodium murale*
32	*Chenopodium rubrum*
33	*Cichorium intybus*
34	*Cichorium pumilum*
35	*Cichorium spinosum*
36	*Cocos nucifera*
37	*Crepis sancta*
38	*Cressa cretica*
39	*Crithmum maritimum*
40	*Cynara cardunculus*
41	*Cynodon dactylon*
42	*Cynomorium coccineum*
43	*Cyperus longus*
44	*Cyperus rotundus*
45	*Dysphania ambrosioides*
46	*Echinochloa crus-galli*
47	*Elymus farctus*
48	*Eryngium campestre* var. *virens*
49	*Eryngium creticum*
50	*Eryngium glomeratum*
51	*Eryngium maritimum*
52	*Glinus lotoides*
53	*Glossonema varians*

(continued)

Sl. no.	Taxa
54	*Glycyrrhiza glabra*
55	*Halogeton glomeratus*
56	*Halopyrum mucronatum*
57	*Halosarcia indica*
58	*Haloxylon griffithii* ssp. *griffithii*
59	*Haloxylon griffithii* ssp. *wakhanicum*
60	*Haloxylon stocksii*
61	*Hibiscus tiliaceus*
62	*Imperata cylindrica*
63	*Inula crithmoides*
64	*Krascheninnikovia ceratoides*
65	*Lepidium latifolium*
66	*Lycium shawii*
67	*Mesembryanthemum crystallinum*
68	*Mesembryanthemum forskahlii*
69	*Mesembryanthemum nodiflorum*
70	*Neurada procumbens*
71	*Nitraria retusa*
72	*Nitraria schoberi*
73	*Oligomeris linifolia*
74	*Oxystelma esculentum*
75	*Pancratium maritimum*
76	*Pedalium murex*
77	*Pentatropis nivalis*
78	*Phoenix dactylifera*
79	*Phoenix sylvestris*
80	*Phragmites australis*
81	*Plantago coronopus*
82	*Plantago lanceola*
83	*Plantago major* ssp. *intermedia*
84	*Polygonum aviculare*
85	*Polypogon monspeliensis*
86	*Portulaca oleracea*
87	*Prosopis farcta*
88	*Rhizophora mucronata*
89	*Rumex vesicarius*
90	*Salicornia bigelovii*
91	*Salicornia perennis*
92	*Salicornia ramosissima*
93	*Salsola soda*
94	*Salvadora oleoides*
95	*Salvadora persica*
96	*Sarcocornia fruticosa*

(continued)

Sl. no.	Taxa
97	*Sarcocornia perennis*
98	*Sesuvium portulacastrum*
99	*Sinapis arvensis*
100	*Solanum incanum*
101	*Suaeda aegyptiaca*
102	*Suaeda fruticosa*
103	*Suaeda maritima*
104	*Terminalia catappa*
105	*Tetraena alba*
106	*Tetraena simplex*
107	*Thespesia populneoides*
108	*Trianthema portulacastrum*
109	*Tribulus terrestris*
110	*Trifolium campestre*
111	*Trifolium repens*
112	*Triglochin maritima*
113	*Typha latifolia*
114	*Vicia sativa*
115	*Zizyphus nummularia*

Appendix II: Halophytes with Potential Fodder Value in Southwest Asia

Sl. no.	Taxa
1	*Acacia saligna*
2	*Acacia tortilis*
3	*Acantholippia seriphioides*
4	*Aegiceras corniculatum*
5	*Aellenia auricula*
6	*Aeluropus lagopoides*
7	*Aeluropus littoralis*
8	*Aeluropus macrostachyus*
9	*Aerva javanica*
10	*Agathophora alopecuroides*
11	*Agrostis stolonifera*
12	*Aizoon canariense*
13	*Alhagi graecorum*
14	*Alhagi pseudalhagi*
15	*Alopecurus myosuroides* var. *myosuroides*
16	*Ammi visnaga*

(continued)

Sl. no.	Taxa
17	*Anabasis articulata*
18	*Anabasis elatior*
19	*Anabasis salsa*
20	*Anabasis setifera*
21	*Anagallis arvensis*
22	*Aristida adscensionis*
23	*Aristida mutabilis*
24	*Artemisia campestris*
25	*Artemisia scoparia*
26	*Arthrocnemum halocnemoides*
27	*Arthrocnemum macrostachyum*
28	*Asparagus persicus*
29	*Aster tripolium*
30	*Astragalus hamosus*
31	*Astragalus kahiricus*
32	*Astrebla lappacea*
33	*Atriplex cana*
34	*Atriplex canescens*
35	*Atriplex confertifolia*
36	*Atriplex dimorphostegia*
37	*Atriplex griffithii*
38	*Atriplex halimus*
39	*Atriplex hortensis*
40	*Atriplex lasiantha*
41	*Atriplex leucoclada*
42	*Atriplex lindleyi* ssp. *inflata*
43	*Atriplex moneta*
44	*Atriplex muricata*
45	*Atriplex patula*
46	*Atriplex polycarpa*
47	*Atriplex portulacoides*
48	*Atriplex prostrata* ssp. *calotheca*
49	*Atriplex sagittata*
50	*Atriplex spongiosa*
51	*Atriplex stocksii*
52	*Atriplex tatarica*
53	*Atriplex verrucifera*
54	*Avicennia marina*
55	*Bassia eriophora*
56	*Bassia hyssopifolia*
57	*Bassia indica*
58	*Bassia prostrata*
59	*Bassia scoparia*

(continued)

Sl. no.	Taxa
60	*Beta vulgaris* ssp. *maritima*
61	*Bienertia cycloptera*
62	*Blepharis ciliaris*
63	*Blysmus rufus*
64	*Bolboschoenus glaucus*
65	*Bolboschoenus maritimus*
66	*Bromus arvensis*
67	*Bromus japonicus*
68	*Bromus tectorum* ssp. *tectorum*
69	*Buchloe dactyloides*
70	*Caesalpinia bonduc*
71	*Calligonum comosum*
72	*Calligonum leucocladum*
73	*Calligonum polygonoides*
74	*Camphorosma monspeliaca*
75	*Capparis spinosa*
76	*Carex divisa*
77	*Carex extensa*
78	*Caroxylon nitrarium*
79	*Caroxylon scleranthum*
80	*Cenchrus biflorus*
81	*Cenchrus ciliaris*
82	*Cenchrus pennisetiformis*
83	*Centaurea postii*
84	*Centaurium spicatum*
85	*Cerastium dubium*
86	*Ceriops tagal*
87	*Chenopodium chenopodioides*
88	*Chenopodium* species
89	*Chloris gayana*
90	*Chloris virgata*
91	*Cichorium intybus*
92	*Cleome brachycarpa*
93	*Convolvulus glomeratus*
94	*Cornulaca aucheri*
95	*Cornulaca monacantha*
96	*Crambe cordifolia* ssp. *kotschyana*
97	*Crepis sancta*
98	*Cressa cretica*
99	*Cynodon dactylon*
100	*Cyperus conglomeratus*
101	*Cyperus fuscus*
102	*Cyperus laevigatus*

(continued)

Sl. no.	Taxa
103	*Cyperus rotundus*
104	*Dactyloctenium aegyptium*
105	*Dactyloctenium aristatum*
106	*Dactyloctenium scindicum*
107	*Dalbergia sissoo*
108	*Desmostachya bipinnata*
109	*Diarthron lessertii*
110	*Dichanthium annulatum*
111	*Digitaria ciliaris*
112	*Echinochloa colona*
113	*Echinochloa crus-galli*
114	*Echinochloa turneriana*
115	*Eleusine indica*
116	*Eleusine tristachya*
117	*Elymus elongatus*
118	*Elytrigia* x *littorea*
119	*Enteropogon macrostachyus*
120	*Eragrostis curvula*
121	*Eragrostis japonica*
122	*Eragrostis superba*
123	*Eryngium campestre* var. *virens*
124	*Fagonia arabica*
125	*Fagonia bruguieri*
126	*Fagonia mollis*
127	*Festuca rubra*
128	*Frankenia pulverulenta*
129	*Girgensohnia oppositifolia*
130	*Glinus lotoides*
131	*Glycyrrhiza glabra*
132	*Halimocnemis mollissima*
133	*Halimocnemis pilosa*
134	*Halimodendron halodendron*
135	*Halocharis hispida*
136	*Halocharis sulphurea*
137	*Halocharis violacea*
138	*Halocnemum strobilaceum*
139	*Halopeplis perfoliata*
140	*Halopeplis pygmaea*
141	*Halopyrum mucronatum*
142	*Halosarcia indica*
143	*Halostachys belangeriana*
144	*Halostachys caspica*
145	*Halothamnus glaucus*

(continued)

Sl. no.	Taxa
146	*Halothamnus subaphyllus*
147	*Haloxylon ammodendron*
148	*Haloxylon recurvum*
149	*Haloxylon salicornicum*
150	*Haloxylon stocksii*
151	*Helianthemum lippii*
152	*Heliotropium bacciferum*
153	*Holcus lanatus*
154	*Hordeum marinum*
155	*Hyparrhenia hirta*
156	*Imperata cylindrica*
157	*Indigofera argentea*
158	*Inula crithmoides*
159	*Iris spuria*
160	*Juncus acutus*
161	*Juncus subulatus*
162	*Kali tragus*
163	*Kalidium caspicum*
164	*Kaviria tomentosa*
165	*Kochia iranica*
166	*Kochia odontoptera*
167	*Krascheninnikovia ceratoides*
168	*Lasiurus scindicus*
169	*Lepidium perfoliatum*
170	*Leptadenia pyrotechnica*
171	*Leptochloa fusca*
172	*Limonium stocksii*
173	*Lobularia maritima*
174	*Lolium multiflorum*
175	*Lotus corniculatus* var. *tenuifolius*
176	*Lotus preslii*
177	*Lycium shawii*
178	*Maireana brevifolia*
179	*Maireana georgei*
180	*Malcolmia grandiflora*
181	*Medicago lupulina*
182	*Medicago minima* var. *minima*
183	*Melilotus indicus*
184	*Melilotus officinalis*
185	*Mesembryanthemum* spp.
186	*Neokochia americana*
187	*Neurada procumbens*
188	*Nitraria retusa*

(continued)

Sl. no.	Taxa
189	*Nitraria schoberi*
190	*Oligomeris linifolia*
191	*Panicum antidotale*
192	*Panicum turgidum*
193	*Paspalum distichum*
194	*Paspalum vaginatum*
195	*Peganum harmala*
196	*Pergularia tomentosa*
197	*Phalaris arundinacea*
198	*Phalaris minor*
199	*Phleum exaratum* ssp. *exaratum*
200	*Phragmites australis*
201	*Phragmites karka*
202	*Plantago major* ssp. *intermedia*
203	*Poa bulbosa*
204	*Poa pratensis*
205	*Polygonum aviculare*
206	*Polypogon maritimus*
207	*Polypogon monspeliensis*
208	*Populus euphratica*
209	*Porteresia coarctata*
210	*Portulaca oleracea*
211	*Potentilla anserina*
212	*Prosopis cineraria*
213	*Prosopis farcta*
214	*Prosopis juliflora*
215	*Puccinellia distans*
216	*Puccinellia koeieana*
217	*Raphanus raphanistrum*
218	*Reaumuria alternifolia*
219	*Reaumuria fruticosa*
220	*Reaumuria halophila*
221	*Reaumuria palaestina*
222	*Reaumuria stocksii*
223	*Rhizophora mucronata*
224	*Ruppia maritima*
225	*Saccharum bengalense*
226	*Salicornia bigelovii*
227	*Salicornia perennis*
228	*Salicornia persica*
229	*Salicornia rubra*
230	*Salsola abarghuensis*
231	*Salsola arbuscula*

(continued)

Sl. no.	Taxa
232	*Salsola baryosma*
233	*Salsola chorassanica*
234	*Salsola crassa*
235	*Salsola dendroides*
236	*Salsola drummondii*
237	*Salsola gossypina*
238	*Salsola imbricata*
239	*Salsola incanescens*
240	*Salsola jordanicola*
241	*Salsola kali*
242	*Salsola kerneri*
243	*Salsola lanata*
244	*Salsola leptoclada*
245	*Salsola nitraria*
246	*Salsola orientalis*
247	*Salsola sclerantha*
248	*Salsola soda*
249	*Salsola tetrandra*
250	*Salsola tomentosa*
251	*Salsola vermiculata*
252	*Salsola volkensii*
253	*Salvadora persica*
254	*Sarcocornia fruticosa*
255	*Sarcocornia perennis*
256	*Schoenoplectus litoralis*
257	*Schoenoplectus tabernaemontani*
258	*Scirpoides holoschoenus*
259	*Seidlitzia florida*
260	*Seidlitzia rosmarinus*
261	*Senna italica*
262	*Seriphidium quettense*
263	*Sesuvium portulacastrum*
264	*Sonchus maritimus*
265	*Spergularia media*
266	*Sporobolus coromandelianus*
267	*Sporobolus helvolus*
268	*Sporobolus ioclados*
269	*Sporobolus tourneuxii*
270	*Sporobolus virginicus*
271	*Stipagrostis pennata*
272	*Stipagrostis plumosa*
273	*Suaeda acuminata*
274	*Suaeda aegyptiaca*

(continued)

Sl. no.	Taxa
275	*Suaeda altissima*
276	*Suaeda arcuata*
277	*Suaeda asphaltica*
278	*Suaeda confusa*
279	*Suaeda fruticosa*
280	*Suaeda heterocarpa*
281	*Suaeda maritima*
282	*Suaeda microphylla*
283	*Suaeda microsperma*
284	*Suaeda monoica*
285	*Suaeda palaestina*
286	*Suaeda splendens*
287	*Suaeda vera*
288	*Suaeda vermiculata*
289	*Tamarix androssowii*
290	*Tamarix aphylla*
291	*Tamarix aralensis*
292	*Tamarix aravensis*
293	*Tamarix arceuthoides*
294	*Tamarix gallica*
295	*Tamarix hispida*
296	*Tamarix karakalensis*
297	*Tamarix kotschyi*
298	*Tamarix laxa*
299	*Tamarix leptostachya*
300	*Tamarix mannifera*
301	*Tamarix mascatensis*
302	*Tamarix octandra*
303	*Tamarix passerinoides*
304	*Tamarix ramosissima*
305	*Tamarix rosea*
306	*Tamarix szovitsiana*
307	*Taraxacum bessarabicum*
308	*Tecomella undulata*
309	*Tetraena alba*
310	*Tetraena coccineum*
311	*Tetraena simplex*
312	*Thymelaea hirsuta*
313	*Traganum nudatum*
314	*Trianthema portulacastrum*
315	*Trianthema triquetra*
316	*Tribulus terrestris*
317	*Trifolium fragiferum*

(continued)

Sl. no.	Taxa
318	*Trifolium repens*
319	*Trifolium tomentosum*
320	*Triglochin palustris*
321	*Urochondra setulosa*
322	*Vicia sativa*
323	*Xylosalsola richteri*
324	*Zaleya pentandra*
325	*Zizyphus nummularia*
326	*Zoysia macrantha*
327	*Zygophyllum eichwaldii*
328	*Zygophyllum eurypterum*
329	*Zygophyllum fabago*
330	*Zygophyllum oxianum*
331	*Zygophyllum propinquum*

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Chapter 12
How Could Halophytes Provide a Sustainable Alternative to Achieve Food Security in Marginal Lands?

Karim Ben Hamed and Luisa Custódio

Contents

Abstract Food insecurity is a major issue in marginal lands around the world where a large population is at risk of insufficient diet and even severe hunger. Since there is no food productivity in these lands, it becomes necessary to investigate the potential for plants that grow and survive in salty soils or waters (i.e., halophytes) to produce food for humans. They have a high taxonomical diversity, broad geographical distribution, and immense diversity in response to salinity. Their phytochemical profiling has indicated their food relevance in many countries. This diversity can be beneficial if the species are integrated rationally and sustainably in the farming systems of many regions in the world under extreme environments. In this review, by presenting case studies on cultivating some alternative crops like quinoa and new cropping systems in many regions in the world, we will show how halophytes could provide a sustainable alternative to achieve food security in marginal lands.

Keywords Marginal lands · Halophytes · Food security

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12.1 Introduction: Food Security Challenges in 2050

According to the latest UN estimates published in June 2017, the number of individuals that count the planet in 2050 will be 9.8 billion and 11.8 billion in 2100. The situation becomes more challenging when today 793 million people are undernourished globally (according to FAO's 'The State of Food Insecurity in the World 2015'). Looking a little closer to these projections, many reports estimate that in 2050, 21.5% of the population will be over 60 years and 70% live in the city. This means a decreasing number of farmers for a growing number of people to feed, and further and further away from the places of production (which will require optimized means of conservation, processing, and transport), while the proportion of middle classes in the developing countries will also increase. But above all it is in Africa that the demographic will know the most spectacular leap: in 2050, the number of Africans should double compared to 2017 reaching 4.47 billion in 2100, while the prevalence of undernourishment is already 20%, and the water resource and agricultural productivity, already low in many countries, may be negatively impacted by global warming.

To meet the growing demand for food, due to both population and economic growth, FAO estimates that an additional 200 M hectares (ha) of new agricultural land will be required for sustaining the present food levels over the next 10 years. In addition, some 3 billion tons of cereals have to be produced by 2050, compared with 2.1 billion tons today. According to FAO projections, global food production is expected to have increased by 70% between 2005 and 2050, not to mention that the rise of biofuels could disrupt these prospects by further increasing the increase in demand. The most effective solution is to increase the productivity of the already cultivated land. But, this conventional intensification is often associated with a high cost and large consumption of water, energy, and pesticides, in addition to soil depletion, loss of biodiversity, and climate changes. An alternative solution is to exploit an area of about 1 billion ha of uncultivated abandoned or marginal lands situated mainly in South America and sub-Saharan Africa. These lands are home to around 1.7 billion people by one estimate. Considered also as marginal lands, approximately 130 M ha of salt-affected lands in the world's coastal and inland salt desert could be suitable for growing crops using saltwater agriculture (Glenn et al. 1998).

12.2 Challenges in Marginal Lands

According to the FAO (2000), marginal land is defined as "land having limitations which in aggregate are severe for sustained application of a given use; [. . .] with inappropriate management, risks of irreversible degradation." Marginal lands mainly include areas which are affected by degradation processes, e.g., erosion, salinization, and low organic carbon contents, and in most cases triggered by anthropogenic impact. These sites exhibit clear economic inefficiencies with regard to agricultural usability and poor ecological site conditions, as indicated by obviously reduced low soil fertility. These lands are distributed in the entire world, regardless of climatic conditions and geographical occurrence. An Oxfam study in 2009 showed that 45.9% of the poor in Sub-Saharan Africa and 25.3% in Asia live in marginal environments.

A large part of these marginal lands is perennial desert or drylands (United Nations Environment Programme (UNEP) 1997): 43% of the earth's total land. These lands are also home to many extremophile plants ("extremophytes") that are able to tolerate and even thrive in extreme environments where few other plant species, and certainly no conventional crops, are able to grow. Salt-tolerant extremophytes or halophytes are an example of these plants that are halophytes that are able to grow and reproduce in saline growth media and could represent a treasure trove of genes for improving crop tolerance to salt and for developing halophyte-based agriculture (Cheeseman 2015; Ventura et al. 2015). Although the definition of a halophyte depends upon the threshold salt concentration used for that definition, it has been estimated that there are 350 known species that can tolerate at least 200 mM salt (Flowers et al. 2010). The central question around which this chapter is organized is whether halophytes could be a part of alternative solutions to meet the challenge of food insecurity in marginal lands.

Increasing food production to meet the nutritional demand of vast growing population in these lands is a real challenge. This goal can only be realized by bringing new lands under cultivation. For instance, uncultivated land in Egypt desert occupied 96% of the total area and characterized with high evaporation (1500–2400 mm/year) and very low rainfall (5–200 mm/year). Parts of this desert are millions of hectares of coastal sites and salinized farmlands. To solve this situation is the replacement of traditional species, which requires large amounts of water, by species adapted to areas of low rainfall, either as food for people or for animals to produce meat and milk. In this context, water and land are used more efficiently, since it is possible to utilize marginal land and water unsuitable for conventional crops.

12.3 The Diversity of Halophytes Under Extreme Saline Conditions

Although they represent only 2% of terrestrial plant species, halophytes are present in about half the higher plant families and represent a wide diversity of plant forms. The largest number of halophytes is found among the Amaranthaceae, followed by Poaceae, Fabaceae, and Asteraceae families. Among these halophytes are annuals and perennials, monocotyledonous and dicotyledonous species, shrubs, and some trees. Halophytes are present, with the exception of polar regions of the arctic and Antarctica, on all continents. They exist as well at European seacoasts and also in humid, tropical rainforests or arid salt prairies, in beaches of secluded islands in of Ozeania, in salt lakes and salt springs of alpine regions (up to 2500 m), or in the middle of the desert (Sahara) at sodium-rich sands. However, their center of appearance is the tropical and temperate zones. They are found on sand dunes or rocky coasts, in saline depressions (sabkhas), in saline inland deserts, and in salt marshes. In Tunisia, for instance, 1.5 million ha (10% of the whole territory and 18% of arable land area) are affected by salt. One of the most fascinating natural saline ecosystems found in Tunisia are coastal or continental sabkhas where salt concentration reaches or even exceeds seawater salinity level (Souid et al. 2018).

There is a wide range of morphological, physiological, and biochemical adaptation in halophytes which vary widely in their degree of salt tolerance (Flowers and Colmer 2008). Halophytes are divided into two groups, excluder and includer halophytes depending on the mechanism to deal with salt (Ben Hamed et al. 2013). Includer halophytes, mainly dicotyledonous, accumulate more NaCl in shoot tissues than monocotyledonous excluder halophytes (especially grasses). This aspect has several consequences on the suitability of halophytes as crops and their culture conditions (Ben Hamed et al. 2013).

12.4 Traditional and Commercial Uses of Halophytes

Halophytes can cope with adverse stressful conditions, such as high salinity and intense UV radiation, partially due to the synthesis of several bioactive secondary metabolites, for example, phenolic compounds and alkaloids. Besides their protective role for the plant, these molecules display important bioactivities, including antioxidant, anti-inflammatory, antidiabetic, and neuroprotective, which may explain the several ethnomedicinal and veterinary uses of different halophyte species (Ksouri et al. 2012). For example, *Salicornia* species (sea asparagus) are used in traditional medicine against obesity and diabetes, while *Crithmum maritimum* L. (sea fennel) is used as diuretic and antiscorbutic (Pereira et al. 2017a). Halophyte's ethnomedicinal uses and chemical richness literally opens a cornucopia of naturally available bioactive products with a high added value in different commercial segments.

There are several plant species which have shown potential to be used as food crops, depending upon their suitability to the available land and climatic conditions. One of the most promising crops toward future food and nutrition security is quinoa, *Chenopodium quinoa* (Jacobsen 2003), because of its robust character and high nutritional value. Very recently, Vilcacundo et al. (2018) identified 17 potential bioactive peptides derived from quinoa proteins. These proteins might be utilized as new ingredients in the development of functional foods or nutraceuticals with the aim of reducing oxidative stress-associated diseases, including cancer. *Sesuvium portulacastrum* is another halophyte species that has a great potential food value and also utilized as a wild vegetable crop in southern India because of its salty taste and fleshy nature (Lokhande et al. 2013). Considering its nutritional composition, the plant can be used to complement as a vegetable in the coastal region. In addition, the plants growing in the arid and semiarid regions can provide the alternative source of fodder to domestic animals. Also, in many developed countries in Europe and America, halophytes like *Aster tripolium* are already used as vegetables in The Netherlands, Belgium, and Portugal, *Salicornia* as food in West Siberia, many mangroves including *Avicennia marina* and *A. germinans* as food in Columbia, and *Zizania aquatic*a (wild rice) as catch crop in western USA and Canada.

12.5 Think Global, Act Locally: Exploiting Endemic and Minor Halophyte Crops

To date, there is increasing interest both of global initiatives such as Biodiversity International and of the public and private sector toward "new crops," "alternative cultivations," "new uses," and "new markets" (Padulosi et al. 2013). The interrelated problem of malnutrition and disease is still the world's greatest challenge (Padulosi et al. 2013).

To date, agricultural research is expected to develop effective strategies not only to produce more food worldwide but also to improve global, regional, and local access to more nutritious food and fodder crops to feed people most at risk for food insecurity due to soil salinity or groundwater salinization. Ninety percent of the world's food is coming from only 30 plant species. Only four crops (wheat, rice maize, and potato) contribute to up to 50% of calories and proteins obtained by humans from plants (Panta et al. 2014). In many developing countries like Bangladesh, India, Pakistan, Egypt, and Tunisia, these crops are mainly affected by the problem of salinization. Data from local researchers showed that these countries are seriously deficient in wheat, maize, and species for the production of oils. For example, in Tunisia where 2/3 of the total area is considered as arid and semiarid regions, and salinity affects more than 10% of the total area, wheat constitutes 96% of cereals consumed and over half of the daily caloric intake per person. Tunisia relies heavily on grain imports, mainly wheat, even in good production years. Cereal imported in the 2015/2016 marketing year (July/June) reached about 3.5 million tons, which is 15% higher than the previous 5-year average. The situation in other developing countries like Egypt, India, Pakistan, and Bangladesh (Timsina et al. 2018) seems more challenging in achieving food security due to their high population and density, diet changes, and limited room for expanding cropland and cropping intensity.

A change in attitude is noticed over the last 5–10 years among policy makers and the public with regard to the quality of life as related to the quality of food as well as diverse sources of food. This global "opening" toward alternatives crops is the result of a gradual change of attitude toward biodiversity and plant genetic resources by many organizations, institute, countries, etc.

According to experts' opinion (International Plant Genetic Resources Institute, International Center for Underutilized Crops, FAO, etc.), numerous neglected species, also called minor or alternative crops (Table 12.1), are species cultivated on

Table 12.1 List of minor field crops

Category	Crops
Feed and forages	Bird seed (sunflower, proso millet, canary grass, etc.), pearl millet, sorghum, forage brassicas – turnips, rutabagas, kochia, medics, sainfoin, switch grass, quinoa, *Salicornia*
Fiber, fuel, edible, and industrial oils	Canola, castor beans, comfrey, corn (for oil), *Crambe*, *Cuphea*, flax, guayule, jojoba, kenaf, *Lesquerella*, lupine, meadow-foam, milkweed, *Perilla*, safflower, sesame, sunflowers, *Vernonia*, *Salicornia*
Food grains, pseudocereals, legumes, etc.	Amaranth (food and feed), barley, buckwheat, dry edible beans (field beans), field peas (food and feed), Jerusalem artichokes (food and feed), pearl millet, quinoa, sesame (seeds), sorghum (syrup), triticale, wheatgrass, wild rice

small areas or which normally grow in specific geographical regions and which create market opportunities. These species offer the potential to not only diversify the human diet but also increase food production levels and, thus, enable more sustainable and resilient agro-food systems (Baldermann et al. 2016). Most of these species have a comparative advantage in marginal lands, where they have been naturally selected to withstand stress conditions and can, therefore, contribute to low-input sustainable production systems (Thompson et al. 2007).

The year 2013 was exceptional for alternative crops as it was the International Year of Quinoa celebrated by the Food and Agriculture Organization (FAO). This reflects the importance of research conducted on quinoa and other alternative crops in many regions of the world.

12.6 Halophytes Food: From the Field to the Market

12.6.1 Nutritional Properties and Health-Enhancing Properties

Halophytes are traditionally consumed for their organoleptic properties (Davy et al. 2001; Ventura and Sagi 2013). For example, species belonging to the *Salicornia* L. and *Sarcocornia* L. genera produce succulent shoots that are highly valued in gourmet cuisine due to their salty taste (Ventura et al. 2011a). In Europe, the young fleshy tips of those species are commercialized with the name "samphire" or "sea asparagus" (Ventura and Sagi 2013). Other Medicinal and aromatic halophytes like *Helichrysum italicum* subsp. *Picardii* (everlasting) and *Crithmum maritimum* L. (sea fennel) are traditionally used in many countries as spice or pickle, due to their interesting sensory properties (Castroviejo et al. 2003; Franke 1982; Renna and Gonnella 2012¸ Pereira et al. 2017a, b). Besides their pleasant organoleptic properties, several edible halophytes display a nutritional profile adequate for human consumption. Generally, halophytes have higher ash contents than other edible plants and are valuable sources of essential minerals, such as Na, K, Mg, Ca, and Fe (Borah et al. 2009; Barreira et al. 2017). Halophytes also tend to contain high fiber and protein contents and are poor in fat (Díaz et al. 2013; Barreira et al. 2017) and are thus considered as a healthy food. Halophytes can also contain appreciable levels of other nutritional elements, for example, tocopherols (Davy et al. 2001; Ksouri et al. 2012; Barreira et al. 2017) which are fat-soluble antioxidants that play an important role in the prevention of lipid peroxidation by reactive oxygen species (Bernal et al. 2011). Overall, and due to their contents in nutritional elements with possible benefits for human health, halophytes can be exploited as crop halophytes in the context of food security.

12.6.2 Production Systems

12.6.2.1 Saline-Seawater Agriculture

Halophytes can be cultivated in conditions where other crops (glycophytes) can't. In fact, their high salt tolerance enables their use in sustainable saline agriculture and production systems using a range of saline irrigation water resources and/or underutilized soils. Halophytes can be commercially produced, for example, in greenhouse aquaponic systems using saline water (e.g., *Salicornia* sp. in RiaFresh, Portugal (http://www.riafresh.com), and Koppert Cress, The Netherlands (http://www.koppertcress.com)) or in saline soils (e.g., *Salicornia ramosissima* L. and *Inula chrithmoides* L. – golden samphire in Horta Salgada, Portugal https://www.facebook.com/HORTASALGADA.pt/). Moreover the levels of secondary metabolites that are responsible for the medicinal properties of halophytes may be manipulated by agrotechnical practices, for example, irrigation water quantity and salinity, fertilization, harvest time and cycle, and harvested plant material (young or old leaves) (Ventura et al. 2010, 2011a, b, 2013).

Halophytes can also be farmed via integrated multi-trophic aquaculture (IMTA) system (Waller et al. 2015; Custódio et al. 2017). IMTA systems are innovative technologies allowing the recycling of materials and energy and are considered as an important tool for the sustainable development of aquaculture at a global level (Granada et al. 2015; Alexander and Hughes 2017). In IMTA the by-products (wastes) from one species are recycled to become inputs (fertilizers, food, and energy) for another species through the cultivation, in the right proportions, of fed aquaculture species (e.g., finfish) with organic extractive species (e.g., suspension and deposit feeders) and inorganic extractive aquaculture species (e.g., seaweeds or plants) (Chopin et al. 2008; Troell et al. 2009; Barrington et al. 2009).

For example, there are reports of the successful growth of *S. europaea* with effluents from a shrimp, sole, and turbot farming (Webb et al. 2012) and of *Tripolium pannonicum* (Jacq.) Dobrocz., *Plantago coronopus* L., (buckshorn plantain), and *S. dolichostachya* (moss). Coupled with the production of European sea bass (*Dicentrarchus labrax* L.), *Sesuvium portulacastrum* (sea purslane) and *Batis* *maritima* (saltwort) were also successfully grown hydroponically in a marine aquaponic system (Boxman et al. 2017).

12.6.2.2 Halophyte-Glycophyte Associations: Toward Sustainable Intercropping Systems in Marginal Lands

The soils in many arid and semiarid regions are saline and are not thus proper for the cultivation of traditional crops. In these soils, many glycophytes or salt-sensitive species (like barley and *Medicago*) are capable of growing in association with perennial halophytes. The latter are capable of desalinizing and fertilizing soils, thus creating microhabitats favorable for the development of annual glycophytic plants (Ben Hamed et al. 2014). Small-scale experiments showed that the cultivation of the salt-accumulating halophyte *Sesuvium portulacastrum* on saline soils led to a significant decrease in soil salinity. Indeed this plant can remove the equivalent of 6.5 tons of NaCl/hectare/year (Rabhi et al. 2010; Panta et al. 2014). Other results showed that barley plants grown on a saline soil previously desalinated by the halophyte *S. portulacastrum* showed a better development and produced large biomass compared to those grown on unsalted soil.

These properties can be exploited to ameliorate growth performance of many food crops in saline soils by cultivating them in mixed cropping with halophytes. Recently, Nanhapo et al. (2017) mixed cowpea cropping with ice plant (*Mesembryanthemum crystallinum*), a salt-accumulating halophyte that alleviates the salinity stress of cowpea. The mixed cropping system using ice plant has not been applied, probably because ice plant is still considered as a “minor crop.” However, ice plant is utilized as a raw or cooked vegetable (Abd El-Gawad and Shehata 2014; Herppich et al. 2008) and is principally used for medicinal purposes (Abd El-Gawad and Shehata 2014; Deters et al. 2012; Bouftira et al. 2012). Mixed cropping system using halophytes might reduce the ion content in the leaves of salt-sensitive crops of drier tropical regions such as cowpea. Moreover, crop farmers will harvest the produce from both crops of the mix cropping system for consumption and/or generate income, which will improve their livelihoods at low production input.

Other studies showed that it is possible to cultivate the fodder halophyte grass *Panicum turgidum* together with the salt accumulator halophyte *Suaeda fruticosa* in marginal lands under brackish water irrigation (Khan et al. 2009). This intercropping system is one way to use the 130 M ha of abandoned saline land and brackish water for producing economically viable and environmentally sound agriculture. This example of a successful intercropping culture supports the possibility to adopt the polycultural practices in marginal lands instead of conventional monoculture system.

12.7 Conclusion

Halophytes can be used for human food consumption in 2050. At the same time, the need to expand agricultural production into extreme marginal lands to meet the 2050 challenge of feeding over nine billion people requires immediate and drastic action. One of the most obvious solutions is to find potential uses of halophyte in harsh saline environments. Inland and coastal cultivation of halophytes will contribute to the establishment of innovative farming systems in marginal lands allowing for a significant increase in the productivity and quality of commercial crops typical in that area, to reduce the levels of soil salinization, and to identify new salt-tolerant cash crops that can be cultivated under the extreme conditions of such lands. Aquaponic halophytes production will be enhanced upon the reuse of nutrients originating from the marine aquaculture production. All these halophyte-based opportunities will provide an increase in farmers' income while preserving agroecosystems' integrity and services. Figure 12.1 summarizes all the ideas developed in this review to show how the utilization of halophytes could transform marginal saline habitats into new productive areas.

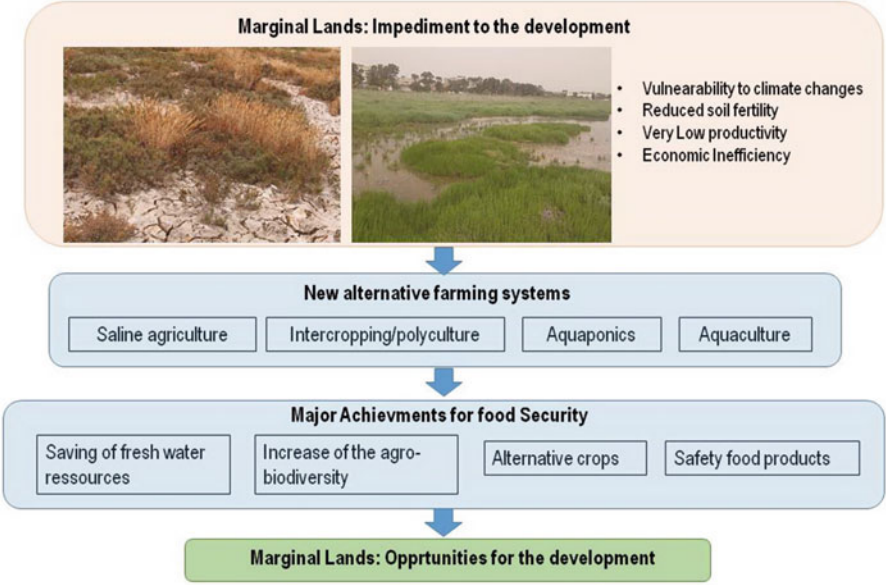

Fig. 12.1 Halophytes in marginal lands: from impediment to opportunities to the development and food security. (Photos in the figure are taken in Tunisian Sabkhas by K. Ben Hamed)

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Chapter 13
Halophytes: The Plants of Therapeutic Medicine

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Contents

Abstract Halophytic plants that grow in an extensive range of saline soils have significant economic importance, with potential for use in environmental restoration and therapeutic medicine. Halophytes live in coastal regions, from salt-marshy mudflats to inland deserts. They are traditionally used for medicines and the release of bioactive compounds, such as terpenes, phenols, antioxidants, and anticarcinogenics. These compounds can also be potentially used as medicines. The literature reveals that different types of medicines obtained from coastal and near-coastal species have been used by local inhabitants. The present review focuses on the potential use of halophytes as medicines and their utilization at local and industrial levels.

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13.1 Introduction

The term halophyte is used to describe native flora grown in high salt concentrations with osmotic pressure of at least 3.3 bars, which are characterized by high physiological plasticity and the ability to thrive in a salinity-stressed environment (Jennings 1976). Halophytes have substantial economic potential by contributing enormously to environmental refurbishment and as potential sources of medicine. Halophytes have the ability to remediate the soil, accumulating large amounts of sodium salts through roots, improving nutrient availability, and creating microclimates favorable for the growth of fodder glycophytes, which contribute to the productivity of this ecosystem (Abdelly et al. 2011). Several species of halophytes are used as folk medicine and prove that halophytes have antipathogenic activity toward plants, animals, and humans. Recent reports reveal that secondary metabolites are responsible for their bioactivities in the pharmaceutical industry and medicine (Phillips et al. 2006; Falleh et al. 2011a, b). The Ayurveda system relies heavily on preventive medicine and the promotion of positive health. Ayurvedic preparations called Rasayanas are used to promote health. The Rasayanas are preparations from several plant extracts, containing strong antioxidants, and are used as rejuvenators or nutritional supplements (Govindarajan et al. 2005; Thyagarajan et al. 2002). In recent years, pharmacognostics and researchers of medicinal plants have identified the therapeutic properties of halophytes (Qasim et al. 2017).

Halophytic plants are salt-tolerant and have latent medicinal and nutraceutical properties that can potentially be used as a source of functional compounds in nutritional diets, such as flavonoids, high-molecular-weight tannins (Meot-Duros and Magné 2009; Falleh et al. 2011a), polyunsaturated fatty acids (Ksouri et al. 2009), and proteins and vitamins (Ksouri et al. 2011). In the Vedic period of India about 3500 years ago, the first medicine records books on Ayurveda and *Charaka Samhita* (600 BC) came about. Globally, approximately 25,000 halophyte species are known to grow under saline environments to date and are used as edible plants, animal fodder, biofuel, medicine, bioactive secondary metabolites (e.g., terpenes, phenols, antioxidants, anticarcinogenics), and ornamental plants (Abdelly et al. 2006). The species of halophytes from the genera *Acanthus*, *Aegiceras*, *Avicennia*, *Bruguiera*, *Ceriops*, *Exoecariaceae*, *Kandelia*, *Rhizophora*, *Sonneratia*, *Suaeda*, and *Xylocarpus* plants grow in brackish soil because they have the ability to survive in high-saline environments and in anaerobic soil (Thatoi et al. 2014). These genera of halophyte plants contain a number of phenolic compounds, such as anthocyanins, catechins, coumarins, flavones, flavonoids, isoflavones, isocatechins, and lignans, which are used as a rich source of antioxidants (Schwarzlander et al. 2008).

Currently, halophytes are attracting attention because of their nutraceutical potential, their strong antioxidant powers, and their therapeutic role in curing a number of diseases such as autoimmune pathological conditions, digestive system disorders, inflammation, neurodegenerative disorders, and viral infections. They are also used as an external source of antioxidants to detoxify the excess production of free radicals in the human body (Ramchoun et al. 2009). The antioxidants obtained from halophytes are in the form of herbal drugs used to protect against free radical-induced injury (Ksouri et al. 2009). The present review reports the pharmaceutical and therapeutic medicinal roles of halophytes for economic and safety reasons. They are the sources of natural antioxidants and biologically active compounds that may be used as potential substitutes in the pharmaceutical industry to replace synthetic medicine from natural biologically active compounds.

13.2 Folk Halophyte Species Used for Medicinal Value

The scarce literature available reveals that halophytes have been used in traditional medicine up to the present day. In this chapter, we discuss some of the medicinal halophyte species and their uses in folk medicine around the world.

Sea fennel or rock samphire (*Crithmum maritimum*) is an aromatic perennial plant present on cliffs and rocks or on the beach (Males et al. 2003). Guil-Guerrero et al. (1996) showed a keen interest in folk medicine, such as diuretics, antiscorbutics, and its digestive and purgative properties.

The root and rhyzomes of the salt-tolerant plant *Glehnia littoralis*, a perennial herb native to sandy seashores, of which the young flower buds and leaves are edible, have been customarily used as a diaphoretic, an antipyretic, and an analgesic (Rozema et al. 1985; Masuda et al. 1998; Um et al. 2010). Another salt-tolerant plant, *Cynara cardunculus,* commonly named “cardoon,” of the family Asteracae, is naturally grown under adverse environmental conditions, such as drought, high salinity, and high temperature (Fratianni et al. 2007). The plant leaf and stem are used in soups, salads, and sweet dishes (Gominho et al. 2000), the flowers are used in the preparation of cheese (Valentão et al. 2002), whereas leaves are mainly used in folk medicine as diuretic, antidiabetic, cholagogue, choleretic, and antimicrobial agents (Krizková et al. 2004; Fratianni et al. 2007).

In folk medicine, *Inula viscosa*, a member of the Asteracae family used as an anti-inflammatory, with antiscabies, antipyretic, antiseptic, and antiphlogistic activity for wound healing (Lauro and Rolih 1990; Ali-Shtayeh and Abu Ghdeib 1999) and in the treatment of diabetic patients (Yaniv et al. 1987). Also, the plant has been used in gastroduodenal disorders, in the treatment of tuberculosis, bronchitis, anemia, and as a promoter of female sterility and abortion induction (Al-Dissi et al. 2001). *Cakile maritima L.*, an annual succulent halophyte, belongs to Brassicaceae and is distributed globally in sandy coastal areas (Clausing et al. 2000). It is traditionally used for its antiscorbutic, diuretic, digestive, and purgative properties (Guil-Guerrero et al. 1996; Davy et al. 2006). The weed *Chenopodium album* L. is a widely distributed halophyte. Its dried fruits have been used in folk medicine for their laxative, sedative, diuretic, hepatoprotective, and antiparasitic properties for many years (Fournier

1999; Dai et al. 2002). Roots of *Asparagus officinalis* are used to cure pains of the joints, hips, and back, and to rinse out the harmful substances of the bladder that cause gout in the feet. The roots of *Asparagus racemosus* are used against rheumatism and inflammation in traditional medicine (Goyal et al. 2003).

Thespesia populnea is a large halophytic plant found in the coastal regions of India. The above-ground part, such as the bark, leaves, flowers, and fruits, are used for medicinal purposes against dysentery, cholera, hemorrhoids, and infections such as eczema, guinea worm, psoriasis, ringworm, and scabies (Ilavarasan et al. 2003a, b), whereas the root, bark, and fruits are used against dysentery, cholera, and hemorrhoids (Ilavarasan et al. 2003b). The fruits are used to control diabetes, as vividly described in Ayurveda (Sathyanarayana et al. 2004). In southern India and Sri Lanka, the leaves and bark used for oil production are also used for fracture wounds and as an anti-inflammatory poultice applied to ulcers and boils (Jayaweer 1982). The plant *Limoniastrum monopetalum* is used in folk medicine for its antidysenteric, antibacterial, and anti-inflammatory properties against infectious diseases that cause body pain, bloody diarrhea, and for treating hemorrhage and menstrual disorders in women (Chaieb and Boukhris 1998; Aniya et al. 2002; Murray et al. 2004). A broad range of halophytes are used as natural medicines for a number of diseases, such as asthma (*Evolvulus alsinoides*), as a diuretic (*Portulaca quadrifida*), for the eyes (*Zygophyllum simplex*), gonorrhea (*Portulaca oleracea*), heart disease (*Capparis decidua, Kochia indica*), as a laxative (*Capparis decidua*), pain killer (*Solanum surattense*), for pneumonia (*Corchorus depressus*), as a sedative (*Withania somnifera*), for skin diseases (*Salsola imbricata*), snakebites (*Rumex vesicarius*), and ulcers (*Ceriops tagal*) (Khan and Qaiser 2006; Ksouri et al. 2011).

13.3 Release of Bioactive Compounds, Properties, and Medicinal Uses

Medicinal halophytes have a wide range of bioactive compounds that can used to treat human infirmities. They are consumed either as whole plants or specific parts only for medicinal purposes. Currently, a huge range of medicinal halophytes are being used in salads, vegetables, coloring, flavoring, and as spicing agents in food (Qasim et al. 2014). Halophytes have a broad range of bioactive complexes (primary and secondary metabolites), i.e., essential oils (terpenes), polyunsaturated carotenoids, fatty acids, glycosides, polysaccharides, sterols, phenolic compounds, and are a rich source of vitamins. These bioactive substances have potent anti-inflammatory, antimicrobial, antioxidant, and anticarcinogenic activity, and the complexes avert various diseases (such as atherosclerosis, cancer, cardiovascular disorders, and chronic inflammation). They are a modern source of health products such as nutraceuticals, growth regulators, and are cost-effective medicines. Bioactive compounds that are beneficial to health are the primary and secondary metabolites discussed in this chapter.

13.3.1 Primary Metabolites

A primary metabolite (central metabolites) is one that plays a direct role in growth, development, and differentiation. Usually synthesized directly by sunlight, it has a physiological function in the organism and is a major constituent of organisms or cells (Bernal et al. 2011). Primary metabolites are mainly carbohydrates and their derivatives, lipids, certain amino acids, and related compounds (Ksouri et al. 2011).

13.3.2 Carbohydrates and Glycosides

Carbohydrates are primarily synthesized by the photosynthetic activity of plants acting as storage and structural components. These compounds have a probiotic effect or commonly have antioxidant or anti-inflammatory activity (Bernal et al. 2011). Macrophages stimulated by *S. herbacea* play a substantial protagonistic role in the host–pathogen defense mechanism by releasing nitric oxide and cytokines (Im et al. 2003) and have an inhibitory effect on tumor cell growth and microorganism infection (Lee et al. 2006). Many halophytic plant glycosides have antidiabetic, antibacterial, anti-obesity, and cancer prevention activity, in addition to antineoplastic effects (Erkucuk et al. 2009). A metabolite, namely a glucosinolate derived from amino acid biosynthesis (Podsedek 2007), is one of the most important metabolites of the Brassicaceae family and acts as a cholesterol-reducing agent, an anticarcinogenic substance, and has folk pharmacological effects in humans (Cieslik et al. 2007). Radwan et al. (2008) reported that glucotropaeolin, ethyl glucosinolate, 2-methyl butyl, and 4-pentyl glucosinolate are major constituents of the halophyte *C. maritima*. These four glucosinolates display robust antioxidant activity against molluscicidals caused by *Biomphalaria alexandrina*. Cardiac glycosides (bufadienolides) are synthesized by *Urginea maritima* (Adams et al. 2009) and extract obtained from this halophyte is widely used for the prevention of heart failure and kidney disorder (Hänsel et al. 1994). Saponins are amphipathic glycosides and have hemolytic, immunological, antibacterial and antidiabetic properties, increase testosterone levels, and stimulate muscle growth (Kimura et al. 2006; Li et al. 2009). The pharmaceutical industry requires saponins, because researchers believe them to be a major constituent of drugs and folk medicines obtained from natural plants and used in the cosmetic and phytotherapy industries (Estrada et al. 2000). Bioactive compounds obtained from the extract of *Tribulus terrestris* have anti-hypertensive activity in rats and are also involved in smooth muscle relaxation via membrane hyperpolarization and in releasing nitric oxide (Phillips et al. 2006).

13.3.3 Lipids

Natural lipids and their derivatives quarantined from halophytic plants show important biological activity and antibacterial qualities, including phototoxic, antimicrobial, anticarcinogenic, and antifungal medicinal properties (Dembitsky 2006). Lipids are a large cluster of regular compounds that include carotenoids, natural fats, fat-soluble vitamins (A, D, E, and K), phospholipids, sterols, mono- and di-glycerides, and waxes (Ksouri et al. 2011). Lipids obtained from halophytic plant species are used as nutraceuticals and for medicinal purposes in humans. Halophyte seeds and stems are an original source of unsaturated fatty acids with a *cis*-configuration double bond between carbon skeleton C_{16} and C_{20} (Stuchlik and Zak 2002). Humans cannot synthesize certain fatty acids, such as ω-3 (α-linolenic acid), ω-6 (linoleic acid), and ω-9 (oleic acid), but halophytes are a good source of these polyunsaturated fatty acids (Herbaut 2006). Eicosapentaenoic acid and docosahexaenoic acid are synthesized from ω-6 (linoleic acid), which is converted to eicosanoids (hormone-like compounds), for vital organ functioning and intracellular activity (Reiffel and Mc Donald 2006). 5-hydroxyindoleacetic acid in cerebrospinal fluid can cause depression and suicide, but is neutralized by docosahexaenoic acid extracted from *Salicornia bigelovii* (McNamara et al. 2009). γ-Linolenic and arachidonic acids are precursors of prostaglandins in the human body, which protect the blood vessels of the brain and prevent oxygen deficiency. *Descurainia sophia*, commonly known as a Chinese halophyte, contains 76.6% polyunsaturated fatty acid, 53.7% linolenic acid with α-linolenic acid, γ-linolenic acid, and the arachidonic acid content is 5.3% (Yajun et al. 2003) (Tables 13.1 and 13.2).

The halophyte species *Crithmum maritimum* contains 81% total fatty acids, and has resilient antimicrobial activity against *Bacillus cereus, Candida albicans*, *Erwinia carotovora*, *Micrococcus luteus*, *P. aeruginosa*, *P. marginalis*, *Pseudomonas fluorescens*, and *Salmonella arizonae*, with a low concentration ranging between 1 and 100 μg ml^{-1} (Zarrouk et al. 2003; Meot-Duros et al. 2008). The genus *Thapsia* has a high level of petroselinic acid, an isomer of oleic acid, which is interestingly used as a oleochemical in the cosmetics and pharmaceutical industries (Murphy 1994; Avato et al. 2001).

Halophytes are rich sources of phytosterols and tocopherols because they have lipophilic constituents, protecting against lower risk cancer and long-lasting diseases, maintaining the concentration of serum cholesterol, and preventing the risk for atherosclerosis (Ortiz et al. 2006; Patel and Thompson 2006). Oils obtained from the unsaponifiable fraction of halophytes, biological active emulsifiers, and the high content of phytosterols maintain the structure and permeability of the membrane, interacting with alcohol, lipids, phenol, and some heterocyclic ingredients (Gusakova et al. 1998). Isolation from halophyte species *Teucrium abutiloides* and *Teucrium betonicum* extract results in a wide range of biologically active complexes, i.e., poriferasterol, clerosterol, and (24*S*)-24-ethylcholesta-5, 22, 25-trien-3β-ol (Gaspar et al. 1996; Fontana et al. 1999). Oil from *Teucrium* seeds is rich in tocopherols, with a total content varying between 534 and 569 mg/kg of seed oil (Hachicha et al. 2009). The alpha-tocopherol level in *T. nabli* it is 296 mg kg^{-1}), in

Table 13.1 Halophytes traditionally used as folk medicine

Species	Medicinal uses	References
Artemisia capillaris	Anti-inflammatory, cholagogic, diuretic in jaundice and cholecystitis, antipyretic	Yao and Chen (2007)
Artemisiae scoparia	Sedation, protects the liver, reduces blood pressure, decreases body temperature, anti-inflammatory, antibacterial, antipathogenic microbes, and anticarcinogenic action	Zhang et al. (2002), Ramezani et al. (2004), and Cha et al. (2005)
Atriplex halimus	Diabetes control, glycemic and antiparasitic in cattle	Sokolowska-Krzaczek et al. (2009)
Chenopodium album	Hepatoprotective and antiparasitic properties	Dai et al. (2002)
	Laxative and sedative agent	
Cocos nucifera	Diarrhea, arthritis, taeniasis, bleeding, schistosomiasis, and ancylostomiasis	Blini and Lira (2005)
Ficus microcarpa	Fever and pain relief, folk remedies to decrease perspiration	Chiang et al. (2005) and Krishnaiah et al. (2011)
Hordeum vulgare	Applied like a plaster to joints externally against gout and rheumatism	Adams et al. (2009)
Nitraria retusa	Folk medicine as anti-arrhythmic, antineuropathic, and antispasmodic agents	Xing (1991)
Plantago	Cold cure, viral hepatitis, respiratory organs, skin, digestive organs, reproduction, circulation, and cancer prevention	Chiang et al. (2002) and Adams et al. (2009)
Rubia cordifolia	Chronic bronchitis, hemorrhage, trauma, and cancers	Gao et al. (2000)
Salicornia herbacea	Constipation, obesity, diabetes, and cancer	Han and Kim (2003)
Tamarix gallica	Leucoderma, spleen trouble, and eye diseases, anti-inflammatory, antidiarrheic, cicatrizing, and antiseptic agents	Younos et al. (2005) and Saïdana et al. (2008)
Terminalia catappa	Hepatoma prevention, hepatitis, dysentery, and diarrhea cure	Chen et al. (2000)
Tribulus terrestris	Cardiovascular diseases such as hypertension and coronary heart disease	Sharifi et al. (2003) and Phillips et al. (2006)
Verbena officinalis	Analgesic and antiphlogistic	Calvo (2006) and Jarić et al. (2007)

T. alopecurus it is 316 mg kg^{-1}), and in *T. polium* it is 277 mg kg^{-1}, whereas the lowest amount of β-tocopherol is detected. *Hippophae rhamnoides* L. pericarp oil is enriched with triacylglycerols (palmitoleic 16:1(9) acid), vitamins E and F, carotenoids (cryptoxanthin, carotene, physalin, zeaxanthin), alkanols, phytosterols, and tocopherols (Gusakova et al. 1998). *Teucrium* (and *Batis maritima* and *Hippophae rhamnoides* oil) (Kallio et al. 2002; Hachicha et al. 2009) contains phytosterols and tocopherols in higher amounts than *Glycine max, Medicago sativa*, *Avocado persea, Olea europeae*, and *Zea mays*, but protects from melanocyte-forming processes and skin diseases (Hachicha et al. 2009). *Apium graveolens* root extract contains high amounts of falcarindiol, falcarinol, and panaxadiol (Zidorn et al. 2005).

Table 13.2 Bioactive compounds of halophytes and their medicinal uses

Bioactive compound	Obtained from	Medicinal uses	Part used
Nimbin	*Azadirachta indica*	Antipyretic, antiseptic, cholera, cold diabetes, piles, ulcer, urinary complaint, tumors, small pox, and scabies	Whole plant
Punarnavine	*Boerhavia diffusa*	Epilepsy, heart disease, and rheumatism	
Protoine and corlumine	*Corydalis govaniana*	Antipyretic, eye disease, gastric pain, and muscle pain	
Saponin	*Solanum nigrum*	Urine disorder, sprain, liver complaints, jaundice, and seasonal fever	
Tannin-astrin	*Anogeissus latifolia*	Diarrhea, headache, snakebite, and stomach disorder	Bark
Homoferreirine and isoflavanone	*Ougeinia oojeinensis*	Asthma, bronchitis, and fish poison	
Keno-tannic acid	*Pterocarpus marsupium*	Cooling, diarrhea, tonic, toothache, and dysentery	
Colloturine	*Symplocos racemosa*	Blood purifier, cough, bronchitis	
Acorin, calamenol and asarone	*Acorus calamus*	Body ache, asthma, and abdominal pain	Roots
Berberine	*Berberis aristata*	Rat and snake bites, boils, eye complaints	
Propeimine	*Fritillaria roylei*	Bronchitis, burns, stomach disease	
Jatamansic acid	*Nardostachys grandiflora*	Blood purifier, cooling, cough, diuretic, tonic ulcers, snakebite	
Serpajmaline	*Rauwolfia serpentina*	Blood pressure, fever, vomiting, intestine trouble, malaria, nervous disorder	
Glucoside munjistin	*Rubia cordifolia*	Chest complaints, leucoderma, inflammation, menstrual disorder, paralysis, postnatal, and ulcers	
3α-tigloylooxytropane	*Withania somnifera*	Asthma, bronchitis, cough, dyspepsia	
Marmelosin	*Aegle marmelos*	Constipation and gastric trouble	Fruits
L-ascorbic acid	*Emblica officinalis*	Constipation, fever, laxative, vaginal complaints	
Astrin and chebulinic acid	*Terminalia chebula*	Cold, cough, indigestion, pneumonia, and pregnancy	
Aloin and uronic acid	*Aloe barbadensis*	Breast tissue hardening, jaundice, rheumatism, spleen disease, and sexual vitality	Leaf
d-α-phellandrene	*Cinnamomum tamala*	Heart and throat complaints	
Skimnianine	*Skimmia laureola*	Antiseptic, gastric pains, rheumatism, and scabies	
Alpaline and taxanine	*Taxus baccata*	Anticancer	

13.3.4 Secondary Metabolites

The term secondary metabolite, or phytochemical, refers to a broad spectrum of plant metabolites that have low molecular weights and are widely distributed in plants (Acamovic and Brooker 2005; Edreva et al. 2008). Plants produce secondary metabolites to protect themselves against environmental stresses and they are defined as those substances (Smitha Patel et al. 2013) generated in natural food stuffs by the normal metabolism of species and by different mechanisms, for example, the inactivation of some nutrients, the diminution of the digestive process, or the metabolic utilization of food that exerts effects contrary to optimal nutrition (Kumar 1991).

13.3.4.1 Phenolic Compounds

Phenolic compounds are simple phenol derivatives of hydroxybenzoic acid (hydrolyzable tannins) to condensed tannins (Tania da et al. 2012). The two types differ in their effects on animals, one with respect to nutrient digestibility and the second causes toxic manifestations owing to hydrolysis in the rumen (Smitha Patel et al. 2013). A wide range of phenolic compounds are present in different halophyte species, such as flavonoids, isoflavones, coumarins, and phenolic acids, which are widespread in the leaf, stem, flower, and seed of halophytes (Miniati 2007). The main difference between usual phenolic and biological active phenolic complexes is that they act as folk medicine and have nutraceutical properties without any antagonistic effect (Bernal et al. 2011). Nowadays, in human food, halophytes are supplementary in the promotion of health care activities such as reducing body weight, having anticarcinogenic and anti-inflammatory properties, decreasing blood sugar levels, and having antithrombotic and anti-aging actions (Senevirathne et al. 2006). A finding from Sharifi et al. (2003) showed that *Tribulus terrestris* roots and fruit are rich sources of alkaloids, flavonoids, glycosides, saponins, and play a potential biological role in growth and development.

The species *Atriplex halimus* and *Nitraria tangutorum* have potent antioxidant activity owing to abundant flavonoids (isorhamnetin, kaempferol, patuletin, quercetin, spinacetin, and tricin) in food (Benhammou et al. 2009). Phenol derivative compounds, i.e., ferulic acid betacyanin, flavonol, hyperoside, and rutin isolated from the shoots of *Mesembryanthemum edule*, are used to prevent oxidative stress-related diseases and nutritional food in folklore (Van Der Watt and Pretorius 2001; Falleh et al. 2011a, b). These compounds are derived from a phenolic structure, with -OH groups showing antibacterial, anticancer, and antiviral activities (Okuda 2005). *Mesembryanthemum edule* has antioxidant properties and detoxifies the superoxide, 2,2'-azino-bis-3-ethylbenzothiazoline-6-sulfonic acid, and 2,2-diphenyl-1-(2,4,6-trinitrophenyl) hydrazyl radicals that accumulate during oxidative stress. Herba Artemisiae Scopariae is found in abundance in phenolic bioactive compounds, i.e., chlorogenic acid, *P*-hydroxyacetophenone, and caffeic acid, and is clinically used for the treatment of severely icteric contagious oral ulcer and hepatitis (Xu 1995).

Seo et al. (2003) also found that methanolic extract from *Artemisia capillaris* shows strong antioxidant activity in hyperlipemia. Cynarin is a caffeoyl derivative phytocompound of poly-phenols in the halophyte species *Cynara cardunculus*, which acts as an antioxidant, cholesterol synthesis inhibitor, and hepato-protector (Gebbart 1998). *Limoniastrum monopetalum* leaf extract, which is rich in polyphenol content, shows antioxidant, superoxide scavenger, and antimicrobial activity (Trabelsi et al. 2010). *Cocos nucifera* leaf and stem extract has larger amounts of bioactive polyphenol compounds, i.e., vanillic, chlorogenic, and ferulic acids, as identified by Ralay Ranaivo et al. (2004). Five different classes of bioactive complexes have been identified in *Plantago major*, namely vanillic acid (benzoic compound), baicalein, luteolin (flavonoids), aucubin (iridoid glycoside), caffeic acid, *p*-coumaric acid (hydroxy-cinnamic acids), and ursolic acid (triterpenes) (Duke 1992; Samuelsen 2000).

Tungtungmadic acid, quercetin 3-O-glucoside, and isorhamnetin 3-O-glucoside with 1,1 diphenyl-2-picrylhydrazyl have a scavenging effect against oxidative stress and have been reported in *Salicornia herbacea* (Park and Kim 2004; Rhee et al. 2009). Chenopodiaceae and Plumbaginaceae families have a number of bioactive compounds that play pharmacological and bio-technological roles (Saïdana et al. 2008) in the development of new drugs. The halophyte *Suaeda fruticosa* has been found to have hypolipidemic and hypoglycemic properties (Benwahhoud et al. 2001). A wide range of secondary metabolites in *Rubia tinctorum* extract, i.e., di-hydroxyanthraquinones, tri-hydroxyanthraquinones, and purpurin derivatives, show bactericidal, antifungal, antipruritic, antinociceptive, and anti-inflammatory effects (Bányai et al. 2006).

Terminalia catappa has a great antioxidant, antibacterial, and antisickling potential, in addition to antisteroidogenic and hepatoprotective activity owing to bioactive punicalagin, punicalin, quinones, and tannin components of inflammation induced by carrageenan in rats, and genotoxicity induced by bleomycin in rabbits (Chen et al. 2000). *Asparagus officinalis* root extract contains an active amino acid and its derivatives, flavonoids, oligosaccharides, and steroidal saponins (Fukushi et al. 2000; Hayes et al. 2006). Two halophyte species, *Cakile maritima* and *Thellungiella salsuginea*, have been found to have a high degree of salt tolerance and a potential rich in antioxidants owing to higher amounts of phenolic compounds, glucosinolate compounds, ascorbic acid, alkaloids, coumarins, flavonoids, sterols, sulfur glycosides, and triterpenes (Jahangir et al. 2008; Radwan et al. 2008). *Hippophae rhamnoides* fruits, which are rich in fatty acids, flavonoids, and other healthy components (vitamin C, E, and other nutrients), are used in the formation of soft gelatin capsules for treating cardiovascular disease (Rosch et al. 2004).

13.3.4.2 Uses of Bioactive Compounds

Usually, halophytes contain a wide range of primary and secondary compounds in bioactive form and they are used as a potential source of natural vitamins, fatty acids, amino acids, flavonoids, alkaloids, terpenes, and isoflavonoids. Halophytes have been used since ancient times in folk medicine and play an important role in community health and safety owing to confirmed roles in human growth and development, in addition to reducing the risk of disease (Lagos et al. 2015). Halophytes contain nutritional components required for the healthy survival of humans, or nutraceuticals, when the aim is to treat/prevent a disease or disorder (Kalra 2003), with various reported bioactive functions (e.g., antioxidant, antimicrobial, immunomodulatory, hypocholesterolemic, etc.), often because of the incorporation of functional enzymes, fibers, isoflavones, peptides, phytic acids, phytosterols, prebiotics, probiotics, proteins, and saponins (Stankovi et al. 2015; Jdey et al. 2017).

13.4 Conclusion

Halophytes are exclusive sources of folk medicine and are of nutraceutical value for most of the world's population (Hamburger and Hostettmann 1991). A variety of plant chemicals have therapeutic importance, such as low-molecular-weight proteins and peptides or glycosides. These metabolites, which include alkaloids, essential oils, flavonoids, phenolic acids, phytoalexins, saponins, and tannins, could also form part of a plant's defense against microbes (Van Etten et al. 1989; Maher et al. 1994), and show antifungal, antimicrobial, anti-inflammatory, antioxidant, and anticarcinogenic activity (Robert and Seletrennikoff 1986; Terras et al. 1992). In addition, they can cure various diseases and are a novel source of nutraceuticals and growth regulators. Despite the wide use of halophytes, their therapeutic value has not been fully substantiated and the mode of action of bioactive compounds against diseases has not yet been established. Alkaloids, flavonoids, and glycosides isolated from halophytes may be responsible for their pharmacological activities. The road ahead consists in establishing the specific bioactive molecules that might be responsible for these actions. Therefore, the cultivation, collection, and further pharmacological exploration of halophytes are essential.

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Chapter 14
Halophyte Species as a Source of Secondary Metabolites with Antioxidant Activity

Milan Stanković, Dragana Jakovljević, Marija Stojadinov, and Zora Dajić Stevanović

Contents

Abstract As naturally salt-tolerant plants, halophytes can grow in a variety of saline habitats due to the development of special adaptations, particularly secondary metabolites with antioxidant properties. Since, in order to overcome harsh environmental conditions, halophytes have the ability to produce phenolic molecules with powerful biological capacities, this interesting ecological group of plants gets more attention in recent years because of a rapid increase in demand for natural bioactive substances. Having in mind that specific conditions of saline habitats cause specific responses of biochemical pathways of plant metabolites, which is related to their biological activities, the developmental stage and yield of individual plant species together with environmental factors must be considered in further studies. In this paper, halophyte secondary metabolites with antioxidant properties were reviewed in terms of their contributions to ecophysiological adaptations. Additionally, a complete experimental screening – from plant sampling through the methodological procedure to the presentation of the obtained results – was displayed in order to

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enable the selection of appropriate screening method together with the proper methods of extractions and applications of obtained results.

Keywords Salt-tolerant plants · Halophytes · Phenolic acids · Flavonoids · Antioxidant activity · Screening · Extraction

14.1 Introduction

Salinity is common phenomena for the world arid and semiarid regions. Saline habitats and conditions of increased salinity cause development of special adaptations and different adaptive mechanisms of the salt-tolerant plants. These mechanisms are not yet clearly understood but include osmotic adjustment and succulence, ion transport and uptake regulation, ion compartmentation, salt exclusion and excretion, maintenance of redox and energetic status, regulation of Na^+/K^+ selectivity, as well as a range of biochemical and signaling pathways under complex genetic control (Hasegawa et al. 2000; Dajic 2006; Hasanuzzaman et al. 2013). As naturally salt-tolerant plants, halophytes can grow in a variety of saline habitats and extreme locations characterized with high temperature and salinity conditions such as coastal sand dunes, salt marshes, salt flats, and steppes (Ksouri et al. 2010). In the case of halophytes occurring in arid and semiarid regions, combined stresses (salinity and drought) resulting in the appearance of the reactive oxygen molecules, such as singlet oxygen ($^1O_2$), superoxide anions (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH•) (Xiong et al. 2002). The scavenging of reactive oxygen species (ROS) in plants exposed to salt and drought stress is associated with activity of the different enzymes involved in antioxidant defense mechanisms (Sekmen et al. 2012; Jakovljević et al. 2017), osmoprotectant compounds (Xiong et al. 2002), as well as nonenzymatic antioxidant compounds and secondary metabolites (Xiong and Zhu 2002; Ksouri et al. 2007).

Biosynthesis and accumulation of polyphenols as well as other secondary metabolites in plants is evolutionary response of biochemical pathways under environmental influences (biotic/abiotic constraints), including increased salinity and drought (Navarro et al. 2006; Meot-Duros et al. 2008; Selmar and Kleinwachter 2013). Consequently, to overcome harsh environmental conditions, halophytes have a particularity which lies in their ability to produce secondary compound, mainly phenolic molecules, with powerful biological capacities (Trabelsi et al. 2012). Those molecules originated from halophytes, including vitamins, phenolics, polysaccharides, and glycosides, displaying a wide variety of biological activities, including antioxidant, antimicrobial, and anti-inflammatory, and may be crucial for the prevention of several human diseases, e.g., inflammation, cancer, and cardiovascular disorders (Ksouri et al. 2012; Rodrigues et al. 2015). Since halophyte plant species have been evaluated as natural sources of phenolic compounds, as well as other secondary metabolites with biological properties in adaptive responses to stress conditions (Ksouri et al. 2007; Benhammou et al. 2009), and because of a rapid increase in demand for natural bioactive substances on the world market, there is a need for further phytochemical investigation of species from this specific ecological group. Additionally, potential of some halophytic species for antioxidant activity and demonstration of antimicrobial, antiviral, anticancer, and other biological effects have been recently reported (Meot-Duros et al. 2008; Trabelsi et al. 2010; Lee et al. 2011; Oueslati et al. 2012).

This chapter aims to provide short insight into the salinity and environmental problems in saline habitats together with main characteristics of a halophytes as a specific ecological group adapted to these conditions. Plant secondary metabolism and plant secondary metabolites in these plants were discussed in the terms of their physiological adaptations. Having in mind that specific conditions of saline habitats cause specific responses of plant metabolism, which is related to their biological activities, halophytes were considered as a source of secondary metabolites with antioxidant activity. Finally, eight halophyte species were selected to serve as a model to display a complete experimental screening – from plant sampling through the methodological procedure to the presentation of the obtained results.

14.2 Plant Secondary Metabolites

Unfavorable growth conditions are a complex process leading to coordinated changes at different levels of plant metabolism. Plant secondary metabolites, the products of plant secondary metabolism which is a resumption of the essential primary metabolism, have a main role in their interaction in the environment. As per definition given by Verpoorte (2000) “secondary metabolites are compounds with a restricted occurrence in taxonomic groups, that are not necessary for a cell (organism) to live, but play a role in the interaction of the cell (organism) with its environment, ensuring the survival of the organism in its ecosystem.”

Major roles in the adaptation of plants to their environment belong to the products of secondary metabolism, and plant secondary compounds are usually classified according to their biosynthetic pathways (Bourgaud et al. 2001). Quantitative and qualitative composition of secondary metabolites in plant tissues and organs depends on numerous abiotic and biotic ecological factors (Oh et al. 2009). Secondary metabolites isolated from plants, in addition to the different roles in processes of the plant adaptation, exhibit many in vitro and in vivo biological effects. The mechanism of their biological actions is the stimulation or inhibition of the different metabolic processes (Faggio et al. 2015a, b, 2016; Korkina 2007; Trischitta and Faggio 2006, 2008). Therefore, the investigation of plant secondary molecules and their biological potential have the possibility of a number of scientific and practical applications (Stanković et al. 2015). Biosynthesis of phenylpropanoid compounds is passed from shikimate pathway and regulated by different enzymatic pathways (Ziaei et al. 2012). In the first step of the general phenylpropanoid biosynthetic pathway, the phenylalanine is deaminated by the enzyme phenylalanine ammonium lyase (PAL), and metabolites resulting from PAL activity can be classified as phenolic compounds including phenolic acids, coumarins, flavonoids, lignin, and other compounds (Ziaei et al. 2012; Rigano et al. 2016).

14.2.1 Phenolic Derivatives

The general structural characteristic of all phenolic derivatives is the hydroxyl group attached to the aromatic ring. A large group of natural products with this structural fragment is known as “natural aromatic compounds.” They can be systematized in two groups: phenolic compounds and flavonoids. The first group consists of phenols, phenolic acids, and condensation products of phenol – dephides, phenylpropane, tannins, and stilbene – while the other group consists of flavonoids and anthocyanins (Crozier et al. 2006; Quideau et al. 2011). Different amounts of phenolic compounds from plant sources depend on their function in the plant itself, i.e., role in photosynthetic apparatus protection and then protection against herbivores and pathogens, as well as other biotic and abiotic factors to which the plant is exposed during growth and development (Alonso-Amelot et al. 2004). Physiological drought, as one of the common abiotic factors in saline habitats, caused increased intensity of synthesis and accumulation of secondary metabolites (usually phenolic compounds) in order to prevent the negative consequences of drought.

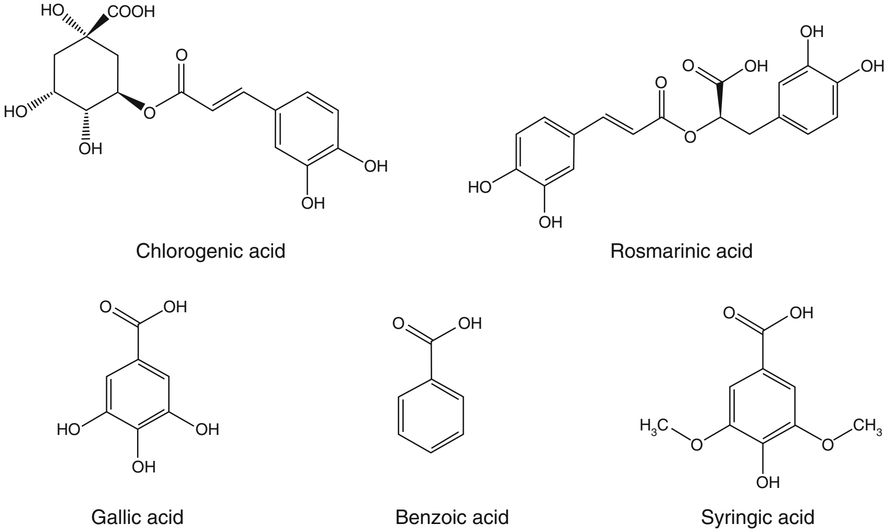
In the previous investigations of quantitative and qualitative characteristics of secondary plant metabolites, several thousand types of phenolic derivatives have been identified. Among them, phenolic compounds are present in all plant organs and are most commonly found in leaves (Stanković et al. 2012). The diversity of the phenolic compounds is the result of their ability to bond different sugar components that occupy different positions in the binding process (Boskou 2006). Phenolic compounds are characterized by a variety of applications in the pharmaceutical industry, medicine, and agricultural and food production. A wide spectrum of the use of phenolic compounds of plant origin is related to the structural properties of the molecule, in which their antioxidant, antimicrobial, and anticancer activity is observed, as well as numerous therapeutic effects (Manach et al. 2004; Tapas et al. 2008; Quideau et al. 2011). Due to the diverse chemical structure, phenolic compounds exhibit an effect at all levels of the organization in biological systems, which is the reason for their intensive application (Fraga 2010). The mechanism of antimicrobial action of phenolic acids is based on an intense increase in the permeability of the membrane, resulting in a loss of selective permeability where important biomolecules are uncontrolled out of the cell (Zaixiang et al. 2011). In addition, the mechanism of antimicrobial activity of phenols is based on interfering or completely blocking some of the functions of the cytoplasmic membrane, as well as inhibition of the enzymes necessary in the process of replication of bacteria. Characteristic of terpenoids is effects of disintegration of the cell membrane; coumarins exhibit antimicrobial activity by inhibition of cellular respiration, while tannins are characterized by inhibition of cell membrane functions and the activity of some important enzymes (Cushine and Lamb 2005). The mechanism of antitumor activity of secondary plant metabolites is different – some of them are carcinogenic inactivation, cell cycle blocking, proliferation inhibition, apoptosis induction, angiogenesis inhibition, control of the enzyme activity involved in the regulation of the cell cycle, and transport through the membrane (Ren et al. 2003; Khantamat et al. 2004; Khoo et al. 2010; Duangmano et al. 2010)

Phenolic acids are one of the many classes of phenolic compounds in plants. Based on their origin, they can be divided into benzoic acid or cinnamic acid derivatives (Robbins 2003). The biological role of phenolic acids as secondary metabolites in herbs is multiple. A very important role is reflected in the part of biochemical communication in the ecosystem, i.e., in the process of adaptation to biotic and abiotic stress (Mandal et al. 2010). Phenolic acids are presented in all types of herbs, especially in medicinal and herbal plants, fruits, and vegetables. They can be found in leaves, flowers, fruits, and seeds, but their quantitative and qualitative relationship varies and is not the same in all plant organs during the vegetative phases because of the influence of the abiotic and biotic factors under which the plant is exposed (Wang et al. 2011). Phenolic acids are with ether or ester bonds related to some protein molecules, carbohydrates, other phenolic acids, or some organic acids and secondary metabolites such as terpenes, lignin, or lignans. In addition, phenolic acids are necessary precursors in the process of biosynthesis of some flavonoids and other complex phenolic acids (Gorshkova et al. 2000; Ascensao and Dubery 2003; Bunzel et al. 2004). In addition to the high number of biological effects in plants, phenolic acids isolated from the plants show strong biological effects in in vitro and in vivo conditions by exhibiting antimicrobial, antioxidant, anticancer, and many other activities (Merkl et al. 2010; Maistro et al. 2011; Kang et al. 2011). Previous investigations of halophyte species in terms of major specialized metabolites revealed the significant amount of different phenolic acids. Among them, caffeic, chlorogenic, gallic, syringic, ellagic, rosmarinic, and ferulic acid were found to be predominant in extracts obtained from *Statice gmelinii*, *Mentha pulegium*, *Salvadora persica*, and *Crithmum maritimum* and species from the genus *Artemisia* (Serkerov and Aleskerova 1984; Korulkina et al. 2004; Meot-Duros and Magne 2009; Ivanescu et al. 2010; Tahira et al. 2011; Pereira et al. 2017a, b; Qasim et al. 2017). The chemical structures of several phenolic acids from halophyte species are presented in Fig. 14.1.

14.2.2 Flavonoids

To date, about 9000 different flavonoids of plant origin are known. Main structural characteristic of these secondary metabolites is the presence of a heterocyclic molecular structure consisting of two benzene rings associated with an aliphatic sequence. Due to numerous modifications of the basic skeleton regarding the change in the oxidation state of the aliphatic sequence, plant possess wide variety of structurally different flavonoids located in plant cell vacuoles (Buer et al. 2010; Mierziak et al. 2014).

Flavonoids are the derivatives of 2-phenyl-benzyl-γ-pyrone whose biosynthetic pathway, as part of phenylpropanoid metabolism, begins with the condensation of one *p*-coumaroyl-CoA molecule with three molecules of malonyl-CoA with the formation of chalcones (4,2,4,6-tetrahydroxychalcone). The next step in the synthesis of flavonoids is the isomerization of chalcones to flavanone, and from this step,



Chlorogenic acid

Rosmarinic acid

Gallic acid

Benzoic acid

Syringic acid

Fig. 14.1 The chemical structures of some phenolic acids from halophyte species

the synthetic pathway branches to several different classes of flavonoids, including aurones, dihydrochalcones, isoflavones, flavones, flavonols, anthocyanins, proanthocyanidins, and others (Buer et al. 2010; Mierziak et al. 2014).

The resulting flavonoids undergo further modifications followed by changes in solubility, reactivity, and stability. Due to the diversity in the chemical structure resulting from the diversity of substituents, flavonoids exhibit several significant functions in plants such as protection against pathogens, pollen germination, ultraviolet radiation protection, antioxidant functions, etc. The antioxidative role of flavonoids is based on the ability to neutralize free radicals, thereby preventing cell damage and allowing plant adaptation to different environmental conditions. This antioxidative role of flavonoids in correlation with the number and position of hydroxyl groups bound to the phenolic ring (Gill and Tuteja 2010; Mierziak et al. 2014). The important biological role of flavonoids in plants is associated with biochemical communication of plants in ecosystems, and the distribution together with the quantitative and qualitative composition of these compounds varies depending on both genetic and ecological factors (Stanković et al. 2012).

The predominance of the polyphenol family in particular the flavonoids was found in different plant species from the saline habitats. The naringin and naringenin 7-O-glucoside are very common in species of Chenopodiaceae family (Al-Jaber et al. 1991). High concentration of flavonoids was obtained from *Atriplex hortensis* (Yang et al. 2008) and *A. halimus* (Benhammou et al. 2009). Moreover, the flavonol class forms the major chemical compounds of species from the *Atriplex* genus (Sanderson et al. 1988). Also, Chenopodiaceae family is characterized by the presence of glycinebetaine as an alternative osmolyte to protect from salt and water stress (Benhammou et al. 2009). High content of flavonoids was also reported

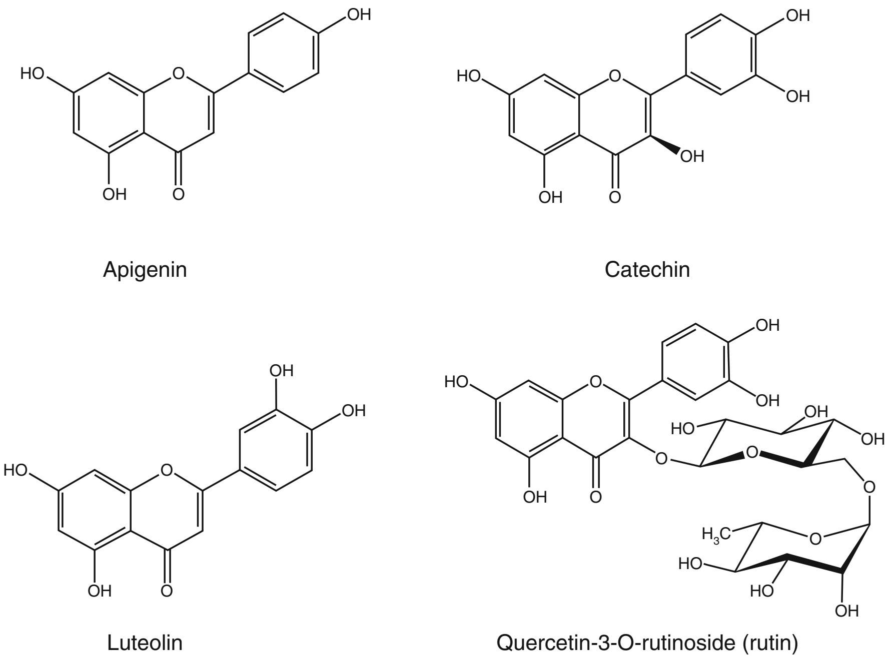


Fig. 14.2 The chemical structures of some flavonoids from halophyte species

in the case of *Limoniastrum guyonianum* (Trabelsi et al. 2012); *Limonium algarvense* (Rodrigues et al. 2015); species from saline habitats of the south of Portugal including *Halopeplis amplexicaulis*, *Cladium mariscus*, *Frankenia pulverulenta*, and *Salsola vermiculata* (Lopes et al. 2016); as well as Tunisian halophytes *Thespesia populneoides*, *Salvadora persica*, *Ipomoea pes-caprae*, *Suaeda fruticosa*, and *Pluchea lanceolata* (Qasim et al. 2017). Different studies also revealed the presence of epicatechin, pyrocatechol, catechin, rutin, luteolin, quercetin, myricetin, apigenin, avicularin, phloretin, and procyanidin B2 as major flavonoids in different halophyte species (Falleh et al. 2011; Ksouri et al. 2009, 2012; Rodrigues et al. 2014; Medini et al. 2015; Jdey et al. 2017; Oueslati et al. 2012a; Pereira et al. 2017a, b; Qasim et al. 2017). The chemical structures of several flavonoids from halophyte species are presented in Fig. 14.2.

14.3 Antioxidant Activity of Phenolic Compounds

The overproduction of reactive species (ROS, RNS), together with the imbalance between their production and the detoxification system capacity, leads to the generation of oxidative stress. The equilibrium between positive and negative effects of free radicals is essential for living organisms, since the oxidative stress may represent underlying causes of several stress-related human diseases including cancer, diabetes, cardiovascular disorders, inflammatory disease, and Alzheimer (Shoham et al. 2008; Benhammou et al. 2009; Hajhashemi et al. 2010). Humans possess endogenous antioxidant defense system against free radicals; however, this system sometimes is not sufficient to prevent the occurrence of cell damage (Rechner et al. 2002). Since it is well known that antioxidants neutralize harmful effects of free radicals, synthetic antioxidants like butylated hydroxytoluene (BHT) and butylated hydroxyanisole (BHA) are widely used in food industry. Although synthetic antioxidants have widespread use in many countries, there are growing evidences that these molecules may be implicated in toxic and carcinogenic effects (Sasaki et al. 2002; Jennings and Akoh 2009; Sindhi et al. 2013). Hence, it is necessary to replace synthetic compounds with natural antioxidants.

Natural antioxidants are secondary metabolites produced naturally in plant organism. They are mainly phenolic compounds in the function of plant defense mechanisms to counteract reactive oxygen species (ROS) to avoid consequences of oxidative stress. Antioxidant properties of secondary metabolites from the group of phenolic compounds arise from their redox properties and high reactivity as hydrogen or electron donors, from the ability of the polyphenol-derived radical to stabilize and delocalize the unpaired electron (chain-breaking function), ability to scavenge a variety of reactive species (superoxide, hydroxyl, and peroxyl radicals), and ability to chelate transition metal ions (Halliwell et al. 2005; Rohma et al. 2010; Falleh et al. 2012; Jdey et al. 2017). Additionally, polyphenolic constituents demonstrate several biological properties useful in the management of the stress-related diseases (Sousa et al. 2015; Zengin et al. 2015).

Plants represent a significant source of natural antioxidants. In this sense, in recent years, extracts of many plant species become popular in attempts to characterize their antioxidant activity and potential utilization as rich sources of antioxidants (Gourine et al. 2010; Ksouri et al. 2012). Plant phenolic compounds, among the various types of natural antioxidants, represent the leading and most powerful plant secondary metabolites with multiple applications such as additives, functional food, and medicinal and pharmaceutical materials (Povichit et al. 2010). The mechanism of action of plant antioxidant substances is based on their role as a donor of an electron or a hydrogen atom. The antioxidant ability of phenolic compounds depends on the number and position of hydroxyl groups. In addition, bond dissociation energy (BDE) and ionization potential (IP) are also very important characteristics. One of the main mechanisms of the antioxidant activity of phenolic compounds is the role of hydrogen donor (*HAT – hydrogen atom transfer*) and the role of electron donors (*SET – single electron transfer)* to the molecule exposed to the oxidation process (Quideau et al. 2011). The mechanism of these reactions has the following form:

$$\mathrm{R}^{\bullet} + \mathrm{ArOH} \rightarrow \mathrm{RH} + \mathrm{ArO}^{\bullet}$$

$$\mathrm{R}^{\bullet} + \mathrm{ArOH} \rightarrow \mathrm{R}^{-} + \mathrm{ArOH}^{\bullet +}$$

As natural antioxidants, phenolic compounds significantly contribute to antioxidant activity of the plants. To date, halophytes are recognized as plants with high amount of total phenolic content together with significant antioxidant activity. Significant content of phenolics as well as antioxidant activity has been confirmed in the case of *Atriplex halimus* (Benhammou et al. 2009); *Inula crithmoides* (Jallali et al. 2014; Jdey et al. 2017); *Crithmum maritimum* (Meot-Duros and Magne 2009; Jallali et al. 2014; Pereira et al. 2017a); *Halimione portulacoides* (Vilela et al. 2014); *Limoniastrum guyonianum* and *L. monopetalum* (Ksouri et al. 2008; Trabelsi et al. 2012; Lopes et al. 2016); *Limonium algarvense*; *L. tetragonum* and *L. gmelinii* (Korulkina et al. 2004; Lee et al. 2011; Rodrigues et al. 2015, 2016); *Mesembryanthemum edule* (Falleh et al. 2011); *Frankenia laevis* and *F. pulverulenta* (Lopes et al. 2016; Jdey et al. 2017); *Lythrum salicaria*, *Cladium mariscus*, *Aster tripolium*, and *Typha domingensis* (Lopes et al. 2016); species from the genus *Suaeda* (Oueslati et al. 2012a, b; Stanković et al. 2015; Qasim et al. 2017); *Tamarix gallica* (Ksouri et al. 2009); *Plantago coronopus* (Jdey et al. 2017); *Statice gmelinii*, *Mentha pulegium*, *Camphorosma monspeliaca*, *Salicornia europaea*, *Suaeda maritima*, *Artemisia santonicum*, *Achillea collina*, and *Aster tripolium* (Stanković et al. 2015); and *Thespesia populneoides*, *Salvadora persica*, *Ipomoea pes-caprae*, *Suaeda fruticosa*, and *Pluchea lanceolata* (Qasim et al. 2017). Halophyte species from the genus *Mentha* also demonstrated significant content of phenolic compounds. According to Sarikurkcu et al. (2012) high content of phenolic compound can be obtained from methanolic extracts of *Mentha pulegium* (97.20 mg GA/g of extract), while, according to Hajlaoui et al. (2009), extracts from *Mentha longifolia* also possess high content of phenolics (89.1 mg GA/g).

Ksouri et al. (2007) analyzed content of phenolic compounds together with antioxidant activity of *Cakile maritima* leaves from dry and humid habitats, under limited substrate conditions. It has been found that plants from dry habitat are more resistant, and the resistance is probably associated with higher values of phenolic compound and antioxidant activity comparing the plants from the humid habitat. Meot-Duros and Magne (2009) analyzed the content of total phenolic compounds, the amount of chlorogenic acid, and the antioxidant activity in leaves obtained from populations of this species in different habitats – sand and rocks. It was found that the plants from the sand habitat had a higher content of chlorogenic acid than plants with rocky substrate, but certainly both populations had a high content of phenolic compounds. By comparing physiological parameters of the typical coastal species *Calystegia soldanella* from natural habitats and cultivated conditions, obtained results indicated that the phenol content was significantly higher in plants from natural habitats compared to cultivated plants. This may suggest that phenolic substances play a key role in response to these plants to the limitations of coastal habitats (Spano et al. 2013). Quantitative and qualitative composition and antioxidant activity of metabolites from halophyte species depend on taxonomic affiliation of a species, biological (organ or developmental stage), environmental, and technical (extraction solvent) factors (Ksouri et al. 2008).

14.4 Example for Experimental Screening of Phenolic Content and Antioxidant Activity of Halophytes

Due to the natural specificity of the composition of secondary metabolites – active substances with biological activity – halophytes are the subject of many aspects of laboratory testing. As in the case of testing of other potential medicinal plants from different ecological groups, from natural or laboratory conditions, laboratory testing of halophytes is differentiated into two important ways – testing of quantitative and qualitative composition of secondary metabolites and testing of biological activity using different model systems. In the experimental process, extracts are obtained using a variety of solvents such as methanol, ethanol, water, acetone, ethyl acetate, etc. as well as tinctures and decocts prepared according to the different procedures.

Before a detailed analysis using chromatographic methods, a group of spectrophotometric methods is used to determine their total amount or preliminary quantification of important groups and subgroups of secondary metabolites. Chemical identification and detailed determination of the amount of secondary metabolites are carried out using various chromatographic methods. Chromatography methods are also used to isolate the target components and their further laboratory processing. Biological activity testing involves the application of several levels of in vitro testing of antioxidant, antimicrobial, anticancer activity, etc., followed by in vivo testing on different systems. Standard substances, such as synthetic compounds with antioxidant activity, or extracts of known herbs with the described industrial use are indispensable in both directions of the assay. In the study of the amount of active substances, their content in extracts, decocts, tinctures or other, is expressed in the form of equivalents of standard substances. In the study of biological activity, standard substances are examined in parallel in the goal of the comparison and evaluation of the results obtained. For the purpose of efficient presentation and interpretation of the obtained results, a large number of special statistical programs are used. In addition to noninfectious statistical evaluation, tests are used to determine the correlation between the amount of active substances and their biological activity, determining the dosage dependence, etc.

14.4.1 Experimental Procedure

The experimental procedure of the presented model for the screening of the antioxidant activity of the halophyte species contains a description of the methods starting from the preparation of the samples to the presentation of the obtained results. The methods enable preliminary screening of the total amount of phenolic compounds, flavonoids as an important phenolic group, as well as in vitro antioxidant activity using the DPPH reagent.

14.4.1.1 Plant Material

Halophytes *Echinophora spinosa* L., *Crithmum maritimum* L. and *Eryngium maritimum* L. (Apiaceae), *Medicago marina* L. (Fabaceae), *Halimione portulacoides* (L.) Aellen (Amaranthaceae), *Calystegia soldanella* L. (Convolvulaceae), *Cakile maritima* Scop. (Brassicaceae), and *Limonium gmelinii* (Willd.) Kuntze (Plumbaginaceae) were collected from natural habitats in south Adriatic coastal zone (Fig. 14.3). *Crithmum maritimum* L. and *Cakile maritima* Scop. were collected from coastal rocks of Mogren, Budva (Montenegro), while other species were sampled from the location of Ada Bojana, Ulcinj (Montenegro), in May 2014. The voucher specimens were confirmed and deposited at the Herbarium of the Department of Biology and Ecology of Faculty of Science, University of Kragujevac. The collected plant material was air-dried in darkness at ambient temperature. The dried plant material was cut up and stored in tightly sealed dark containers until needed.

14.4.1.2 Preparation of Plant Extracts

The air-dried plant material (10 g) was coarsely crushed in small pieces of 2–6 mm by using the cylindrical crusher and extracted with ethanol 200 ml. The extract was filtered using a paper filter (Whatman, No. 1) and evaporated under reduced pressure by the rotary evaporator. The obtained extracts were stored in dark glass bottles until use.

14.4.1.3 Determination of Total Phenolic Content in the Plant Extracts

The content of phenolic compounds in the plant extracts was determined by using spectrophotometric method with Folin-Ciocalteu reagent (Singleton et al. 1999). Folin-Ciocalteu reagent contains, in its constitution, phosphomolybdic/ phosphotungstic acid complexes. The determination assay is based on the transfer of electrons in alkaline medium from plant phenolic compounds to molybdenum, forming blue complexes that can be monitored spectrophotometrically at 750–765 nm. Therefore, the spectrophotometric measurement is based on quantification of the reducing capacity of phenolic compounds from the plant extract. Proton and a phenoxide anion formed in their discharge reaction reduce the Folin-Ciocalteu molecule to the ion responsible for the blue color of the reaction mixture (Magalhães et al. 2008). The reaction mechanism can be presented according to the following equations:

Fig. 14.3 *Echinophora spinosa* L., *Crithmum maritimum* L., *Eryngium maritimum* L., *Medicago marina* L., *Halimione portulacoides* (L.) Aellen, *Calystegia soldanella* L., *Cakile maritima* Scop., and *Limonium gmelinii* (Willd.) Kuntze

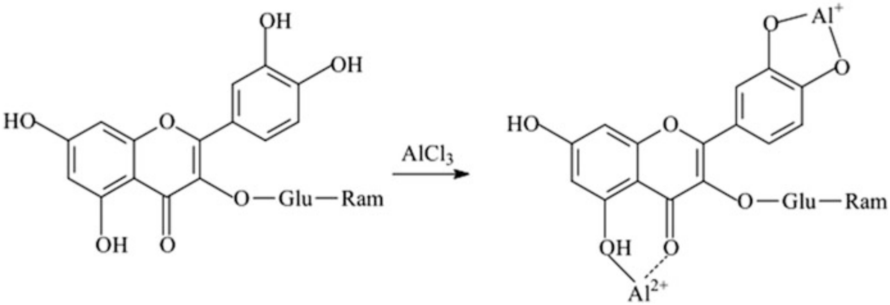
$$\mathrm{Na_2WO_4/Na_2MoO_4 + phenol \rightarrow (phenol - MoW_{11}O_{40})^{4-}}$$

$$\mathrm{Mo(VI)(yellow\ \ color) + e^- \rightarrow Mo(V)(blue\ \ color)}$$

The methanolic solution of the plant extract in concentration of 1 mg/ml was used in the analysis. The reaction mixture was prepared by mixing 0.5 ml of methanolic solution of the extract, 2.5 ml of 10% Folin-Ciocalteu reagent dissolved in water, and 2 ml of 7.5% $NaHCO_3$. The blank was concomitantly prepared containing 0.5 ml of methanol, 2.5 ml of 10% Folin-Ciocalteu reagent dissolved in water, and 2 ml of 7.5% of $NaHCO_3$. The samples were thereafter incubated at 45 °C for 15 min. The absorbance was measured spectrophotometrically at $\lambda_{max} = 765$ nm. The samples were prepared in triplicate for each analysis, and the mean value of absorbance was obtained. The same procedure was repeated for the gallic acid, and the calibration curve was construed. Based on the obtained absorbance, the content of phenolics was calculated (mg/ml) from the calibration curve; then the content of phenolics in the extracts was expressed in terms of gallic acid equivalent, GAE (mg of GA/g of extract).

14.4.1.4 Determination of Total Flavonoid Content in the Plant Extracts

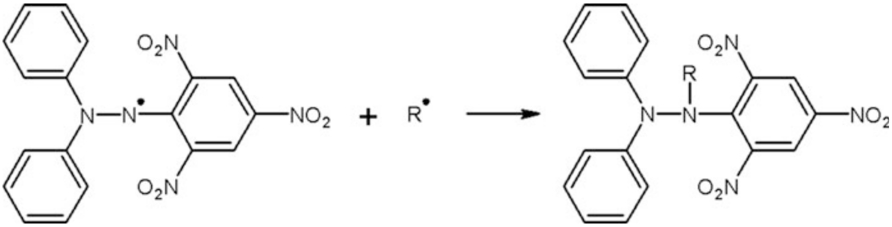
The values for flavonoid content in the examined plant extracts were measured using spectrophotometric method (Quettier et al. 2000). This assay is based on formation of acid-stable complexes with the C-4 keto group and either the C-3 or C-5 hydroxyl group of flavonoids in addition with aluminum chloride. Aluminum chloride also forms acid labile complexes with the ortho-dihydroxyl groups in the A or B ring of flavonoids. The spectrophotometric measurement is based on the quantification of the color change in this reaction, at 400–420 nm. The mechanism of this reaction – the formation of metallocomplex in the case of the rutin molecule – is the following:



The sample contained 1 ml of methanolic solution of the examined extract in concentration of 1 mg/ml and 1 ml of 2% $AlCl_3$ methanolic solution. The samples were incubated for an hour at room temperature. The absorbance was determined using spectrophotometer at of $\lambda_{max} = 415$ nm. The samples were prepared in triplicate for each analysis, and the mean value of absorbance was measured. The same procedure was repeated for the solution of rutin, and the calibration curve was construed. Based on the measured absorbance, the content of flavonoids was calculated (mg/ml) on the calibration curve; then, the amount of flavonoids in extracts was expressed in terms of rutin equivalent, RUE (mg of RU/g of extract).

14.4.1.5 Evaluation of Antioxidant Activity of the Plant Extracts

The capacity of the plant extract to scavenge 1,1-diphenyl-2-picrylhydrazyl (DPPH) free radicals was determined by the standard method (Takao et al. 1994), adopted with some corrections (Kumarasamy et al. 2007). Molecules of 1,1-diphenyl-2-picrylhydrazyl radical (DPPH) are, based on the chemical structure, stable free radicals. In dry form, the DPPH powder is characterized by a dark-purple to black color with absorption peak at 517 nm. After dissolution, color loses its intensity, depending on the concentration. After reduction, the color of the solution changes to yellow, depending on the concentration of the reduced molecules in the reaction mixture. Antioxidant compounds as donors of the hydrogen atom reduce the stable 1,1-diphenyl-2-picrylhydrazine radical by transforming it into 1,1-diphenyl-2-(2,4,6-trinitrophenyl)-hydrazine. The reduction process can be presented by the following reaction:



During this process, the purple color of the initial solution derived from the stable DPPH radical is changed to yellow due to the presence of a newly formed 1,1-diphenyl-2-(2,4,6-trinitrophenyl)-hydrazine resulting in a decrease in absorbance at 517 nm. This property allows visual and spectrophotometric monitoring of the reaction, i.e., the quantity of radicals at the beginning can be determined by changing the absorbance at 517 nm or by the ECP signal of the DPPH radical. In an experimental study of the antioxidant activity of plant extracts, the intensity of color change from violet to yellow is in correlation with the antioxidative potential of the plant extract (Fig. 14.4), which can be monitored by spectrophotometric measurement. Based on this, the DPPH method is widely used to measure the ability of different substances to act as free radical scavengers or hydrogen donors as well as to evaluate antioxidant activity of plant compounds as plant extracts or isolated metabolites.

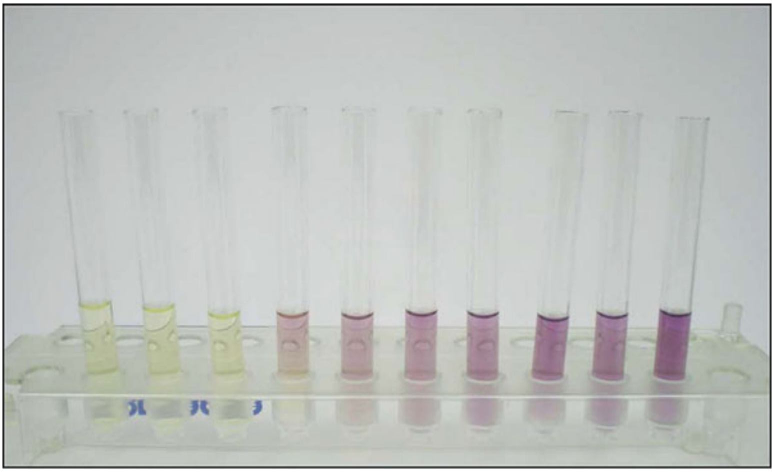


Fig. 14.4 Series of samples with a decreasing gradient of the plant extract concentration after the reaction with the DPPH reagent

For the experimental procedure when applying this method, DPPH (20 mg) was dissolved in methanol (250 ml) to obtain the concentration of 80 μg/ml. The start solution of the examined extracts was prepared in methanol to obtain the concentration of 1 mg/ml. Dilutions were made to achieve concentrations of 500, 250, 125, 62.5, 31.25, 15.62, 7.81, 3.90, 1.99, and 0.97 μg/ml. Obtained extract samples (1 ml each) were combined with DPPH solution (1 ml).

After 30 min of incubation in darkness at ambient temperature, the absorbance was measured at 517 nm. The control samples contained all the reagents except the plant extract. The percentage inhibition was obtained using Eq. (14.1), while IC_{50} values were estimated from the percentage inhibition versus concentration plot, using a nonlinear regression algorithm. The data were presented as mean values ± standard deviation ($n = 3$):

$$\% \text{ inhibition} = \left(\frac{A \text{ of control} - A \text{ of sample}}{A \text{ of control}}\right) \times 100 \qquad (14.1)$$

14.4.2 Results and Further Implications

14.4.2.1 Total Phenolic Content of the Plant Extracts

The obtained values of total phenolic content for the studied halophytes, quantified by measuring of the amount in the ethanolic extracts using Folin-Ciocalteu's reagent, are presented in Table 14.1. The values obtained for the total content of

Table 14.1 Total phenolic content in the extracts of analyzed halophytes, expressed as gallic acid equivalent – mg GA/g extract

Species	mg GA/g of extract
Echinophora spinosa	104.66 ± 0.82
Crithmum maritimum	106.08 ± 1.37
Eryngium maritimum	44.79 ± 0.58
Medicago marina	34.30 ± 0.87
Halimione portulacoides	30.51 ± 0.41
Calystegia soldanella	74.39 ± 0.72
Cakile maritima	62.06 ± 1.37
Limonium gmelinii	90.81 ± 0.79

Values in the table are shown as the mean value of the obtained results for the three samples ± standard deviation

phenolic compounds in plant extracts of analyzed halophytes were expressed as the equivalent of gallic acid – mg of gallic acid per gram of extract (mg GA/g).

The obtained values for the total amount of phenolic compounds in the plant extracts of analyzed halophytes have a range from 30.51 to 106.08 mg GA/g of extract. The highest value was obtained for the species *Crithmum maritimum* (106.08 mg GA/g) and *Echinophora spinosa* (104.66 mg GA/g), followed by *Limonium gmelinii* (90.81 mg GA/g). The average amount was obtained for plant extracts of *Calystegia soldanella* (74.39 mg GA/g) and *Cakile maritima* (62.06 mg GA/g), as well as the lowest value for *Eryngium maritimum* (44.79 mg GA/g), *Medicago marina* (34.30 mg GA/g), and *Halimione portulacoides* (30.51 mg GA/g).

14.4.2.2 Total Flavonoid Content of the Plant Extracts

The obtained values of flavonoid content in plant extracts of the studied halophytes, determined by described method using ethanolic extracts and $AlCl_3$ as reagent, are showed in Table 14.2. The values obtained for the flavonoid content were presented as the equivalent of rutin – mg of rutin per gram of extract (mg Ru/g). The values obtained for the total content of flavonoids in the plant extracts of the investigated halophytes are in the range from 15.71 to 22.15 mg Ru/g. The highest value was obtained for the species *Limonium gmelinii* (22.15 mg Ru/g) and *Cakile maritima* (22.13 mg Ru/g), followed by *Medicago marina* (21.86 mg Ru/g), *Crithmum maritimum* (21.36 Ru/g), and *Halimione portulacoides* (20.93 mg Ru/g). The average amount was obtained for plant extracts of *Echinophora spinosa* (18.69 mg Ru/g) and *Calystegia soldanella* (18.24 mg Ru/g), as well as the lowest value for *Eryngium maritimum* (15.71 mg Ru/g).

14.4.2.3 Antioxidant Activity of the Plant Extracts

Obtained values for antioxidant activity of examined plant extracts, expressed in terms of IC_{50} ($\mu g\ ml^{-1}$) values, are presented in Table 14.3.

Table 14.2 Total flavonoid content in the extracts of analyzed halophytes, expressed as rutin equivalent – mg Ru/g extract

Species	mg Ru/g of extract
Echinophora spinosa	18.69 ± 0.25
Crithmum maritimum	21.36 ± 0.45
Eryngium maritimum	15.71 ± 0.15
Medicago marina	21.86 ± 0.19
Halimione portulacoides	20.93 ± 0.41
Calystegia soldanella	18.24 ± 0.20
Cakile maritima	22.13 ± 0.32
Limonium gmelinii	22.15 ± 0.07

Values in the table are shown as the mean value of the obtained results for the three samples ± standard deviation

Table 14.3 Antioxidant activity of the extracts of analyzed halophytes, expressed as IC_{50} values (μg/ml)

Species	IC_{50} (μg/ml)
Echinophora spinosa	163.55 ± 0.62
Crithmum maritimum	195.26 ± 1.41
Eryngium maritimum	827.85 ± 0.67
Medicago marina	1317.95 ± 1.98
Halimione portulacoides	1237.14 ± 1.81
Calystegia soldanella	547.52 ± 0.95
Cakile maritima	365.36 ± 0.42
Limonium gmelinii	196.79 ± 0.56

Values in the table are shown as the mean value of the obtained results for the three samples ± standard deviation

For the results of antioxidant activity displayed in this way, the intensity of activity is inversely proportional to the numerical IC_{50} (a lower numerical value indicates better activity of the plant extracts) values. Values for antioxidant activity of examined plant extracts ranged from 163.55 to 1317.95 μg ml^{-1}. The strong antioxidant activity was detected in the *Echinophora spinosa* plant extract (163.55 μg ml^{-1}), followed by *Crithmum maritimum* (195.26 μg ml^{-1}) and *Limonium gmelinii* (196.79 μg ml^{-1}). The average antioxidant activity was measured for plant extracts of *Cakile maritima* (365.36 μg ml^{-1}) and *Calystegia soldanella* (547.52 μg ml^{-1}) and *Eryngium maritimum* (827.85 μg ml^{-1}) as well as the lowest value for *Halimione portulacoides* (1237.14 μg ml^{-1}) and *Medicago marina* (1317.95 μg ml^{-1}).

The obtained results point to a wide variability of phenolic compounds among the analyzed species, as well as different variations among species of the same genus. As shown in Table 14.1, the total phenolic content for *E. spinosa* species is 104.66 mg GA/g of extract, which is approximately the value measured for the *C. maritimum*. Bearing in mind that these two species belong to the same family (Apiaceae), it can be said that there is a similarity in the origin and evolution of plants, and this is the reason for their similar content of phenolic compounds. However, the species *Eryngium maritimum*, which also belongs to this family, showed a deviation when it comes to the content of phenolic compounds. The value obtained for this species is

44.79 mg GA/g extract, which is significantly less than the value of previous two species. Based on this, it can be said that species from the same family do not always have the same or similar values of phenolic compounds. Differences in the content of total phenolic compounds in the investigated halophytes from the same family may refer to specific evolutionary paths of this taxon, and the reason may be the specific response of species to increased salinity, which relates to tolerance of these plants on salinity stress (Quideau et al. 2011).

The results obtained in Table 14.1 confirm the existence of halophytes characterized by a relatively high content of secondary metabolites such as phenol compounds (Oh et al. 2009). Based on the values shown in Table 14.1, it has been established that ethanol is a good solvent for the extraction of secondary metabolites during the examination of selected halophytes and that the measured high content of phenolic compounds in certain species originates from their high solubility in ethanol.

As shown in Table 14.2, the highest content of flavonoids among the examined halophytes has *Limonium gmelinii* (22.15 mg Ru/g), which is very similar to the value obtained for the *Cakile maritima* (22.13 mg Ru/g). It can be noticed that the mean values among the examined halophytes are of the species *Echinophora spinosa* of 18.69 and *Calystegia soldanella* with 18.24 mg Ru/g extract. The convincingly minimal flavonoid concentration (15.71 Ru/g of extract) was measured in the *Eryngium maritimum* which, according to this value, is distinguished from all investigated species.

Based on the obtained results, it can be concluded that the quantities of flavonoids, as well as the values of phenolic compounds, differ in the extracts of overground parts of investigated halophytes. The obtained flavonoid values indicate that these secondary metabolites constitute the most represented group among phenolic compounds, where some of the examined halophytes have a high, while others have a lower content of flavonoids. Thus, the differences in amount of phenolic compounds are reflected in the difference in concentration of flavonoids, as their most important groups. The differences in concentration of flavonoids in the examined halophytes are related, both with different phylogenies and morphologies and with physiological and molecular factors that are related to the response to stressful environmental conditions.

By comparing the values obtained in the first three species in Table 14.2 (*Echinophora spinosa*, *Crithmum maritimum*, and *Eryngium maritimum*) belonging to the same family (Apiaceae), it was concluded that the amount of flavonoids in them significantly varies and that all of three species have different contents of these secondary metabolites. Based on this, it can be said that species from the same family do not necessarily have the same or similar values of flavonoids, since different factors affect the plants and therefore the content of phenolic compounds and flavonoids in them. Factors that affect the difference in the quantities of phenolic compounds cause a difference in flavonoid concentrations in the investigated halophytes.

When assessing the content of phenolic compounds and the antioxidant activity of certain halophytes, it was determined that their variability depends to a great extent on biological (different types, organs, and developmental phases), ecological, and technical (extraction) factors.

Considering that the three species (*Echinophora spinosa*, *Crithmum maritimum*, and *Eryngium maritimum*) among the investigated halophytes belong to the same family (Apiaceae), it is useful to compare the value of the antioxidant effect obtained from the extracts of their overground parts. It can be concluded that the first two species have the highest antioxidant activity among the examined halophytes, while the third significantly deviates with its value and among the examined halophytes belongs to the group with a small antioxidant effect. The first two species can be said to have similar evolutionary pathways (Quideau et al. 2011), and the deviation in the third species can be attributed to biotic and abiotic factors that affect plants and their antioxidant activity (Lattanzio et al. 2006).

Based on a parallel comparison of the values for the total amount of phenolic compounds and the antioxidant value for the abovementioned three species from the same family, it can be concluded that there is a correlation between the obtained values. Namely, the species *E. spinosa* and *C. maritimum* had the highest amount of phenolic compounds, as well as the highest antioxidant activity among the examined halophytes, while *E. maritimum* deviated from the previous and had lower values of the amount of phenolic compounds and antioxidant activity. A comparative analysis of the value of phenolic compounds and antioxidant activity in extract of overground parts of other investigated halophytes also confirms the connection between these two parameters, since species with higher content of phenolic compounds have a higher antioxidant effect and vice versa. This correlation indicates that phenolic molecules in these halophytes are the key active substances that exhibit antioxidant activity.

14.5 Conclusion

Based on the attention that is given in recent years together with more intensive and significant researches directed toward the plants from saline habitats, it may be concluded that halophytes represent interesting ecological group of plants in several aspects. Findings from plenty of studies indicate that halophyte species generally represent important sources of secondary metabolites with significant biological activity, in particular antioxidant activity, and that habitat specificity leads to specific composition of secondary metabolites in these plants. However, in order to obtain significant amount of metabolites from interests originated from halophytes, moderations are needed between plant yield, plant exploitation, and biodiversity conservation. Therefore, the appropriate screening method together with the proper methods of extractions and applications of obtained results should be studied firstly and precisely. Additionally, the further search for biologically active metabolites from halophyte species must take into account the developmental stage and yield of individual plant species together with environmental factors.

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Chapter 15
Phytoamelioration of the Salt-Affected Soils Through Halophytes

Arvind Kumar, Ashwani Kumar, Anita Mann, Geeta Devi, Hariom Sharma, Rachna Singh, and Satish Kumar Sanwal

Contents

Abstract In recent years scarcity of fresh water and the secondary salinization of agricultural lands are becoming much more challenging worldwide. The use of these salt-affected marginal lands for crop production is an increasing trend as they are valuable resource that cannot be neglected and will be crucial for ensuring sufficient food to a burgeoning population. The present global scenario is also a pointer to the urgent need for bringing salt-affected marginal lands under cultivation. Previously reclamation of salt-affected soils has been predominately achieved through the application of chemical amendments, although the costs of these chemical amendments like gypsum or pyrite for reclamation of alkali soils have increased prohibitively over the past two decades because of competing demands from industries and reductions in government subsidies for their agricultural use. Therefore, calls for phytoamelioration of degraded lands through growing halophytic crops/grasses/trees seem to be one of the alternative methods of reclamation of these lands. Additionally alkali soils of India and Pakistan contain high levels of insoluble calcium carbonate ($CaCO_3$), which can be made soluble by adding acid or acid formers. It could be best

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done by enhancing biological activity either through the addition of organic matter or cultivation of halophytes. Thus phytoamelioration is one of the more effective approaches for resource-poor farmers and community-based reclamation management of moderately saline-sodic and sodic soils. Currently it has become viable approach in many parts of the world including India.

Keywords Phytoamelioration · Phytodesalination · Salinization · Halophytes

15.1 Introduction

Agricultural productivity in many parts of the world especially arid and semiarid regions is threatened by the occurrence of salt-affected soils. Reclamation of such type of soils is a most urgent requirement for sustaining world food production in the twenty-first century. In addition to naturally occurring saline soils, anthropogenic salinity which is the result of improper agricultural management practices is creating a great threat to the biodiversity, world food and fodder production. Although, in context with the secondary salinization, irrigation with excessive saline groundwater may transform productive land into unproductive salinized soil, consequently every year, a large area of productive land is going out from agricultural production (Sehgal et al. 1990). If we characterized the salt-affected soils, alkali soils contain excess of salts capable of alkaline hydrolysis such as sodium carbonate ($NaCO_3$), sodium bicarbonate ($NaHCO_3$), sodium silicate (Na_2SiO_3) and sufficient exchangeable Na^+ ion in the soil solution phase. However in the saline soils, chlorides and sulphates of Ca and Mg are the predominant salts, while ever predominance of Na along with excess of natural salts comes under saline-sodic category. Most of the saline-sodic soils contain soluble carbonates in addition to excess natural salts manifesting alkaline properties. From the management point of view, the saline-sodic soils that do not contain soluble carbonates are grouped with saline soils and others with alkali soils. Cleaning up of sites contaminated with natural salts usually requires extensive washing which usually consumes a large amount of water. In arid and semiarid regions, water resources are very scarce, in such conditions leaching or washing of excess salts is not recommended for the reclamation of dry land salinity. Therefore biological approaches can be used such as phyto salt accumulators which remove the salt from the soils and accumulate in plant parts. Phytoremediation of salt-affected soils has been proved an efficient and low-cost strategy and potential substitute of cost-intensive chemical amelioration (Qadir and Oster 2002). In this bioremediation approach, dissolution of native calcite enhanced within the root zone and provides Ca^{2+} for Na^+– Ca^{2+} exchange at the cation exchange sites. Phytoremediation of saline-sodic combination remains suitable, because it helps in maintaining adequate soil structure and aggregate stability that prevent a reduction in soil permeability to air and water. This chapter highlights the role of halophytes for phytoamelioration of calcareous sodic and saline-sodic soils and evaluation of the efficiency of phytoamelioration and chemical amendments for their effects on salt and Na^+ removal from the soil. An attempt has also been made to identify the suitable and luxuriantly growing halophytes and to assess the feasibility of salt bioaccumulation. This information will assist researchers in choosing appropriate halophyte to achieve maximum benefit during the amelioration process.

15.2 Salinization: Challenge for the World

Salinization is one of the most serious challenges in semiarid and arid regions of the world confronting sustainable agriculture in irrigated production systems. High levels of sodium chloride and other soluble salts directly affect plant growth and other parameters. Although plant absorbs salt through osmotic adjustment, it can result in ion toxicity and nutrient imbalances (Marschner 1986). At the global level, every continent consists of salt-affected soils, and at least 75 countries have the problem of serious salinization (Goudie 1990). Globally 397 million ha areas are under salinity and 434 million ha under sodicity have been reported. However out of the 230 million ha of irrigated land, 45 million ha (19.5%) are salt-affected soils. In case of dryland agriculture, out of 1500 million ha, 32 million ha (2.1%) are salt-affected soils (FAO 1980). Salt-affected lands are mainly located in arid and semiarid zones of the world. Majority of the countries affected by salinity are extended from the sub-Saharan Africa through the Middle East and into Central Asia. Soil salinization particularly affects developing countries located in arid climate zones (including Pakistan, India, Egypt, Tunisia, Morocco, Peru and Bolivia); on the other hand, developed countries are much less threatened by salinity, but not immune. Crop productivity had already been affected in 20–30% areas of irrigated lands over salinization and additional 1.5 million hectares area affected annually (WCD 2000). Researchers and farmers have been shown that salt-affected barren land can be brought back to the cultivation using plant-assisted amelioration approach that does not depend on chemical amendments (Kaur et al. 2002). In arid and semiarid climatic zones, improper irrigation approaches and secondary salinization are affecting fresh water and soil health. Ridiculously saline water irrigation accumulates salt in the rooting zone of arable land as high rate of evaporation and transpiration draw soluble salts from deep layers of soil profile. In drylands salt and water balance has been disturbed following agricultural practices which allow salt present in the groundwater to reach the surface (Rangasamy 2006). Additionally continuous sea level rising in a warming world due to climate change threatened to coastal low land areas as fertile land is becoming salinized (Munns 2005). In arid regions salinization is an irreversible process because fresh water is not available to leach out the accumulated salts in rhizosphere. Evolution of plant life started 3 billion years ago on earth in saline ocean water; with the improvement of land plants about 450 million years ago, primitive adaptation mechanisms of plants to the high concentrations of Na^+ and Cl^- were effectively lost (Rozema 1996). Presently only about 1% of plant species can grow and reproduce in coastal and inland saline habitats. Among these monocot and dicot salt-adapted plants, shrubs, and tress, some are annuals, and others are perennials in nature. There is a wide range of morphological, physiological and biochemical adaptations in such plants, which vary extensively in their degree of salt tolerance (Flowers and Colmer 2008). Salinity is not inimical to all plants; a wide range of naturally grown plant species in salt deserts and salt marshes survive under salt concentration equal to or greater than that of seawater. These plants compartmentalize ions in the vacuoles and accumulate the compatible solutes in the cytoplasm, having the genes for salt tolerance confer salt resistance (Gorham 1995). Reclamation of saline soils may be carried out by leaching, subsurface drainage, mechanical remediation, organic or mineral amendments and using halophytic vegetation, although the cost of leaching, drainage system and chemical is higher (Carty et al. 1997). Revegetation of halophytes on a salt-affected land is an example of proactive phytoremediation (Yensen et al. 1999). Phytoremediation of sodic and saline-sodic soils is achieved through the plant roots ability to increase the dissolution rate of calcite, through which levels of Ca^{2+} in the soil solution enhanced. Phytoremediation of saline-sodic soils involves cultivation of certain halophytic plant species that can tolerate ambient soil salinity and sodicity levels and accumulate salts in their aerial plant parts. Several plant species of agricultural significance appear suitable to be an effective phytoremediation tool (Qadir et al. 2002). Researchers suggest that if harvest of aerial plant portion of hyper salt accumulators is not added back to the same soil, it can significantly contribute to the removal of salts and amelioration processes (Owens 2001).

15.3 Chemical Amelioration vs. Phytoamelioration

Salt-affected soils differ from arable soils in two different aspects, i.e. soluble salt and soil reaction. Soluble salt in the soil may influence its behaviour for crop production through changes in its proportion of exchangeable cations, soil reactions, physical properties and the effect of osmotic and specific ion toxicity. Based on the influence of two common kinds of salts (neutral and alkali) on soil properties and plant growth, salt-affected soils are broadly grouped as either saline or alkali soils (Bhumla and Abrol 1979). The first requisite for crop production on salt-affected soils is to lower the salinity within acceptable level which is accomplished through reclamative leaching. Salt leaching involves the dissolution of soluble salts in the soil and displacement of the salty solution through out of root zone. In fact desalinization of soils by ponding with low salinity, rainwater is considered to be the only practical and effective way for removing salts in the initially barren saline soils. However adequate drainage is necessary for saline soils with shallow water table before undertaking leaching. In developing countries where the water resources are very scarce, leaching is not recommended. However, other phytoamelioration approaches can be used such as planting of hyper salt-accumulating plants where salts are accumulated in the aerial parts by these plants and removed from the soil. Many saline regions are found in poorly drained low-lying areas within semiarid and arid climates in which large quantities of salts have leached from regions of higher elevation. These leached salts accumulate in the slow flowing groundwater and are brought to the soil surface, in these low-lying areas, through high evapotranspiration rates (Goudie 1990). Whereas the application of appropriate chemical amendments is required for reclamation of alkali soils, it requires the removal of exchangeable sodium and its replacement by calcium. This is accomplished by the application of gypsum or any other chemical amendment including phosphogypsum, distillery spent wash, sulphur, sulphuric acid, pyrites, press mud, molasses and fly ash. Waterlogged saline soils are one of the major problems associated with land degradation in irrigated agriculture. The rising water table, a consequence of excessive deep percolation losses from irrigation fields and/or seepage from irrigation networks, results in waterlogging in root zone leading to build-up of soluble salts causing twin problems of waterlogging and soil salinity simultaneously. In waterlogged saline soils, water table remains within 1.5–2.0 m from the soil surface, and soils are saline with ECe more than 4 dS m^{-1}, pHs less than 8.2 and an ESP less than 15. These soils are often found in irrigation commands of arid, semiarid and subhumid coastal regions. However, there are saline soils without waterlogging and have been developed due to irrigation with saline groundwater. These soils have abundance of chlorides and sulphates of sodium, calcium and magnesium, are generally flocculated showing little signs of structural degradation and have high infiltration rate. Such type of problems could be handled by flushing and drainage. In the absence of drainage system, the reclamation of saline and saline waterlogged soils is not possible through leaching and subsurface drainage. Intermittently, the cost of the leaching and subsurface drainage is beyond the limit of land holder. In such type of situations, alternative for reclamation, i.e. phytoamelioration approach, could be applied. This approach utilizes halophytes to reclaim salt-affected soils. For resource-poor farmers, phytoremediation approach is very useful as it requires low initial investments and improves the soil quality. Two major constraints with chemical amelioration in several developing countries have emerged during the last two decades: firstly deterioration of amendment quality due to large fraction of impurities and secondly availability and increased costs of amendments due to high competing demands by industries and reductions in government subsidies for their agricultural use (Qadir et al. 2006). Owing to the over-riding importance of the last factor, chemical amelioration has become prohibitively expensive for resource-poor farmers.

15.4 Applied Phytoamelioration: Removal of Salts from the Soil

Boyko (1966) firstly suggested that halophytic plants could be used to desalinate soil and water. Consequently, Singh et al. (1994) reported that economic plants can also be used for reclamation of saline and sodic soils. Several studies have been conducted for comparable performance of phytoamelioration and chemical approaches in various countries for sodic soil reclamation. Field experiment conducted on a barren, calcareous, alkali soil indicated that amelioration efficiency of para grass (*Brachiaria mutica* (Forssk.) Stapf) and karnal grass (*Leptochloa fusca* (L.) Kunth) was comparable with gypsum application of 12.5 tonne ha^{-1} (Kumar and Abrol 1984). Grain yield of first crop (rice) in the gypsum treatment averaged 3.7 tonne ha^{-1} as compared to 3.8 and 4.1 tonne ha^{-1} during the first year with para and karnal grass treatments, respectively, while rice yields were 5.3 and 6.1 tonne ha^{-1} after second year cropping of grasses. Hamid et al. (1990) also have been reported that amelioration efficiency of Kallar grass was higher in comparison to gypsum-treated soil. Comparative study of sesbania (*Sesbania bispinosa* (Linn.) w.f. Wight), Kallar grass and sordan (*Sorghum x drummondii* (Steud.) Millsp. & Chase) against gypsum application of 13 tonne ha^{-1} on a calcareous, sandy clay loam, saline-sodic soil ($pH = 8.2–8.6$) showed that treatment efficiency for grain yield of wheat (*Triticum aestivum* L.) crop was higher in sesbania (3.79 tonne ha^{-1}) and gypsum (3.68 tonne ha^{-1}) treatment followed by Kallar grass (3.14 tonne ha^{-1}), sordan (2.27 tonne ha^{-1}) and control (0.65 tonne ha^{-1}) after two cropping seasons (Ahmad et al. 1990). In another field experiment conducted by Qadir et al. (1996), amelioration efficiency of Kallar grass, sesbania, millet rice and finger millet was tested against gypsum application of 14.8 tonne ha^{-1} on a calcareous saline-sodic soil ($ECe = 9.1–11.0$ dS m^{-1}). The treatment effectiveness of gypsum was equivalent to sesbania and higher than Kallar grass, millet rice and finger millet in terms of decreasing soil ECe and SAR. Forage yields of all the species were found directly proportional to their soil amelioration efficiency. However effectiveness of Amshot grass (*Echinochloa stagninum*) was more in comparison to ponding (5–10 cm water depth) and gypsum (~24 tonne ha^{-1}) to reducing the alkalinity and salinity of the highly saline-sodic soil. The initial ESP of the sites, i.e. 79.3, 73.3 and 67.3%, was reduced up to 55.0, 47.0 and 33.6% at the surface layer for ponding, gypsum, and Amshot, respectively, in 2 years of experiments (Helalia et al. 1992). In a reclamation experiment of saline-sodic soil ($pH_s = 9.1$, $EC\ e = 9.8$ dS m^{-1}), comparative study of Kallar grass (*Leptochloa fusca*) and gypsum treatments (control, gypsum at 50% and 100% GR) reveal that effectiveness of 100% GR amendment was highest followed by karnal grass, 50% GR and control for soil reclamation. The cumulative salt removal efficiency of gypsum amendment was equivalent to karnal (Qadir et al. 1996). The bioremediation treatment was more persistent in terms of maintenance of electrolyte concentration in leachates and removal of soluble salts than gypsum; possibly plant roots were affecting the $Na^+–Ca^{2+}$ exchange at the cation exchange sites and finally Na^+ concentration in soil chemical environment and increased the leaching of soluble salts (Robbins 1986; Qadir et al. 1996). Theoretically it is estimated that *Suaeda salsa* can remove 3.0–3.8 tonne Na ha^{-1} with population density of 15 plants m^{-2}. However with the bulk density of 1600 kg m^{-3} of soil, reduction of 1.25 tonne and 1.92 tonne Na^+ ha^{-1} with the population density of 15 and 30 plants m $^{-2}$, respectively (Zhao (1991). Sodium (Na^+) and chloride (Cl^-) hyperaccumulating halophytes *Kalidium folium* and *Suaeda salsa* produce 7.70 tonne and 8.70 tonne ha^{-1} biomass and can accumulate 2.29 tonne and

2.79 tonne NaCl per hectare of soil, respectively (Zhao et al. 2005). In a field experiment, amelioration efficiency of *H. recurvum*, *S. nudiflora* and *S. baryosma* was tested. Result of the experiment showed that plantation of these halophytes considerably decreases the soil pH, EC, exchangeable Na^+, exchangeable Ca^{2+} and exchangeable sodium percentage (ESP) and *Suaeda nudiflora* was the most efficient halophyte in increasing soil exchangeable calcium content (Shekhawat et al. 2006). It is estimated that *Suaeda maritima* and *Suaeda portulacastrum* could remove 0.50 and 0.47 tonne of NaCl ha^{-1}saline land, respectively, in the time duration of 4 months and these could be good sources for phytoamelioration of saline lands (Ravindran et al. 2007). Expansion of halophyte cultivation gradually declines Na^+ and Cl^- in natural saline soils correspondingly; electrical conductivity (EC) of soil samples was also reduced with increase in plant samples. Halophytes accumulate the salts in plant tissues through osmotic adjustment and compartmentation under saline environment. Compartmentation takes away the toxic ions from the cytosolic compartment and allowing NaCl as cheap osmolytes in addition to organic compounds. The halophytes *S. maritima* and *S. portulacastrum* compartmentalize the toxic Na^+ into vacuoles, and membrane-bound transport system regulates cytosolic ions (Na^+, K^+ and Ca^{2+}), and ion accumulates through increasing the volume of the vacuole. Therefore *S. maritima* and *S. portulacastrum* could be used successfully to reclaim the highly salinized areas for crop production after a few repeated cultivation and harvest (Ravindran et al. 2007). The cultivation of *Tamarix aphylla*, *Atriplex nummularia* and *Atriplex halimus* decreased an average electrical conductivity of soil paste of 84 mS/cm to 5.46, 5.04 and 6.3 mS/cm at the top layer (0–30 cm depth) and, however, in the lower layer (30–60 cm depth) 49.6 mS/cm to 5.46, 13.45 and 7.14 mS/cm for *Atriplex halimus*, *Atriplex nummularia* and *Tamarix aphylla*, respectively. Higher reduction in electrical conductivity was observed in the upper surface which may be attributed to high root density (Farah Al-Nasir 2009). *Tamarix* is one of the best halophyte species used to rehabilitate the saline-sodic soil. Under field experiment, *Tamarix indica* exhibited much higher phytodesalination capacity (77.7–94.4% of the whole shoot removed sodium) as compared to *S. fruticosa*. The phytodesalination capacity of *T. Indica* was 3.5 and 16.7 times higher than that of *S. fruticosa* in winter and summer season, respectively. *S. fruticosa* decrease the soil salinity through roots that released sodium ions from the exchange sites and facilitated their leaching to the deeper horizons (Rabhi et al. 2010). *Sesuvium portulacastrum* is one of the most efficient halophytes for phytodesalination which produced 7.7 tonne dry weight ha^{-1} during 189 days and exhibited a phytodesalination capacity of 1.0 tonne Na^+ ha^{-1} (Rabhi et al. 2010a). In a field experiment, *S. portulacastrum*, *T. indica* and *S. fruticosa* reduced the electrical conductivity (EC_e) of 29%, 35%, and 45%, respectively, in comparison to control. Highest phytodesalination capacity of 2.5 tonne NaCl ha^{-1} was observed in *Sesuvium portulacastrum* with the dry biomass production of 6.6 tonne ha^{-1} (Zorrig et al. 2012). Another field experiment was conducted on three halophytes, *Salicornia europaea*, *Suaeda salsa* and *Atriplex aucheri*, in saline-irrigated condition. A total of 0.98 tonne ha^{-1} salt is imported by irrigation each year; however, the removal of salt recorded 7.62 tonne ha^{-1}, 5.26 tonne ha^{-1} and 4.83 tonne ha^{-1}, respectively, in

A. aucheri, *S. salsa* and *S. europaea* during the first year and 7.62 tonne kg ha^{-1}, 5.19 tonne ha^{-1} and 4.71 tonne ha^{-1}, respectively, during the second year of experiment. *Atriplex aucheri* was more effective for desalinisation than *S. salsa* and *S. europaea* (Zhao et al. 2013). The accumulation of salts was highest in *Suaeda monoica* with the reduction in electrical conductivity of soil from initial 5.1 to 1.8 dSm^{-1} after 120 days of plantation. Simultaneously EC was found increased in plant sample from 3.9 to 18.8 dSm^{-1} which indicates a reduction of salts in the field. Consequently a total of 0.45 tonne NaCl salt ha^{-1}was removed by *Suaeda monoica* in 120 days of plantation (Ayyappan et al. 2013). On the other hand, the desalinization capacity of *Sulla carnosa* was 0.30 tonne Na$^+$ha^{-1} with the dry biomass production of 5.0 tonne ha^{-1}, which is 24% of the added salt quantity after 80 days of plantation (Jlassi et al. 2013). Kilic et al. (2008) have reported that considerable amounts of salt from soil were removed by *Portulaca oleracea*. Chaudhari et al. (1964) have also reported the ability of *Suaeda fruticosa* for the accumulation of Na$^+$ and other ions. Approximately 100 g of salt can be accumulated in aerial tissue by a single plant of *Suaeda fruticosa*. Another experiments on *Sporobolus arabicus*, *Leptochloa fusca*, *Suaeda fruticosa*, *Atriplex lentiformis* and *Kochia indica* also confirmed that cultivation of these halophytes is effective in reducing the soil SAR, consequently reclamation of sodic soils (Ashraf 2007). The phytoamelioration treatments caused 52% decrease in soil sodicity by cultivating salt-tolerant halophytes comparable to 62% decrease in soil sodicity through gypsum (Qadir and Oster 2004).

15.5 Selection of Plant Species for Phytoamelioration

The selection of a particular plant species for phytoamelioration is based on the ability of the species to tolerate soil salinity and sodicity and economically useful. A significant variation normally exists among different crop plant to withstand various saline-sodic conditions (Maas and Grattan 1999). To locate the exact inter- and intracrop diversity, field trials should be conducted to determine the adaptability to saline-sodic soil conditions (Shannon 1997). The appropriate resources for this could be local farmers, farm advisors and researchers, who are familiar with local conditions, including crop response to adverse soil conditions and cropping strategies that fit into the local economic conditions, and hence appropriate recommendations can be suggested. An additional approach is to develop crop genotypes with enhanced salt tolerance through breeding approaches (Pitman and Lauchli 2002). Several authors have used different crops, shrubs, trees and grasses as vegetative bioremediation tools to ameliorate sodic and saline-sodic soils, e.g. Kallar grass (Kumar and Abrol 1984), sesbania (Ahmad et al. 1990), alfalfa (Ilyas et al. 1993), Bermuda grass (Oster et al. 1999) or sordan (Robbins 1986), which have been explored for sodic soil amelioration measures. Several other plant species, e.g. plant species of *Atriplex* and *Maireana* (Barrett-Lennard 2002, Malcolm 1993), *Kochia scoparia* (Garduno 1993), *Salicornia bigelovii* (Glenn et al. 1996), *Echinochloa crus-galli* (Aslam et al.

1987) and *Portulaca oleracea* (Grieve and Suarez 1997), have been suggested to grow well and produce adequate biomass on salt-affected soils. The use of crops with high medicinal value along with aromatic species with potential survival on sodic and saline-sodic soils will be an addition to such studies. Some tree species also have been grown on sodic and saline-sodic soils for phytodesalinization, for example, *Terminalia arjuna* (Jain and Singh 1998), *Prosopis juliflora* (Bhojvaid and Timmer 1998), *Dalbergia sissoo* and *Acacia nilotica* (Kaur et al. 2002), *Parkinsonia aculeata* and *Prosopis cineraria* (Qureshi and Barrett-Lennard 1998), *Sesbania sesban* and *Tamarix dioica* (Singh 1989) and *Leucaena leucocephala* (Qureshi et al. 1993) among others.

15.6 Impact of Phytoamelioration on Soil Health

The experiment conducted with sesbania, sordan, or Kallar grass was designed for vegetative bioremediation. It was observed that after 15 months of plantation of these crop plants and grasses, there was an increase in phosphorus (P), zinc (Zn) and copper (Cu) availability in the soil which may be released through root exudates and dissolution of some nutrient-coated calcite. On the other hand, the soil/field without these plant species with gypsum treatment decreased the availability of these nutrients. This may be due to adsorption of nutrients on some newly formed CaCO3, a secondary consequence of gypsum dissolution. Nitrogen content was increased from 0.49 to 0.53 g kg^{-1} with sesbania plantation (Qadir et al. 1997). Soil microbial biomass plays as potent reservoir for most of plant available nutrients and also transforms the organic matter. The microbial biomass characterizes the health status of a soil. Dehydrogenase activity (DHA) in soils provides the status of microbial populations, respiration activity, and soil organic matter, thus giving an index of overall soil microbial activity (Włodarczyk et al. 2002). An experiment was conducted by Batra et al. (1997) on alkali soils ($pH_{1:2} = 10.6$) by growing karnal grass for 1 or 2 years (harvested biomass removed or left to decompose on the soil surface) along with the following treatments, gypsum application (at 14 tonne ha^{-1}) + karnal grass, gypsum + sorghum, gypsum + rice, and gypsum + sesbania. The DHA activities in post-amelioration soil were greater (118.7 μg triphenyl formazan g^{-1}) in the bioremediation treatments than gypsum + crop treatments (96.1 μg triphenyl formazan g^{-1}). On the other hand, MBC values were higher in gypsum + crop treatments (206.3 mg kg^{-1} soil) than in the cropped treatments (161.7 mg kg^{-1} soil). The overall microbial biomass carbon (184 mg kg^{-1} soil) for all the treatments was more than three times the initial level of 56.7 mg kg^{-1} soil. In addition to soil amelioration effects, cultivation of suitable crops, shrubs and trees on sodic and saline-sodic soils has the potential to mitigate accelerated greenhouse effects by increasing soil C through biomass production.

It has been reported that shisham (*Dalbergia sissoo*) and mesquite (*Prosopis juliflora*) decrease sodium levels in soil and thus are more efficient in terms of biomass production. The microbial activity in upper 60 cm of soil was higher under these species due to accumulation of humus from decomposition of leaf litter and root decay and thus increased soil organic C. A spontaneous slow increase in soil organic carbon C with these three species was observed for the first 2–4 years, exponential between 4 and 6 years, and the plateau at a low rate for 6–8 years (Garg 1998). In sodic field soil, organic carbon of the top 120 cm soil increased from 11.8 to 13.3 tonne C ha^{-1} with 5-year plantations of mesquite along with 34.2 tonne C ha^{-1} in 7 years and 54.3 tonne C ha^{-1} in 30 years (Bhojvaid and Timmer 1998). After harvesting of the halophytes, decay of roots left behind pores in the soil; such pores may be more than 100 cm in diameter. Bipores created by thick roots promote infiltration of rainwater and good aeration and are helpful to rapid and extensive root growth to uptake of moisture and nutrients for new plantation of halophytes (Yunusa and Newton 2003).

15.7 Future Research Directions

Basically phytoamelioration approach worked well on moderately sodic and saline-sodic soils, where adequate fresh irrigation water is not available for leaching of excess soluble salt. In such type of situations, the performance of vegetative remediation is to be comparable with chemical amendments. On highly sodic and saline-sodic soils, chemical treatment was better than the cropped treatments. Under several studies economics of sodic soil ameliorations has been drawn based on cost and benefit analysis. A net economic loss (cost/benefit, 1:0.75) has been reported during vegetative bioremediation although the growth of karnal grass was adequate, which helps in reduction of soil sodicity. Additionally the economic loss may be compensated through grass production based on market-derived demand (Singh and Singh 1989). Under other situations bioremediation strategy has been found economically beneficial when there was a market demand or local utilization of the crops at the farm level (Chaudhry and Abaidullah 1988, Sandhu and Qureshi 1986). In another study Qureshi et al. (1993) reported that agroforestry systems containing several tree species have been found to be economically feasible for the reclamation of saline-sodic soils because of firewood demand in local markets. In an economic perspective, phytoamelioration approaches can only be economically viable if the selected plant species (crops/grasses/tress) have a market demand or local utilization. Certainly it required improvement programme, i.e. screening of large number of halophytes in terms of higher salt accumulation and genetic improvement of selected halophytes to enhance their phytoamelioration efficiency. New avenues of biotechnology could be used to isolation and transfer of salt-tolerant genes in other crop plants.

15.8 Conclusion

Halophytes have the potential for phytoamelioration of salt-affected soils. Consequently phytodesalination has attracted much attention for the desalination of salt-affected soils with the use of salt-accumulating halophytes. The property of halophytes to accumulate high concentrations of salt in their aboveground tissues consequently reclaims the saline soils after harvesting the plants. During recent decades, phytoamelioration have reported an efficient, inexpensive, and environmentally acceptable strategy to ameliorate sodic and saline-sodic soils. Comparative performance with the chemical amendments highlights the effective role of halophytes in the amelioration of salt-affected soils. Phytoamelioration could be better in several aspects including (a) cost-effectiveness, (b) improvement of soil hydraulic properties and root proliferation through bipores, (c) carbon sequestration after post-amelioration process and (d) productive use of marginal and degraded soils in eco-friendly manner. Although phytoamelioration approach gradually achieves positive change than chemical approaches, it is commonly effective to most sodic and saline-sodic soils of arid regions. Further scope of phytoremediation approach is limited on highly sodic soils where the growth of the halophytes is likely to be variable and patchy, and the use of chemical amendments such as gypsum is inevitable. Definitely, phytoamelioration is a cost-effective approach for resource-poor farmers and has the potential for large-scale adoption through government- and community-based programmes to improve the productivity of degraded salt-affected soils.

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Chapter 16

Multidisciplinary Studies on a Pilot Coastal Desert Modular Farm Growing *Salicornia bigelovii* in United Arab Emirates

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Contents

Abstract Global population growth is putting severe pressure on agricultural production, since food supplies need to increase by 50–70% to meet expected future demands. Arable land that is used to grow crops for food is in short supply, and freshwater is being depleted. One way to increase production is to utilize marginal land and water resources such as coastal desert areas and seawater. Aquaculture

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effluents enriched in nutrients can be utilized to irrigate highly salt-tolerant plants such as halophytes which constitute the best candidates for the development of biosaline agriculture. Among the halophytic crops that have high potential to be grown with seawater and can be economically viable are mangroves and *Salicornia* species. In particular, *Salicornia bigelovii* (dwarf glasswort) is a halophyte that grows in salty water and can be utilized in multiple ways. Since 2015, a seawater-based system has been implemented in a coastal desert area in Umm Al Quwain in the United Arab Emirates, exploring the growth potential of four high-yielding *S. bigelovii* genotypes using four saline water treatments (seawater; canal water which is the drainage water coming from a marine research station that flows into a mangrove area; and aquaculture effluents from tilapia and sherry farming) and two types of irrigation system: bubblers and open pipes. A multidisciplinary study was conducted to examine several soil and water attributes, various growth parameters of *S. bigelovii* genotypes, the seed oil content, and the profitability of the system. Results showed that by selecting the suitable *S. bigelovii* germplasm combined with appropriate water and soil management practices, proper growth of salicornia plantation could be achieved in a coastal desert ecosystem. However, continuous exploration of the long-term environmental impact of implementing saline water resources and improvement of the economic sustainability of such biosaline production systems are needed.

Keywords Seawater-based farms · Halophytes · Biosaline agriculture · Multidisciplinary analyses · Desert environments

Abbreviations

ICBA	International Center for Biosaline Agriculture
MERD	Marine Environment Research Department
MOCCAE	Ministry of Climate Change and Environment
UAE	United Arab Emirates

16.1 Introduction

The increasing global population, which is estimated to reach 9.8 billion in 2050 compared with 7.6 billion in 2017 and 11.2 billion in 2100 (United Nations 2017), requires a marked rise in global food production. Despite the considerable growth in crop yield, the most recent forecast of 25–70% increase toward 2050 is challenging (Hunter et al. 2017). Meeting the global food demand while continuously maintaining the proper functioning of the ecosystems will require a sustainable intensification strategy and development of production systems that can meet both production and environmental targets while incorporating future challenges of constraints on water availability (Falkenmark 2013) and climate change (Challinor et al. 2015). The global agricultural area is being exhausted, due to erosion, acidification, and salinity making land unfavorable for cultivation of traditional crops. Salinity accounts for 831 million hectares, where 397 million hectares are saline and 434 million are sodic, and every year 1.5 million hectares are taken out of production due to salinization (Hasanuzzaman 2014). Hence, salt-affected soils contribute in aggravating the global problems in agriculture, and alternative cost-effective solutions are urgently needed, to utilize marginal saline lands. Additionally, alternative water resources are sought to be used for irrigation purposes since they constitute a valuable option for fresh water saving solutions.

Halophytes could be an option to utilize salt-affected soils, bringing them back into production. Many halophytic species have shown good potential used for human consumption; for forages and animal feed; as oilseed, protein, energy, and medicinal crops; and for phytoremediation purposes (Panta et al. 2014; Ventura et al. 2015). *Salicornia bigelovii Torr.* is a small, annual, leafless, succulent halophyte with extremely high salt tolerance (Ventura et al. 2015). It is a native plant in coastal salt marshes of North America and the Caribbean (Bresdin et al. 2016). *S. bigelovii* and its related species are of special commercial interest due to the wide range of valuable products they can provide: the high oil content of the seeds makes it favorable as oilseed crop; the seedcake as fodder has high protein content (45%) (Glenn et al. 2013); the fresh leaf tips can be consumed as vegetable and the straw as a forage for different ruminants (Glenn et al. 1992; Attia et al. 1997; Abdal 2009); and it can also be used as medicinal plant (Rhee et al. 2009). The cultivation of *S. bigelovii* was primarily targeted for biofuel production, and it has been the most preferred species to be included in the majority of large commercial scale biosaline agriculture systems (Marriot and Pourazadi 2017). Coastal areas were found to be the most suitable lands for *S. bigelovii* cultivation in the United Arab Emirates (Al-Yamani et al. 2013). Under saline conditions, biomass yield of halophytes is comparatively larger than from any other conventional crop such as wheat, maize, or rice (Flowers and Colmer 2008).

Halophytic species are indispensable parts of integrated agri-aquaculture systems or else modular farms when saline water resources are considered for irrigation purposes. Modular farms combine different production components such as agriculture and aquaculture. This type of farming schemes increases nutrients and water recycling and can provide a multisource income to the farming communities. Aquaculture is the world's fastest-growing food production system and now accounts for over 50% of all fish products; however it is often associated with considerable environmental problems due to eutrophication of coastal waters, caused by the nutrient-rich aquaculture effluents (FAO 2016). Use of drainage water from aquaculture farms to irrigate various crops is a practice that is applied in several countries worldwide in small scale (Kumar et al. 2012), and due to its multifold advantages, there is an increasing interest for its further expansion and implementation. Such synergistic solutions maximize farm productivity and decrease dependency upon chemical fertilizers while promoting greater sustainability of the systems by biofiltering the aquaculture effluents (Sphigel et al. 2013). Brackish or saline aquaculture effluents can be utilized to irrigate halophytic plants which constitute the best candidate plants for seawater-based agricultural systems (Sànchez et al. 2015; Sphigel et al. 2013). This synergy could alleviate some of the expected future environmental consequences associated with expansion of the aquaculture industry and utilize marginal saline lands and hence provide additional agricultural products for a growing population.

The International Center for Biosaline Agriculture (ICBA) has a long experience with the use of marginal saline resources to grow salt-tolerant crops, forages, trees, shrubs, and grasses. ICBA, in collaboration with the Marine Environment Research Department (MERD) based in Umm Al Quwain in the United Arab Emirates (UAE), has been exploring the possibility to grow *S. bigelovii* as a high potential halophytic crop adapted to UAE climatic and soil conditions using seawater and drainage water from aquaculture (ICBA 2016). The potential for growing *S. bigelovii* production in a sustainable way in a coastal desert area is assessed through testing different *S. bigelovii* genotypes, irrigation schemes, and treatments.

16.2 A Pilot Seawater-Based Farm Implemented in a Coastal Desert Area in UAE

Four *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10) were cultivated at MERD's experimental station in 2015–2016. These genotypes were the high-yielding ones selected after 3-year evaluation at ICBA's experimental station. In order to guarantee good establishment of salicornia plants in the station, we sowed salicornia seeds in jiffy pellets at the end of December in 2015, and they were irrigated with high saline water. After 2 months, salicornia seedlings were transplanted in the coastal desert area at MERD. Four water treatments were used: canal water (drainage water coming from various aquaculture tanks in MERD that flow into a mangrove area), aquaculture effluents from tilapia fish (*Oreochromis spilurus*) and from sherry fish (*Lethrinus nebulosus*), and seawater. Both tilapia and sherry fish tanks were of 50 m^3 capacity and contained 62 and 15 fish, respectively. The fish density was 0.62 kg/m^3 and 0.45 kg/m^3 for tilapia and sherry, respectively. The average weight for tilapia fish was 500 g and for sherry fish 1500 g. Additionally, two types of irrigation system were used: bubblers and open pipes. Details of the experimental area and the irrigation systems are given in Figs. 16.1 and 16.2. Before sowing, the land was prepared by adding organic compost at 40 t/ha. Seed sowing density was 1 g/m^2 and was covered lightly with soil. All the seedlings/plants were irrigated through flooding and bubblers adjusted to the water requirement including a 30% leaching fraction. After sowing, salicornia plants were not fertilized in order to explore the impact of aquaculture effluents enriched in nutrients on their growth.

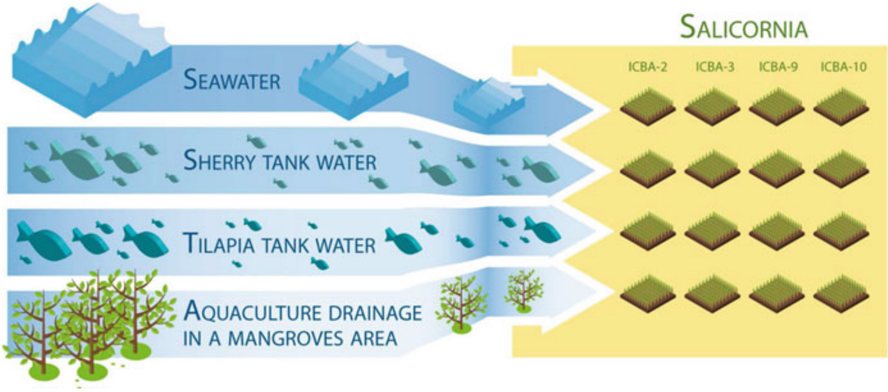

Fig. 16.1 The layout of the coastal modular farm implemented at MERD's experimental station in Umm Al Quwain in the United Arab Emirates. Four high-yielding *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, and ICBA-10) are irrigated with four different water treatments: seawater, canal water, and effluents coming from tilapia and sherry tanks (Design created by A3® for ICBA©)

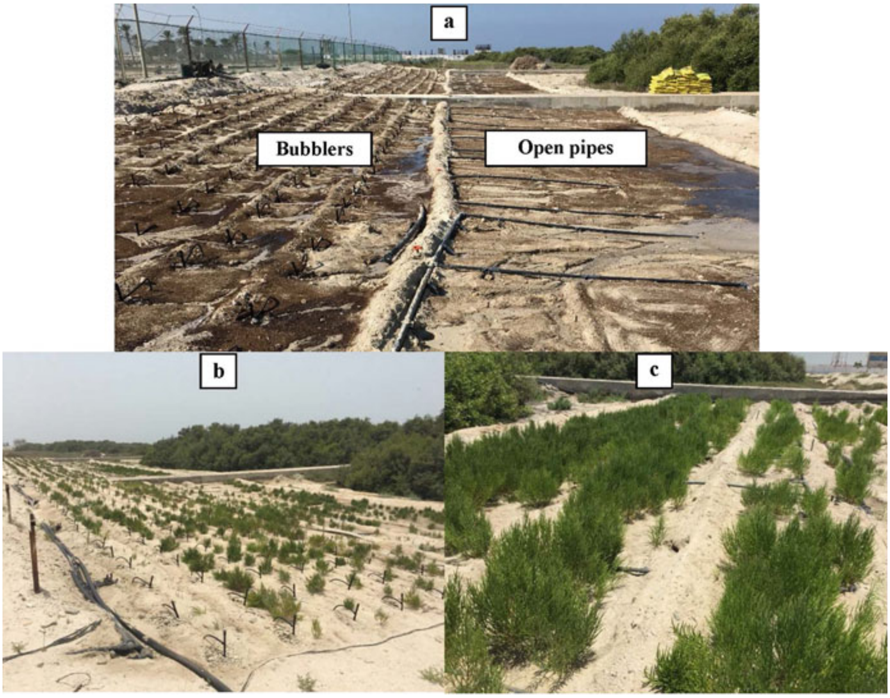

Fig. 16.2 **(a)** Two types of irrigation systems used for salicornia experiment at MERD's experimental station in Umm Al Quwain in the United Arab Emirates: bubblers (left) and open pipes (right). **(b)** *S. bigelovii* plots. **(c)** *S. bigelovii* genotypes treated with canal water

16.2.1 Soil and Water Monitoring

The salinity level of the water irrigation was regularly monitored once per 2 weeks. Soil salinity was evaluated by taking composite soil sample at the root zone (0–30 cm soil depth) from different plots representing different treatments at the beginning, the middle, and the end of the experiment. Soil samples were dried and soil extract was obtained to determine the electrical conductivity. At the end of the trial, soil samples were again collected and analyzed for salinity and pH.

16.2.2 Data Collection and Statistical Analysis

Various growth parameters were taken such as plant height, number of branches, number of spikes, and seed weight per plant. The total oil content of *S. bigelovii* seeds was estimated after drying the seeds to remove the moisture at 80 °C for 12 h in a hot-air oven. Five grams of the powered salicornia seeds was extracted using analytical grade chloroform and methanol, 2:1 ratio (v/v), for 6 h in Behr Serial Soxhlet Extraction apparatus, Germany. The extracted oil was recovered by evaporating the solvent in the hot-air oven overnight to constant weight. All measurements were done in triplicates.

One-way and multifactor analysis of variance (ANOVA) was performed to test whether there were differences among *S. bigelovii* populations, among irrigation treatments, and between the types of irrigation systems. The interaction among factors for all the characteristics was also studied. LSD multiple comparison test was used to detect differences among the means. All statistical analyses were carried out using Statgraphics Centurion XV (StatPoint, USA), and all graphs were constructed with Excel program. The average values, the standard error, and the LSD values were presented in the graphs for each parameter.

16.2.3 Benefit-Cost Analysis

A benefit-cost analysis was performed on the production system in place at Umm Al Quwain. The focus of the current research was on salicornia as a potential biofuel crop (seed production), but the potential market for salicornia as a food crop (fresh tip production) was also considered. This section includes the costs of the production, the benefits, and the implications of the benefit-cost analysis. Because most of the equipment had an expected life of 10 years, the project costs were estimated for a 10-year life span. Equipment and up-front land preparation costs were amortized by dividing the investment cost by the life span, producing an annualized cost of using the investment costs. Variable costs depended on volume of production. A single ha of salicornia production was assumed, and the results of the fish production were based on an output of 10 kg/m^3 fish density. The salicornia results were calculated on a per ha basis, extrapolating from results reported above. Prices were given in US dollars at 2017 values.

16.3 Multidisciplinary Analyses

16.3.1 Water Analysis

Water samples were regularly collected to monitor the salinity level, pH, ammonia, nitrite, nitrate, silicate, and phosphate in all treatments (canal, seawater, and tilapia and sherry effluents) used for irrigating salicornia plants. pH levels ranged from 7.9 to 8.3, 8.2 to 8.7, 8.1 to 8.2, and 8.1 to 8.4 for canal, seawater, and tilapia and sherry effluents, respectively (Fig. 16.3). As a result, pH was characterized as slightly and moderately alkaline for all water treatments except seawater, which pH values were more alkaline. This could be attributed to the higher concentration of salts present in seawater based on the higher values of electrical conductivity. In particular, EC varied between 39.7 and 41, 39.2 and 45, 39.7 and 41, and 39.6 and 40.7 for canal, seawater, and tilapia and sherry effluents (Fig. 16.4). Salinity was maintained in the same levels from 5th of April to 22nd of May with very small fluctuations except seawater. Small variations were also observed for pH values for the same period.

Ammonia, nitrite, nitrate, silicate, and phosphate were measured on 5th of April in all irrigation treatments (canal, seawater, and tilapia and sherry effluents) to

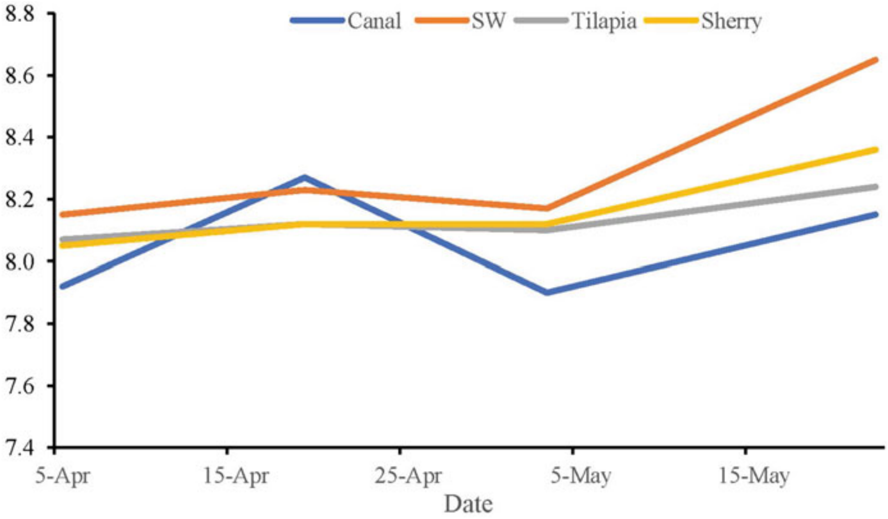

Fig. 16.3 Water pH monitored from 5th of April to 22nd of May for all four water treatments (seawater, canal water, and effluents coming from tilapia and sherry tanks) used to irrigate *S. bigelovii* plants

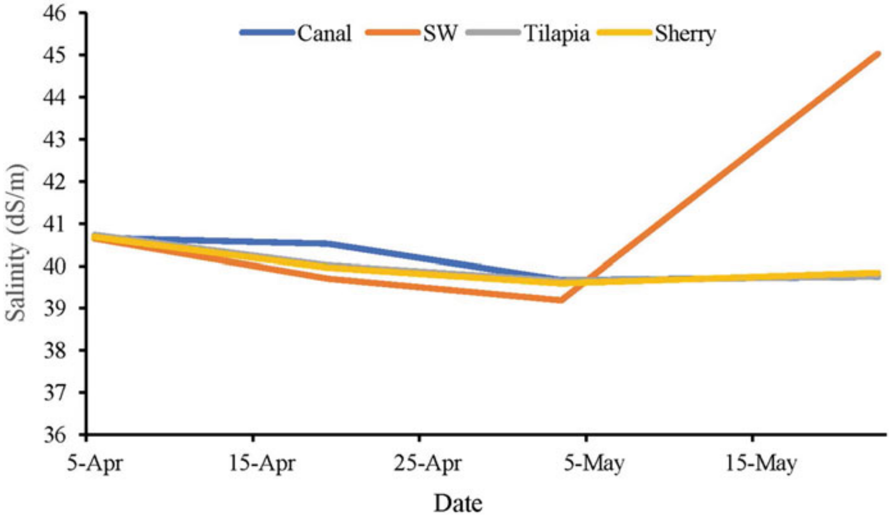

Fig. 16.4 Water salinity (EC) monitored from 5th of April to 22nd of May for all four water treatments (seawater, canal water, and effluents coming from tilapia and sherry tanks) used to irrigate *S. bigelovii* plants

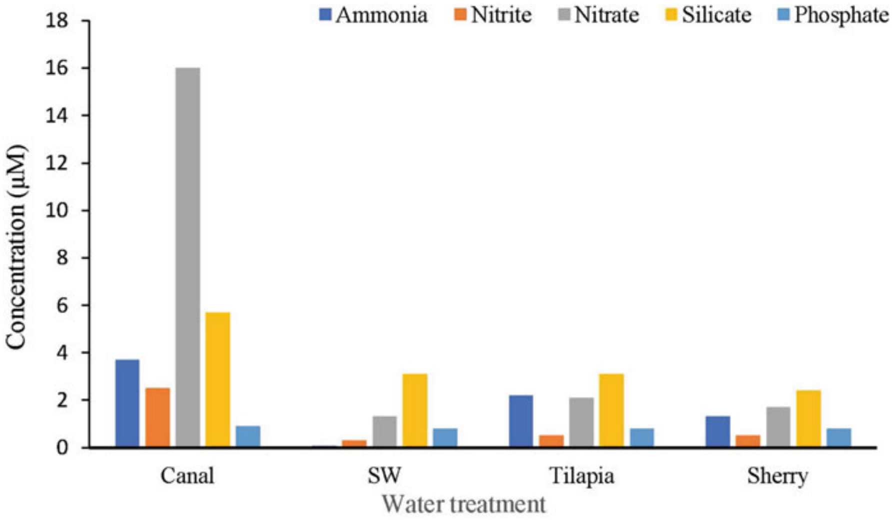

Fig. 16.5 Concentration (µM) of ammonia, nitrite, nitrate, silicate, and phosphate for all four water treatments (seawater, canal water, and tilapia and sherry effluents) used to irrigate *S. bigelovii* plants

examine the differences among water applications (Fig. 16.5). Phosphate values ranged from 0.8 µM (seawater) to 0.9 µM (canal water) and silicate from 2.4 µM (sherry effluents) to 5.7 µM (canal water). Ammonia concentration varied between 0.06 µM (seawater) and 3.7 µM (canal water) and nitrite between 0.3 µM (seawater) and 2.5 μM (canal water). The largest difference was observed among water treatments for nitrate concentration which ranged from 1.3 μM (seawater) to 16.0 μM (canal water). It is obvious from the aforementioned measurements that seawater was characterized by the lowest values of minerals whereas canal water by the highest values. The highest concentration of nitrate in canal water could be attributed to the abundance of nitrifying bacteria present in the water. There could be two sources that generate these bacteria: the first one is the drainage water that is coming from various aquaculture tanks in MERD that flow into this area, and as a result, the load of nitrifying bacteria is higher, and the second source could be the mangrove plantation growing in the area that could contribute in an increase in the number of nitrifying bacteria which are active in their sediment. To understand better nitrogen circle, firstly, the waste from fish releases ammonia. Ammonia is not a stable form of inorganic nitrogen in water, is very toxic to fish, and is converted to nitrite through bacteria activation. These nitrifying bacteria decompose also toxic to fish and short-lived in water nitrite to nitrate. This inorganic form of nitrogen is highly soluble in water and stable over a wide range of environmental conditions and can be used by plants to help them grow.

Another fact that should be taken into consideration is that the nutrients content in tilapia and sherry effluents were not high as expected. This was due to the fact that the fish density in the tanks was very low (0.6 and 0.45 kg/m^3, respectively), almost ten times lower compared to the minimum fish density for commercial scale (10 kg/m^3).

16.3.2 Soil Analysis

Soil samples were collected at two depths 0–25 and 25–50 cm on 20th of April, almost 2 months after transplanting. The samples were air dried, and then saturated extract was obtained under vacuum. Electrical conductivity and pH were measured (Table 16.1). Results showed that EC values differentiated between the two irrigation systems in all water treatments to a higher or a lower extent. EC was higher in samples collected from plots where bubblers were used for irrigating salicornia. The differences were bigger for canal and seawater treatment. This could be attributed to the fact that more salts were leached down through the soil because of the flooding effect that open pipes created in the field. EC measured in soil samples collected from 0 to 25 cm in plots where bubblers were installed was higher in all water treatments, compared to the EC measured in samples collected from 25 to 50 cm. Regarding EC values of soil samples taken from the first 25 cm at plots where open pipes were installed, they were either higher (tilapia and sherry effluents) or lower (canal and seawater) compared to the samples taken from lower depth.

Soil pH ranged from neutral to slightly alkaline (from 7.08 to 7.84) for all the treatments. pH values were higher in samples collected at first 25 cm of soil from plots where bubblers were used to irrigate salicornia plants compared to samples collected from deeper soil layers, except canal water where pH values were almost

Table 16.1 Soil EC (dS/m) and pH measurements for all four water treatments (seawater, canal water, and effluents coming from tilapia and sherry tanks) used to irrigate *S. bigelovii* plants

Soil EC and pH				
Water treatment	Irrigation system	Soil depth (cm)	EC (dS/m)	pH
Canal	Bubblers	0–25	45.1	7.47
Canal	Bubblers	25–50	40.3	7.44
Canal	Open pipes	0–25	34.1	7.21
Canal	Open pipes	25–50	41.5	7.72
Seawater	Bubblers	0–25	40.6	7.58
Seawater	Bubblers	25–50	29.7	7.08
Seawater	Open pipes	0–25	32	7.56
Seawater	Open pipes	25–50	32.8	7.09
Tilapia effluents	Bubblers	0–25	33.3	7.68
Tilapia effluents	Bubblers	25–50	32	7.32
Tilapia effluents	Open pipes	0–25	30.8	7.22
Tilapia effluents	Open pipes	25–50	29.7	7.72
Sherry effluents	Bubblers	0–25	36.5	7.59
Sherry effluents	Bubblers	25–50	34.4	7.13
Sherry effluents	Open pipes	0–25	34.4	7.79
Sherry effluents	Open pipes	25–50	30	7.84

Table 16.2 Multifactor analysis for plant height taking into account the three main effects and their levels: water treatments (seawater, canal water, and effluents coming from tilapia and sherry tanks), *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10), and two irrigation systems (bubblers and open pipes)

Multifactor analysis for plant height		
Source	F-ratio	P-value
Main effects		
A: Water treatment	50.04	$p < 0.001$
B: Genotype	9.62	$p < 0.001$
C: Irrigation system	2.72	NS
Interactions		
A*B	2.22	0.0245
A*C	3.19	0.0261
B*C	5.50	0.0014
A*B*C	6.55	$p < 0.001$

equal for both depths. No other trend was observed between irrigation systems, soil depths, and water treatments.

16.3.3 Agronomic Aspects

16.3.3.1 Impact of Different Treatments on Plant Height

Results showed that plant height was significantly affected by all the treatments and their interactions except the type of irrigation system (Table 16.2). Multiple range

Table 16.3 Multiple range tests among levels of each factor: water treatments (seawater, canal water, and effluents coming from tilapia and sherry tanks), *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10), and two irrigation systems (bubblers and open pipes) based on multifactor analysis for plant height. The same letter implies that the treatments are not significantly different ($LSD_{0.05}$)

Plant height					
Water treatment	Comparison between water treatments	Genotype	Comparison between genotypes	Irrigation system	Comparison between irrigation systems
Tilapia	A	ICBA-9	A	Bubblers	A
Seawater	B	ICBA-10	A	Open pipes	A
Sherry	B	ICBA-2	B		
Canal	C	ICBA-3	B		

Table 16.4 Multifactor analysis for number of branches taking into account the three main effects and their levels: water treatments (seawater, canal water, and effluents coming from tilapia and sherry tanks), *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10), and two irrigation systems (bubblers and open pipes)

Multifactor analysis for number of branches		
Source	F-ratio	P-value
Main effects		
A: Water treatment	12.57	$p < 0.001$
B: Genotype	1.35	NS
C: Irrigation system	1.20	NS
Interactions		
A*B	3.39	$p < 0.001$
A*C	2.95	0.0352
B*C	9.42	$p < 0.001$
A*B*C	3.58	$p < 0.001$

tests revealed the differentiation among water treatments and genotypes but not between the two irrigation systems (Table 16.3). In particular, analyses showed that plant height was high (40.6 cm on average for all salicornia genotypes and both irrigation systems) under canal water irrigation compared to the rest of the water applications, followed by 35.5, 26.6, and 37 cm for seawater and aquaculture effluents from tilapia and sherry, respectively. In addition, ICBA-2 and ICBA-3 plants were taller, 36 and 37.9 cm, respectively, compared to ICBA-9 and ICBA-10 plants, 32 and 33.7 cm, respectively (on average for all water treatments and types of irrigation systems). Finally, the type of irrigation system, bubblers and open pipes, did not show significant differences among plant height values (34.3 and 35.6 cm, respectively, on average for all salicornia genotypes and water treatments).

16.3.3.2 Impact of Different Treatments on Number of Branches

Number of branches was significantly affected by all the treatments and their interactions but not by irrigation system and by salicornia genotype (Table 16.4). As expected, average values differentiated among water treatments; however, no similar observations were made

Table 16.5 Multiple range tests among levels of each factor: water treatments (seawater, canal water, and effluents coming from tilapia and sherry tanks), *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10), and two irrigation systems (bubblers and open pipes) based on multifactor analysis for number of branches. The same letter implies that the treatments are not significantly different ($LSD_{0.05}$)

Number of branches					
Water treatment	Comparison between water treatments	Genotype	Comparison between genotypes	Irrigation system	Comparison between irrigation systems
Tilapia	A	ICBA-9	A	Bubblers	A
Seawater	B	ICBA-10	A	Open pipes	A
Sherry	B	ICBA-2	A		
Canal	C	ICBA-3	A		

among genotypes and between the two irrigation systems (Table 16.5). In particular, multiple range tests revealed that number of branches received the highest values under canal water irrigation among the rest water applications. However, no clear trend was observed among salicornia genotypes and between bubblers and open pipes. Specifically, analyses showed that number of branches received the highest value under canal water irrigation (33 branches on average for all salicornia genotypes and both irrigation systems) compared to the rest of the water applications, 28, 26, and 30 branches for seawater and aquaculture effluents from tilapia and sherry, respectively. ICBA-2, ICBA-3, ICBA-9, and ICBA-10 developed 30, 30, 29, and 28 branches, respectively (on average for all water treatments and types of irrigation systems), so no significant differentiation was observed among salicornia genotypes. Finally, the type of irrigation system, bubblers and open pipes, did not differentiate number of branches (30 and 29 branches, respectively, on average for all salicornia genotypes and water treatments).

16.3.3.3 Impact of Different Treatments on Number of Spikes

Results showed that number of spikes was significantly affected by all the treatments and their interactions apart from salicornia genotype (Table 16.6). Multiple range tests revealed the differentiation among water applications, between the two irrigation systems but not among salicornia genotypes (Table 16.7). In particular, analyses showed that number of spikes received the highest value under canal water irrigation (226 branches on average for all salicornia genotypes and both irrigation systems) compared to the rest of the water applications, 124, 121, and 175 spikes for seawater and aquaculture effluents from tilapia and sherry, respectively. ICBA-2, ICBA-3, ICBA-9, and ICBA-10 developed 161, 170, 152, and 165 spikes, respectively (on average for all water treatments and types of irrigation systems). Finally, the type of irrigation system, bubblers and open pipes, differentiated the number of spikes (146 and 178 spikes, respectively, on average for all salicornia genotypes and water treatments).

Table 16.6 Multifactor analysis for number of spikes taking into account the three main effects and their levels: water treatments (channel, seawater, and tilapia and sherry effluents), *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10), and two irrigation systems (bubblers and open pipes)

Number of spikes		
Source	F-ratio	P-value
Main effects		
A: Water treatment	13.60	$p < 0.001$
B: Genotype	0.32	NS
C: Irrigation system	5.84	0.0171
Interactions		
A*B	2.17	0.0283
A*C	3.19	0.0261
B*C	3.91	0.0103
A*B*C	4.29	$p < 0.001$

Table 16.7 Multiple range tests among levels of each factor: water treatments (channel, seawater, and tilapia and sherry effluents), *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10), and two irrigation systems (bubblers and open pipes) based on multifactor analysis for number of spikes. The same letter implies that the treatments are not significantly different ($LSD_{0.05}$)

Number of spikes					
Water treatment	Comparison between water treatments	Genotype	Comparison between genotypes	Irrigation system	Comparison between irrigation systems
Tilapia	A	ICBA-9	A	Bubblers	A
Seawater	A	ICBA-10	A	Open pipes	B
Sherry	B	ICBA-2	A		
Canal	C	ICBA-3	A		

16.3.3.4 Impact of Different Treatments on Seed Weight per Plant

The majority of *S. bigelovii* genotypes produced more seeds per plant under canal water application compared to the rest irrigation treatments (Table 16.8). This observation could be attributed to the fact that canal water is rich in nutrients such as nitrogen. In particular, ICBA-10 genotype outperformed in both bubblers and open pipe irrigation systems producing 23.0 g and 54.3 g/plant, respectively, when canal water was implemented for irrigation. In contrast, the seed weight per plant for the same genotype ranged from 2.7 to 7.6 g under the rest three water treatments and in both irrigation schemes.

In addition, open pipes seemed to favor the higher production of seeds compared to bubbler irrigation system.

16.3.3.5 Oil Content of *S. bigelovii* Genotypes

The oil content values of salicornia seeds ranged from 18.2% w/w (ICBA-10, seawater, bubblers) to 39.4% w/w (ICBA-9, seawater, open pipes) for all genotypes under all four water applications and both irrigation systems (Table 16.9). The seed

Table 16.8 Seed weight per plant (mean ± s.e.) of four *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10) irrigated with four water treatments (canal, seawater, and tilapia and sherry effluents). Two irrigation systems (bubblers and open pipes) were applied

Seed weight per plant (g)								
	Canal water		Seawater		Tilapia effluents		Sherry effluents	
S. bigelovii genotype	Bubblers	Open pipes	Bubblers	Open pipes	Bubblers	Open pipes	Bubblers	Open pipes
ICBA-2	25.8 ± 6.4	5.2 ± 1.5	7.4 ± 2.1	16.3 ± 5.4	4.7 ± 1.0	3.2 ± 0.4	6.5 ± 2.1	18.5 ± 5.5
ICBA-3	27.4 ± 3.6	13.6 ± 4.7	5.8 ± 2.5	27.8 ± 5.5	3.7 ± 0.9	4.2 ± 1.7	8.5 ± 2.2	3.7 ± 0.7
ICBA-9	12.0 ± 6.5	34.2 ± 4.8	5.7 ± 1.5	20.6 ± 8.2	8.3 ± 1.5	14.8 ± 5.2	4.8 ± 0.9	10.0 ± 2.9
ICBA-10	23.0 ± 12.6	54.3 ± 17.1	4.7 ± 2.2	5.8 ± 1.3	7.5 ± 1.9	7.6 ± 2.4	2.7 ± 0.4	5.4 ± 2.0

Table 16.9 Oil content of four *S. bigelovii* genotypes (ICBA-2, ICBA-3, ICBA-9, ICBA-10) irrigated with four water treatments (canal, seawater, and tilapia and sherry effluents). Two irrigation systems (bubblers and open pipes) were applied

Oil content (%w/w)								
	Canal water		Seawater		Tilapia effluents		Sherry effluents	
S. bigelovii genotypes	Bubblers	Open pipes	Bubblers	Open pipes	Bubblers	Open pipes	Bubblers	Open pipes
ICBA-2	28.2	33.2	32.9	26.1	37.3	30.6	34.6	24.8
ICBA-3	29.1	31.3	25.3	34.3	32.0	29.2	33.9	31.1
ICBA-9	31.2	28.1	32.2	39.4	32.3	33.3	37.6	30.2
ICBA-10	27.9	23.5	18.2	34.2	22.0	33.3	38.1	22.6

oil content for salicornia genotypes irrigated with sherry effluents under bubbler irrigation system was comparably higher to other treatments and ranged from 33.9% w/w (ICBA-3) to 38.1% w/w (ICBA-10). Oil content values varied between 24.8 and 37.3% w/w, 29.1 and 34.3% w/w, 28.1 and 39.4% w/w, and 18.2 and 38.1% w/w for ICBA-2, ICBA-3, ICBA-9, and ICBA-10, respectively. ICBA-9 genotype was characterized by the highest average oil content 33%w/w under both irrigation schemes and all four water applications.

16.3.4 Economic Analysis

16.3.4.1 Input Costs

The production system was comprised of fixed costs that did not vary if production was scaled up or down and variable costs that did vary with the amount of land dedicated to salicornia or the number of fish produced. The aquaculture system in Umm Al Quwain has two large concrete tanks that cost a total of $201,848 to install. The irrigation system costs $53,563, and various other components including preparing new lands for their first agricultural planting cost around $9840. The annualized cost of these components is $9035. The system's variable costs consisted of fish fingerlings, fish feed, pump parts and maintenance, electricity, and labor. The variable costs for the fish came to $28,277 per year and for salicornia $15,595. Thus, the total annualized cost for the system is $52,906.

16.3.4.2 Output Prices

Tilapia is a fish species that grows well in a wide variety of environments, including saline and fresh water. However, due to its ubiquity in fish farms, it is relatively abundant globally and will provide farm gate prices of between 1.30 and 2.70 $/kg. It is possible to harvest tilapia twice per year, so we assume this is the case. Sherry wholesale selling price ranges between $6.20 and $8.50 per kg, so an average of $7 is used. One of the reasons for ongoing interest in salicornia production is the possibility of using it as an input for biodiesel. The oil is reported to be similar in quality and quantity to that of soybeans. As there is no established market for salicornia seeds, we use the price of soybeans as a proxy for the market value. Soybeans wholesale at around $1000 per tonne, so this price is used as a proxy for the value of salicornia seeds. Salicornia tips are a niche gourmet vegetable product known as sea beans or sea asparagus or samphire, among its many monikers. Currently, retailers have either made contracts with specific suppliers or are producing their own supplies of sea vegetables (sources). Recently, 500 g of salicornia tips was selling for £19 in a mainstream British retailer. International trade figures are mainly coming from Israel, although Oman is developing an aquaculture center that is meant to contain a significant salicornia investment. Farmers typically receive between 40% and 60% of the retail price of the fresh product. Assuming the 40% as the low end of the range as a conservative estimate and converting to US currency, the farm price for salicornia tips would be $20 per kg.

16.3.4.3 Net Revenues

Net revenues are calculated as total revenues less total costs. This analysis produces net revenues for the annualized costs of a hypothetical production system consisting of two fish tanks and 1 ha of salicornia. The combinations of production of salicornia seeds or tips are compared to with either two cycles of tilapia or one of sherry production, and the results are summarized in Table 16.10. It is evident that there are no scenarios in which it is economically profitable to produce salicornia for its seed. Seed yields are a fraction of that of soybeans, which results in global yields of between 3 and 30 tonnes per ha (http://www.fao.org/faostat/en/). The highest tip yields were from canal water, roughly doubled the result with water from the fish tanks directly. The nutrient load of the canal water, due to the presence of the mangroves, is assumed to be higher than the water from the fish tanks alone. We have not incorporated the slightly higher harvesting costs for fresh salicornia tips as these would likely be more than compensated for by the high market price. In addition, the salicornia seeds need to be extracted from the plants. The seeds are very adherent to the plant tissue, and there would be additional costs to have seed collection done either manually or automatically. It is likely that the cost of the seed extraction would be higher than that of the harvesting. This reinforces the result of the analysis that the potential value of salicornia lies as a fresh vegetable rather than an oil seed. In this scenario, if we assume the fish tank is working at full capacity of roughly three times the density of the current system, the breakeven salicornia yield is around 1.7 t/ha of tips. Tilapia at three times the density would return $19,278 and sherry $33,075.

16.4 Discussion

This study presented some preliminary data of growing *S. bigelovii* in a coastal desert area in UAE and refers to the first year of experimentation (2015–2016). Results clearly showed that canal water contained more ammonia, nitrite, silicate,

Table 16.10 Benefit-cost analysis for the coastal modular farm cultivating *S. bigelovii* at MERD's experimental station in Umm Al Quwain in UAE. Two scenarios are developed for salicornia use: one for seed production for biofuel purpose and the other one for fresh tip production. All the costs and revenues are calculated in US$. The figures in brackets in the last three columns imply negative net revenues

Water	Salinity (dS/m)	Fixed costs ($)	Variable cost fish ($)	Variable cost *Salicornia* ($)	Total cost ($)	Gross revenue: *Salicornia* seeds ($)	Gross revenue: *Salicornia* tips ($)	Gross revenue: tilapia ($)	Gross revenue: sherry ($)	Net revenue: *Salicornia* tips and tilapia ($)	Net revenue: *Salicornia* tips and sherry ($)	Net revenue: *Salicornia* seeds and tilapia ($)	Net revenue: *Salicornia* seeds and sherry ($)
Seawater	35	18,807	19,555	15,218	53,580	1300	30,000	3213	11,025	9633	(12,555)	(49,067)	(41,255)
Canal water	31	18,807	19,555	15,218	53,580	3200	74,000	3213	11,025	97,633	31,445	(47,167)	(39,355)
Tilapia effluents	31	18,807	19,555	15,218	53,580	1600	36,000	3213	11,025	21,633	(6555)	(48,767)	(40,955)
Sherry effluents	31	18,807	19,555	15,218	53,580	1800	38,000	3213	11,025	25,633	(4555)	(48,567)	(40,755)

and especially nitrate, compared to seawater and tilapia and sherry effluents, and this was reflected at salicornia plants' growth. Salicornia spikes were developed at a faster and higher rate under canal water application compared to the rest irrigation treatments. Plant height, number of branches, number of spikes, and seed weight per plant differentiated under all four water applications. Higher values were observed for salicornia plants irrigated with canal water. *S. bigelovii* genotypes differentiated for plant height, but not for number of branches and spikes. The type of irrigation system that was implemented did not have an impact on plant height and number of branches, but it significantly affected the number of spikes and seed weight per plant. The growth of salicornia plants differentiated under all four water treatments at MERD experimental station. All four salicornia genotypes performed well under the applied irrigation treatments. ICBA-2, ICBA-3, ICBA-9, and ICBA-10 belong to the high-yielding genotypes that were selected after evaluation for several years at ICBA's experimental station, and their good growth potential was also confirmed with the current experiments at MERD (Lyra et al. 2016). Results have shown so far that *Salicornia* is a good candidate halophytic species with high growth potential in coastal desert areas. The drainage water that comes from aquaculture systems is a valuable water source since it contains many fundamental nutrients for plants growth that can be utilized for halophytes crop production. An increase in the fish density (ten times more) should be considered for the next cultivating season to reach at least the minimum commercial scale levels (6–10 kg/m^3), in order to improve the nutrient content in aquaculture effluents and examine the impact on salicornia growth. The following cultivating seasons would give us the opportunity to explore these outcomes and validate the current data.

16.5 Conclusion

Preliminary results suggest that *S. bigelovii* is growing well in a coastal desert area. Especially, canal water was the best water source that boosted salicornia plants' performance due to its higher nutrient content. In order to have more solid and reliable evidence on the dynamics of *S. bigelovii* germplasm and give salicornia plants time to expand their whole growth potential, it is highly recommended to proceed on salicornia sowing at the proper cultivating season (end of October to middle of November). The aim of such seawater-based experiments would be to obtain varieties with high yield and desirable attributes adapted to UAE conditions that could be irrigated with seawater and other highly saline water sources. Given the proper *S. bigelovii* germplasm in combination with suitable agronomic practices, it seems that such halophytic plantations could be economically viable and successful in coastal desert lands. However, additional work following multifaceted approaches should be conducted to explore more the environmental impact of irrigating with saline water resources and to develop feasible economic scenarios of seawater-based production systems.

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Chapter 17
Financial Analysis of Halophyte Cultivation in a Desert Environment Using Different Saline Water Resources for Irrigation

S. M. Robertson, Dionysia Angeliki Lyra, J. Mateo-Sagasta, S. Ismail, and M. J. U. Akhtar

Contents

Abstract Increase in salinity levels poses a threat to many hot and arid farming areas in the Middle East and North Africa region. In some cases, farmers install desalination units to produce freshwater to irrigate high-value crops. However, the produced reject brine is an environmental hazard since it is disposed off in the soil creating a vicious circle of salinity aggravation. The current work focuses on the financial aspect of using the reject brine, generated from reverse osmosis (RO) unit,

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to grow fish (*Sparidentex hasta*, sobaity sea bream) and halophytic species (*Salicornia bigelovii*, *Distichlis spicata*, and *Sporobolus virginicus*) for various uses in an integrated farming approach. Different water treatments (RO brine, RO brine mixed with groundwater, aquabrine, and aquabrine mixed with groundwater) were tested to evaluate their impact on halophytes' growth and production. Irrigating with RO brine resulted in positive net returns for *S. bigelovii*, directed for fresh tips' production, as well as for the grasses *D. spicata* and *S. virginicus*. However, more returns were obtained when RO brine passed through the aquaculture system where it got enriched with more nutrients due to fish waste. Irrigation with brine from the aquaculture system tripled *S. bigelovii* production (23.7 t/ha) and increased returns per ha of approximately US $76,000 over irrigating with RO brine directly, compared to the US $5571 and the US $1884 for *D. spicata* and *S. virginicus*, respectively. Halophytic crops constitute one of the very few sustainable options to improve food and nutrition security in salt-affected regions, contributing in lands' rehabilitation and enhancing farming livelihood income. Halophytes also constitute an imperative component to consider for nutrient-dense production systems such as integrated agri-aquaculture systems (IAAS) implemented in desert environments, and the strengths, weaknesses, opportunities, and threats were explored through a SWOT analysis.

Keywords Integrated agri-aquaculture systems · Halophytes · Biosaline agriculture · Desert environments · Benefit-cost analyses

Abbreviations

FC	Fixed costs
IAAS	Integrated agri-aquaculture systems
ICBA	International Center for Biosaline Agriculture
MENA	The Middle East and North Africa
NR	Net revenue
RO	Reverse osmosis
UAE	United Arab Emirates
VC	Variable costs

17.1 Introduction

Desert regions lie within a marginal environmental context being vulnerable to any climate change impact and human exploitation. Pumping of groundwater by farmers for crop irrigation in desert farming areas has resulted in an increase in groundwater salinity due to either saline intrusion in coastal areas or dissolution of minerals in older aquifers (Mateo-Sagasta and Burke 2010; Van Weert and Van Der Gun 2012). As a result, underground water reservoirs are depleting, increasing the salinization effect that impacts negatively crop yield (van Weert et al. 2009; Munns and Tester 2008). The Middle East and North Africa (MENA) region is among the most vulnerable areas to water scarcity and food security issues worldwide (Bucknall et al. 2007). Despite the hot and arid climatic conditions, a wide variety of crops mainly fruits, date palm, vegetables, and forages have been historically produced in the United Arab Emirates (UAE). Due to rising salinity, farmers are now restricted to grow salt-tolerant species such as dates and forages. In order to increase the productivity and profitability of their lands, farmers install small-scale desalination units to remove the salts from the brackish groundwater. As of 2015, between 1 and 2000 farmers in the UAE are estimated to have installed reverse osmosis (RO) units (https://www.moccae.gov.ae/en/home.aspx). However, the systems generate brine as a waste product of desalination process. In the UAE, the brine is generally dumped outside the farm area or injected back in deep aquifers, exacerbating groundwater salinity issues. In order to guarantee the sustainable use of water resources in a desert environment, the management of the reject brine should be adequately addressed.

Innovative production systems that combine different components (agriculture, aquaculture) were developed in farming areas in Brazil (Sanchez et al. 2015), Egypt (Sadek 2011), and Israel (Appelbaum 2011; Hulata and Simon 2011) where farmers installed desalination units to remove the salts from the brackish groundwater and bring abandoned farms into production. In these integrated agri-aquaculture (IAAS) farms, the desalinated water was used to irrigate vegetables, and the reject brine was utilized to grow marine species (fish and algae). Then the water from the aquaculture, enriched in nutrients, was directed to irrigate highly salt-tolerant plants or else halophytes. Production systems that combine agriculture with aquaculture are attracting more and more interest nowadays due to the system's multiple benefits, including water and nutrient recycling, and the potential increase of revenue from various sources (vegetables, fish, halophytes).

17.2 The Necessity to Shift from Glycophytic to Halophytic Plants in Desert Environments

Rhodes grass (*Chloris gayana*) and alfalfa (*Medicago sativa*) have been the major forages in Arabian Peninsula for several decades, but because of high water requirements (15700–48,000 $m^3ha^{-1}year^{-1}$), their popularity has declined in recent years (https://www.moccae.gov.ae/en/home.aspx). Hence, a great opportunity arises to fill in the gap in degraded farms with alternative crops that can be irrigated with saline water sources and produce reasonably high biomass without compromising the nutritional requirements for livestock.

Five halophytic species that have great potential to be cultivated in a biosaline context are the perennial halophytic grasses *Distichlis spicata*, *Paspalum vaginatum*, *Sporobolus arabicus*, and *Sporobolus virginicus* and the annual multipurpose

Table 17.1 Comparison of common animal forages cultivated in desert environments on different parameters: dry biomass (t/ha), crude protein (%), acid and neutral detergent fiber (%)

Salinity tolerance	Forage species	Dry biomass yield (t ha^{-1})	Crude protein range (%)	Acid detergent fiber range (%)	Neutral detergent fiber range (%)	References
Sensitive	*Chloris gayana* (Rhodes grass)	10–16	4–17	35–50	71–81	Feedipedia
Tolerant	*Medicago sativa* (alfalfa or lucerne)	19–29	16–29	26–35	34–44	http://alfalfa.ucdavis.edu/
Halophyte	*Distichlis spicata* (salt grass)	35–47	10–15	28–38	69–78	USDA Plants Database, Bustan et al. (2005), Al-Shorepy and Alhadrami (2008), Sargeant (2009)
Halophyte	*Sporobolus virginicus* (seashore dropseed)	35–40	6–13	33–37	72–80	USDA Plants Database, Al-Shorepy et al. (2010), and Gawad (2015)
Halophyte	*Salicornia bigelovii* (dwarf saltwort) biomass	31–57	2–6	18–28	34–54	Glenn et al. (1992) and Bresdin et al. (2016)

halophyte *Salicornia bigelovii*. The grasses can substitute Rhodes grass showing remarkable ability to grow in salt-affected areas where Rhodes grass does not perform well contributing in land rehabilitation (Rao et al. 2017). *D. spicata* accessions have a crude protein content between 10% and 15% and low acid detergent fiber values from 28% to 38% comparable to alfalfa (Bustan et al. 2005; Al-Shorepy and Alhadrami 2008; Sargeant 2009) (Table 17.1). *S. virginicus* is reported to be combined with other protein sources to improve the protein content as livestock feed (Gawad 2015). There is no side effect on camels' and lambs' health when their diet is composed of at least 66% of *S. virginicus* grass hay (Al-Shorepy et al. 2010; Gawad 2015). *S. bigelovii* has potential as human food, forage, and biofuel. *Salicornia* is currently a niche vegetable crop known commonly as sea bean, sea asparagus, samphire, or glasswort (Feng et al. 2013). The tips are harvested in coastal areas in summer seasons in various parts of the world. Actually, samphire fresh shoots are very popular in the United Kingdom and United States. They can be consumed fresh or pickled and can be found in high-end restaurants as an exotic ingredient. The seeds have potential to be used as a biodiesel stock as they are high in polyunsaturated fats of 23–35%, of which 70% is linoleic acid (Feng et al. 2013). However, after many years of study, this potential is still unrealized, probably because of the lower-cost options such as soybean or rapeseed oils and the technical difficulties for collecting clean seeds. *S. bigelovii* seed meal could be used as animal feed due to its high protein content (42–45%); however, the seeds contain saponins that need to be separated mechanically or neutralized through treatments such as washing or addition of cholesterol (Shahid et al. 2013; Attia et al. 1997). The high salt content of the plant may result in being unappetizing to some animals, although other studies report that it could be included in animal diets. Goats fed with up to 50% *S. bigelovii*/Rhodes grass mixture got more biomass, they did not drink more water, and they gained the same weight as goats fed with Rhodes grass alone (Glenn et al. 1992). Others have found that animals drink substantially more water and eat only a limited amount of the plant due to its high salt content (Swingle et al. 1996). *S. bigelovii* biomass is characterized by low crude protein content of 2–6% (Bresdin et al. 2016) (Table 17.1), whereas *S. bigelovii* seed meal by 34% (Glenn et al. 1992). It also has the favorable content of acid and neutral detergent fiber.

Halophytes constitute indispensable components of farming schemes in hot and dry regions that combine agriculture and aquaculture targeted to enhance food, nutrition, and livelihood security. Such farms offer solutions to already established agricultural communities in salt-affected areas, but it is also possible to grow halophytes implementing seawater-based systems in coastal desert areas which at present are barren. Despite the strong potential of halophytes and the opportunities for use in salt-affected areas, some weaknesses and threats have been identified which are presented in a SWOT analysis format.

17.3 SWOT Analysis of the Halophytic Component as Part of IAAS

17.3.1 Strengths

Halophytes are naturally evolved salt-tolerant plants that can complete their growth cycle in a highly saline environment where the majority of plants would die because of salt toxicity (Panta et al. 2014). One major strength is that such plant species could be utilized to grow with poor-quality, saline water resources such as the reject brine which is generated by desalination process used for agricultural and industrial purposes and even with seawater (Panta et al. 2016). Independent studies in Brazil and Australia showed that the halophytic forage species *Atriplex nummularia*, *A. halimus*, and *A. lentiformis* could be successfully grown using reject brine water from small- and medium-sized inland desalination units used in agricultural areas and in coal seam gas production plants, respectively (Sanchez et al. 2015; Panta et al. 2016). Reuse of aquaculture effluents, enriched in nitrogen and other fundamental elements for plant cultivation, has been extensively applied in freshwater-based integrated agri-aquaculture production systems worldwide (Neori et al. 2004; Stevenson et al. 2010; Kumar et al. 2012). Similarly, annual and perennial halophytes could be added as components in seawater-based aquaculture systems to make use of the saline, nutrient-rich water coming from the aquaculture system as fertilizer (Lyra et al. 2014).

Another critical strength is the fact that only halophytic plants can be used to rehabilitate degraded saline lands and prevent further deterioration of sabkha areas. In the long term, halophyte cultivation constitutes an effective mitigation measure to combat soil salinity and water scarcity in semiarid and arid regions (Khan 2015). Halophytes also contribute in enriching the biodiversity in both inland and coastal salt-affected areas since no other conventional plant can tolerate such adverse conditions (Breckle 2015; Panta et al. 2014). It cannot be disputed that halophytic vegetation at a saline habitat is preferable to a bare wasteland. Iran, Afghanistan, and other countries severely affected by salinity are characterized by rich halophytic flora where versatile halophytes are investigated to serve biosaline agriculture in salt-induced degraded lands giving hope to the local farmers for new sources of income (Breckle 2015; Akhani 2006). Since the commercial production of halophytes is at very initial stages, more sources of revenues for the farmers could be generated by targeting multipurpose halophytes (food, feed, biofuel, medicinal uses) such as *S. bigelovii* and others (Glenn et al. 2013; Panta et al. 2014; Ventura et al. 2015; Lyra et al. 2016).

17.3.2 Weaknesses

Private farmers are reluctant to adopt new cropping systems in their farms because they do not know how to deal with new management practices and agronomic principles. When considering halophyte cultivation, the water management is a very important issue to be adequately addressed in the farm, so that salt buildup in the soil should be avoided (Glenn et al. 2013). In case the soil is not sandy, hence not characterized by high permeability, effective drainage systems should be constructed for removal of excess salts which implies extra infrastructure expenses that farmers are not willing to cover, unless they receive governmental subsidies.

Seasonality is another weakness that characterizes the halophytic vegetables, as large-scale commercialization generally requires continuous availability (Bogemans and Erdei 2012). Seasonality is a determining factor that defines crop prices in the market.

A critical matter that also needs to be considered is the lack of improved genetic halophytic germplasm to be used for large-scale cultivations (Glenn et al. 2013). Very few existing commercial genotypes of halophytic species are products of multiyear selections, whereas for the majority of halophytes with market potential, the germplasm originates from domesticated wild populations. NyPa grass (*D. spicata* var. yensen-4a) is a perennial halophytic forage, and it is the result of

20 years of selections from the Native American grass. Improved *S. bigelovii* accessions were developed after mass selection and cross among individual plants with distinct characteristics in Tucson, Arizona, and Eritrea; however, further improvements are needed to introduce more desirable traits (Zerai et al. 2010).

17.3.3 Opportunities

There are an increasing number of farmers who install desalination units in their farms to remove the salts from the brackish groundwater and produce water of good quality for vegetable irrigation (Sanchez et al. 2015; Mohamed et al. 2005; Ahmed et al. 2001). Considering the importance of reinforcing the water supply in rural communities in semiarid regions, governmental initiatives have been launched such as the "Agua Doce" program in Brazil that has benefitted 150,000 inhabitants so far through small-size reverse osmosis plants' installation (Sanchez et al. 2015). However, the more desalination units are installed, the more reject brine is produced, and the problem with its disposal increases. Reject brine is a by-product from desalination process that has high salt content. An important opportunity arises to grow halophytes with the reject brine, creating an added value to this by-product of desalination. Multipurpose halophytes directed for human consumption, animal forage, and other uses such as *S. bigelovii* could be targeted achieving multiple sources of income. Production of halophytic forages also constitutes a good option to provide feeding for livestock in desert regions. The reject brine could first go through a fish farming unit, and the aquaculture effluents which are enriched in nitrogen could be used for halophyte cultivation boosting the production.

The aquaculture industry is booming, and it is projected that global production will reach 186 million tons by 2030, up from 142 million tons in 2008 (Msangi et al. 2013). This growth should be combined with technologies that improve environmental and economic sustainability. Future farming production systems should be more biodiverse, resilient, and productive especially when marginal environments are targeted for implementation. IAAS and more intensive aquaponic systems have these characteristics since they optimize the use of available water resources, are less dependent on fertilizers, and significantly increase the economic return per water unit (Stevenson et al. 2010). Kumar et al. (2012) evaluated different components of small-scale integrated farms in East India and found that the more diverse the systems were, including crops, fish, and other livestock, the higher their sustainability was. When seawater is used for fish production, the water cannot be reused for conventional crop farming due to high salinity, so halophytes is the only alternative to make use of the aquaculture effluents.

Another opportunity occurs because of different food campaigns that raise public awareness on healthier eating habits and may contribute in creating additional markets for halophytes with high nutritional potential, i.e., quinoa (Panta et al. 2014). Such nonconventional crops may find a niche in novelty food markets while taking advantage of a range of saline irrigation water sources. Additionally, the growing internationalization of the food industry may enable the emergence and expansion of new products that may reach a wider spectrum of consumers.

Finally, there is a big opportunity to make use of abundant desert, barren, unproductive, and even degraded lands to grow halophytes with marginal water resources providing that proper irrigation schemes are incorporated to minimize the salt buildup in the soil.

17.3.4 Threats

One major threat of growing halophytes is the increase in soil salinity after continuous irrigation with reject brine from desalination units. It is a fact that salinity level may progressively rise due to lack of proper drainage system. Sanchez et al. (2015) observed a gradual rise in soil salinity from 0.6 to 8.2 dS/m over a period of 6 years in several regions in Brazil where desalination units were installed, and the reject brine was used for tilapia-*Atriplex nummularia* production scheme. One major challenge for halophyte farming is the water management issue. A leaching fraction is always needed to control salt content in the soil when seawater is used for halophyte irrigation (Glenn et al. 1999). In addition, proper subsurface drainage systems in the soil could also be considered to increase the removal of salts and maintain lands' productivity (Datta et al. 2000).

Another important weakness is that market strategy for halophytic crops is currently inefficient and needed to be developed. Vegetable markets are oriented today toward ease of use and cooking food. Sea vegetables need only some short stir-frying or steaming to accompany a dish (Bogemans and Erdei 2012). Most halophytic crops should be introduced in less developed agro-food markets by deploying different marketing approaches compared to the ones strategized for staple crops. Halophytes are currently sold as fresh vegetables in niche markets where they are locally produced and consumed. Farmers are not aware of the market potential of halophytic crops as novel foods and novel food ingredients, due to nonexistent market strategies of their products. For example, *S. bigelovii* seeds are characterized by high protein and fatty acid content, and they could be used for animal feed and biofuel production. Saponins extracted from *S. bigelovii* seeds may act as antitumor weapons against human acute leukemia cells (Guan et al. 2013). Additionally, the salt produced from its shoots may reduce hypertension compared to table salt (Patel 2016).

17.4 Background Knowledge on the Financial Aspects of IAAS Components

There are limited numbers of studies on the economic evaluation studies of freshwater-based multicomponent production schemes and aquaculture ventures (Adler et al. 2000; Hulata and Simon 2011; Kumar et al. 2012). Different combinations of cultivations (rice, wheat, moong, maize, mushroom) and livestock (poultry, ducks, goats, cattle, fish) were evaluated at a multilocation study in East India (Kumar et al. 2012). The economic analyses revealed that small and marginal farmers could have profit, only when they are practicing integrated farming approaches. The production scheme crop + goat + duck + fish combination was the most profitable one compared to others with fewer components. Hulata and Simon (2011) observed that the freshwater carp and tilapia production costs per fish unit were much lower when dual-purpose reservoirs (fish stocking and rearing) were used compared to shallow earthen ponds, and the return for the farmer was higher. Parameters such as productivity (t/ha), production costs, gross and net return, capital costs, and depreciation values were considered for both studies. Fixed (FC) and variable costs (VC) were also examined for the economic evaluation of hydroponic production systems and other wastewater treatment options for phosphorus removal in aquaculture effluents (Adler et al. 2000).

Integrated farming systems offer great potential for nutrient-dense food production in desert environments since they can reach high productivity through effective recycling of water and nutrients. Saline water resources, barren lands, and halophytic plants are must-to-consider components in these integrated farming approaches. The challenges related to the economic and environmental sustainability of IAAS increase in this case yet remain unexplored. The introduction of new halophytic crops characterized by a multifaceted profile of uses demands new strategies to be deployed for their market development which is currently very niche. Hence, there is a need to explore the financial viability of halophytes irrigated with saline water resources to design cost-effective large-scale productions. To our knowledge, no financial analysis has been published so far for integrated systems where reject brine from inland desalination units is used for aquaculture and halophyte cultivation.

17.5 Economic Evaluation of the Halophytic Component of an Inland IAAS Implemented in a Desert Environment

An IAAS began operating at the experimental station of the International Center for Biosaline Agriculture (ICBA) in Dubai, United Arab Emirates (UAE), since 2013 in order to explore and add value to the use of the reject brine, the by-product from desalination process, by growing fish and halophytes. Freshwater was produced from an RO unit that desalinated the brackish groundwater (Table 17.2). The unit operates 12 h a day to meet experimental requirements, generating 100 m^3 per day of desalinated water and 150 m^3/day of reject brine. Approximately 100 m^3 of the brine was used to irrigate salt-tolerant forage grasses and halophytes, and the remaining 50 m^3/day was diverted to aquaculture tanks where sobaity sea bream (*Sparidentex hasta*) was raised. The layout of the implemented system is presented in Fig. 17.1. The total surface area is 1 ha. The desalinated water was used to grow winter and

Table 17.2 Salinity levels (ppt) of the water treatments (RO brine, RO brine mixed with groundwater, aquabrine, and aquabrine mixed with groundwater) applied in the IAAS at ICBA's experimental station

Water treatment	Salinity (ppt)
Desalinated	0.2
Groundwater	11.2–19.2
RO brine water	25.6–28.9
RO brine mixed with groundwater	19.5–21.9
Aquabrine water	25.4–25.9
Aquabrine mixed with groundwater	20.7–21.8

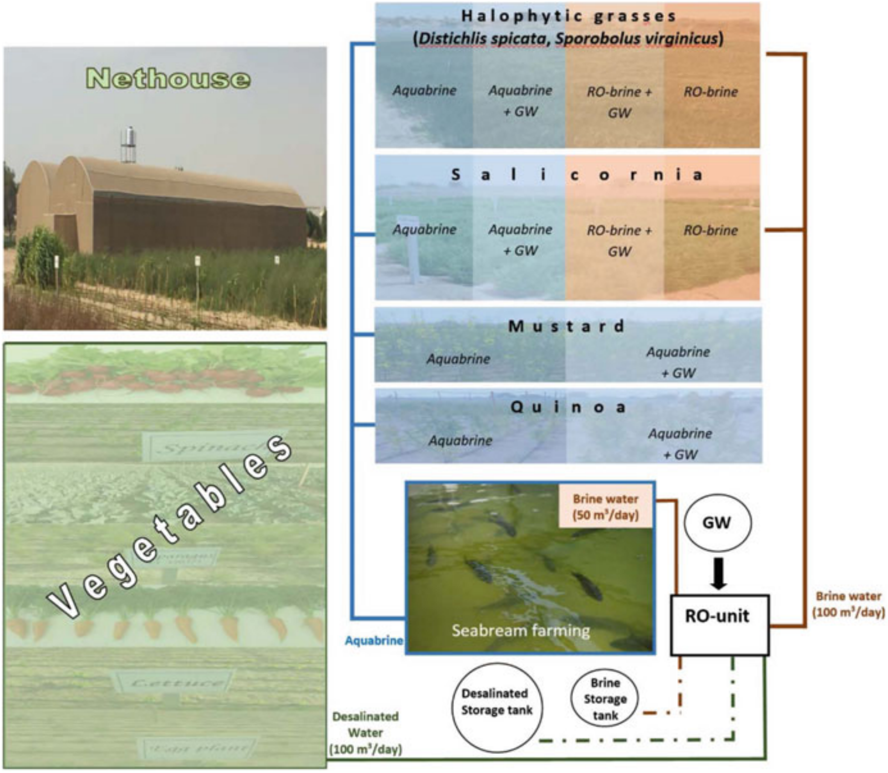

Fig. 17.1 The design of the integrated agri-aquaculture system (IAAS) implemented at ICBA's experimental station

summer crops such as radish, lettuce, spinach, carrot, cauliflower, tomato, eggplant, guar, cowpea, maize, and pearl millet. The vegetables were cultivated in the open field and the net house. *D. spicata*, *S. virginicus*, and *S. bigelovii* were irrigated under four different irrigation treatments: RO brine, RO brine mixed with groundwater, aquabrine, and aquabrine mixed with groundwater (Table 17.2). The first two perennial salt-tolerant grasses were irrigated with sprinkler irrigation system, whereas *S. bigelovii* with bubblers. The financial performance of *D. spicata* and *S. virginicus* was assessed looking into their potential as forage, whereas of *S. bigelovii* as vegetable crop.

Table 17.3 Production costs (US$) for the IAAS at ICBA's experimental station taking into account the following components: land preparation, RO unit, aquaculture system, groundwater pumping, and halophytic seeds. The variable costs of the water are excluded

Cost element	Fixed costs (annualized) (US$)	Variable cost/ha/year (US$)	Total operating cost/ha/year (US$)
Land preparation	220	0	220
RO unit	16,466	25,482	41,948
Aquaculture system	4185	21,976	26,162
Groundwater pumping	220	8491	8711
Seeds	500	0	500

Table 17.4 Variable costs of water/m^3 (US$) for all irrigation treatments (RO brine, RO brine mixed with groundwater, aquabrine, and aquabrine mixed with groundwater) implemented in IAAS at ICBA's experimental station

Irrigation treatment	Water VC/m^3 (US$)
Desalinated	0.70
Groundwater	0.66
Groundwater mixed with RO brine	0.35
RO brine	0.03
Aquabrine	0.03
Groundwater mixed with Aquabrine	0.35

17.5.1 Halophyte Production Costs

The benefit-cost analyses were focused on the halophytic component of the IAAS, and the costs were calculated based on the actual prices and observations of the field station trial plots. The following elements were considered: land preparation, RO unit, aquaculture system, groundwater pumping, halophytic seeds, electricity, and water costs. Costs are shown in Tables 17.3 and 17.4. All values are cited in US$ in 2015 real terms and rounded to the nearest dollar (or cent, where appropriate). Linear depreciation is calculated for each component of the invested FC.

The FC include land preparation involving excavation, establishment of pipe network, and installation of facilities for water and electricity discharge. Land in the UAE has essentially no market value because it is plentiful and completely unproductive without any irrigation infrastructure. UAE citizens who wish to take up farming have only to apply for land ownership from the government. There are no land or income taxes in the UAE, so the sole land costs are to convert desert agricultural land, including tilling. The total amount expended at the research center was $22,000 per ha to prepare the land for agriculture. This cost is amortized over 1000 years as it is a process that would not need to be repeated. There is no salvage value, so the total annualized cost is $22 per year. If we amortized over a smaller timeline, it would just increase the final cost for every treatment tested by some identical amount. This would be relevant for a private firm wanting to calculate return on investment, who would then choose an amortization period based on how long they wished to run their production operation.

The cost of setting up the RO unit included the FC of the unit itself, housing for the unit, associated infrastructure, and two irrigation systems, one for desalinated and the other for saline water. VC for RO unit involved labor expenses, technical support on a weekly basis, and maintenance of the irrigation system and RO unit (replacement of membranes, electric equipment, and pipes). Another start-up costs included the irrigation infrastructure, including pipes, hoses, and bubblers.

The aquaculture system included a concrete foundation where the fish tanks, aquaculture tanks and other storage facilities, net to protect the fish tanks, pump for the aquaculture effluents, and air blowers and diffusers were placed. Annual VC for the aquaculture system include fish fingerlings, fish feed, antibiotics, drugs, and labor.

FC for groundwater consisted of the pumps and irrigation system for water supply and maintenance. The costs of pipes, valves, tubes, and buster pumps were included as FC for the irrigation system, whereas the recurrent costs were directly linked with its maintenance. Data include all capital investment costs as well as labor and other VC of operation. Electrical costs were considered for all the necessary parts required to run and maintain the system.

Water is characterized by the highest VC in fish and halophyte production. Thus, the VC were calculated separately and are presented in Table 17.4. Costs reflect electricity costs to run pumps, irrigation networks, and infrastructure for mixing and storing water, as well as labor expenses to run the system.

17.5.2 Halophytes' Profitability

The wholesale values for salicornia as a fresh vegetable are not widely reported. This is because it is most often wild harvested and locally sold in informal markets. Retail prices vary greatly and can be found higher than $20/kg. Revenue data of salicornia tips are reported from a single source in the California fruit and vegetable wholesale market (http://www.produceone.com/). Salicornia's value as an oilseed crop has not yet been established nor has its value as forage. Thus, it is difficult to estimate how close the values would be to other oilseed or forage supplies. Taking into account the data extracted from the very few reports available on salicornia market value, the price for the economic analyses as the vegetable crop was estimated at 4.73 $/kg (Table 17.5).

Revenue data for *D. spicata* and *S. virginicus* are also not available as there is no market for these halophytic forages. In practice, these are found in coastal or otherwise saline areas and are consumed in situ. Value estimates are made from market data for other forage grasses based on comparative nutritional values. The selling price of Rhodes grass and alfalfa is approximately US $350/t and US $400/t, respectively (http://bakhtertrading.com/en/index; https://www.alibaba.com/; https://www.tradekey.com/). The lower nutritional profile of the two halophytes grown

Table 17.5 Yield data and net revenue calculations (US$) for three halophytic crops (*Salicornia bigelovii*, *Distichlis spicata*, and *Sporobolus virginicus*) irrigated with four different water treatments (RO brine, RO brine mixed with groundwater, aquabrine, and aquabrine mixed with groundwater) as part of the IAAS implemented at ICBA's experimental station. The figures in brackets in the last column (NR/ha) imply negative revenues

Halophytic crop	Irrigation treatment	Observed yield per ha (kg)	Price per kg (USD)	Total revenue per ha	Total costs per ha	NR/ha
Salicornia bigelovii	RO brine	7800	4.73	36,894	10,597	26,296
	RO brine mixed with groundwater	9520	4.73	45,029	87,870.	(42,840)
	Aquabrine	23,700	4.73	112,101	9736	102,364
	Aquabrine mixed with groundwater	12,800	4.73	60,544	86,914	(26,370)
Distichlis spicata	RO brine	56,000	0.30	16,800	5905	10,895
	RO brine mixed with groundwater	63,150	0.30	18,945	38,434	(19,489)
	Aquabrine	74,570	0.30	22,371	5905	16,466
	Aquabrine mixed with groundwater	58,860	0.30	17,658	38,434	(20,776)
Sporobolus virginicus	RO brine	63,430	0.30	19,029	5905	13,124
	RO brine mixed with groundwater	48,280	0.30	14,484	38,434	(23,950)
	Aquabrine	69,710	0.30	20,913	5905	15,008
	Aquabrine mixed with groundwater	58,860	0.30	17,658	38,434	(20,776)

indicates that they should sell for a price that is somewhat lower than either. The price of US $300/t is an estimate based on relative nutritional profiles of the various grasses.

The yield data for the halophytes and the net revenue (NR) calculations are presented in Table 17.5 for all the water treatments applied in IAAS. The results clearly showed that the production increased using the aquabrine in all three halophytic crops. In particular, a threefold rise in yields was observed for *S. bigelovii* production when aquabrine was only used (23.7 t/ha) compared to RO brine (7.8 t/ha). NR of production of all three halophytes was positive with RO brine and aquabrine but negative when brine was mixed with groundwater. The NR was higher in all cases, but there is a much larger effect on yields of the aquabrine used for *S. bigelovii* irrigation, where the total increase in NR from using the aquabrine on a hectare of salicornia is over $76,000 more than RO brine alone (Table 17.6). In comparison, the bump in revenues for the grasses is $5571 for *D. spicata* and $1884 for *S. virginicus* when irrigated with aquabrine over irrigation with RO brine. Thus, the aquaculture tanks are shown to function as a supplier of high-quality fertilization.

Few data on *S. bigelovii* yields are available for comparison. Soliman (1991) reported biomass yields of 20 t/ha for an unspecified type of *S. bigelovii* in Kuwait, whereas 18 t/ha of biomass were produced in Mexico (Ladeiro 2012). Shpigel et al.

Table 17.6 Comparison of the net revenues for three halophytic species (*Salicornia bigelovii*, *Distichlis spicata*, and *Sporobolus virginicus*) between RO brine and aquabrine irrigation treatments

Halophytic crop	RO brine (A)	Aquabrine (B)	NR for aquabrine over RO brine (B-A)
Salicornia bigelovii	28,894	104,930	76,036
Distichlis spicata	13,964	19,535	5571
Sporobolus virginicus	16,193	18,077	1884

(2013) utilized *Salicornia persica* as a biofilter to absorb mariculture waste and obtained fresh biomass yields between 17.4 and 26 kg/m^2, which is roughly ten times more than the obtained one at the current study. However, the yield reported in this chapter refers to *S. bigelovii* tips to be consumed as vegetables, and not to *S. bigelovii* biomass produced at a latter growth stage; hence, the numbers are difficult to compare. However, the results presented at the current study are more comparable to those reported by Shpigel et al. (2013) and Soliman (1991), because of the small plot sizes (194 m^2 and 260 m^2, respectively); hence yield extrapolations up to a full ha seem to be overestimated however, and they are indicative of *S. bigelovii* potential at large scale.

The agriculture sector in UAE is supported by hired labor, an additional cost that increases the operational expenses of the IAAS. However, in other regions, where farmers are poorer and off-farm work is unavailable, we assume that labor would come from the farm family and not constitute a cash expense. With few alternatives, the opportunity costs of using family labor to operate the IAAS would be minimal.

Soils in UAE are very sandy (>90% sand) with very low organic matter (Shahid 2009). Due to the fact that the land used for the study was freshly converted to agricultural land, it is assumed that productivity will increase over time as the soil gains organic matter and its structure and properties get enhanced. Improved water-holding capacity leads to better water usage that may reduce the input costs and potentially leads to an increase of the NR.

The inclusion of the aquaculture unit provides a significant increase in revenue for *S. bigelovii*. The financial analysis showed that the marginal costs of producing the halophytic forages and *S. bigelovii* are extremely low when included as an additional component to an existing integrated aqua-agricultural system (looking at the differences in the production costs for the fish and then the marginal costs is how much more we have to spend to include the halophytes). In particular, *S. bigelovii* value is highly relative to the other crops assessed when sold as a fresh vegetable.

17.6 Conclusions and Future Research Opportunities

The results of the financial analysis indicated that there is a high potential of the halophytic components to be incorporated in an integrated farm using the reject brine from desalination units. The IAAS would reduce brine dumping by reusing the water generating additional revenues especially from *S. bigelovii* directed for fresh tips' production irrigated with aquaculture effluents. However, more work is needed to optimize halophytic crops, and fish production and proper marketing approaches and strategy streams should be developed in order to expand the halophytic agro-food markets and realize this income. Although the IAAS appear promising as climate-resilient and nutrient-sensitive farming systems for hot and dry regions, the long-term effect of using saline water source irrigation should be meticulously explored to secure the environmental sustainability of the systems. Future research targets involve the optimization of the management practices for the fresh vegetables and halophytic crops for open-field cultivation and production in simple protected agricultural structures such as net houses. In order to make the aquaculture system more profitable, an increase in the fish density should be further investigated and examine the impact on halophytic yield. The aquaculture unit currently runs at fish density of 6 kg/m^3 with a potential to increase four to five times more. Changing the fish density in the aquaculture unit will change the nutrient load that the aquabrine carries. The optimal size of the integrated aquaculture and halophyte production system also needs to be further studied, looking into the trade-off between the increase of the fish density and changes in halophyte yields due to changes in nutrient loads in the aquabrine. IAAS incorporating halophytic crops constitute one of the very few options to enhance food and nutrition security in salt-affected regions, contributing in their rehabilitation, sustaining local farming livelihoods, and providing a nutrient-dense production system, so any further study on its proper and sustainable management is one step close to its successful implementation.

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Chapter 18

Rhizophora Biomass of Mangrove Swamp Forests and Its Utilization in Energy and Industrial Production: The Case of Malaysia

I. Faridah-Hanum and A. Latiff

Contents

Abstract The mangrove swamp forests are restricted to the sheltered coasts, estuaries and rivers, and they are important habitats for microbes; wildlife, including fishes and shells; and specialized plant forms. Besides being socio-economically important, mangrove swamps also regulate the hydrology, mitigate floods and buffer against saline water intrusion. They are also important sources of biomass for fuelwood and timber resources and provide various produce used by local communities, small and medium industries. It is herein demonstrated that the biomass of two species of mangroves (*Rhizophora mucronata* and *R. apiculata*) in Malaysia have the potential of producing biomass of charcoal and energy production on a small-scale kilns to industries. Despite their importance, mangrove swamp forests are still being cleared for other land uses, mainly aquaculture and agriculture. In light of their recognized values, it is crucial that more suitable areas of mangrove swamp forests are protected for biodiversity conservation and sustainable management purposes. A long-term, systematic and holistic planning would be the incorporation of conservation and forestry objectives as the best means of achieving sustainable forest management of mangroves.

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Keywords *Rhizophora mucronata* · *R. apiculata* · Biomass · Energy · Swamp forest · Malaysia

18.1 Introduction

Mangrove ecosystems offer many ecosystem goods and services which are provisioning, regulating, supporting and cultural. They are vital for the well-beings, food security and protection of coastal communities worldwide and besides being rich in biodiversity are also valuable both economically and ecologically (Chan and Salleh 1987; Chan et al. 1993; Abbott 1994; Othman 1994) (Figs. 18.1 and 18.2). Together with their living biomass, mangrove swamps are carbon-rich, sequestering carbon over millennial time scales hence playing an effective role as global carbon stores and sinks. Mangroves are nurseries or breeding grounds for a variety of aquatic species, and their existence is crucial for large-scale fisheries. The mangroves' physical presence is a form of natural coastal buffer and defence by reducing strong winds, storms and erosion. Mangroves provide high-value timber and excellent fuelwood which have been harvested in sustainable forestry programmes in some countries for a long time (Chapman 1976).

Fig. 18.1 Community is enhanced through sustainable management of mangroves and fisheries resources

Fig. 18.2 Some wildlife in the mangroves

In Peninsular Malaysia the mangrove ecosystems have been recognized as important resources for the coastal communities, especially by the fishermen and small charcoal producers (Chong et al. 1990; Chong and Sasekumar 2002). These communities have been depending on them for their livelihood for many decades, and they live within the mangrove swamp forests or at their fringes. The mangrove aquatic resources have been the important sources of fishes, shrimps, shells and other gastropods for the fishermen, and these productive forests have been providing fuelwood, poles and other building materials for local constructions (Ong 1982; Ong et al. 1995). In particular, poles of *bakau kurap* and *bakau minyak*, *Rhizophora mucronata* and *R. apiculata*, respectively, have been used widely to protect river banks and lake margin from erosion, while the multipurpose *nipah* palms (*Nypa fruticans*) have been providing free services of its parts to the local communities. Social forestry and fishery have been coexisting harmoniously for generations in the mangrove swamps with minimal impact on the ecosystem (Ali et al. 1996; Adeel and Pomeroy 2002).

Realizing the importance of mangroves to the local communities, all state Forestry Departments had taken steps to conserve some mangrove swamp forests as forest reserves and managing them based on good forestry management and practices. In Peninsular Malaysia the total extent of the mangrove forests reserves has been estimated to be about 105,537 ha of which 77.8% is considered productive. While 90% of these swamp forests are found on the more sheltered west coast of Peninsular Malaysia in the states of Kedah, Perak, Selangor and Johor, the remaining

Fig. 18.3 Mangrove Forest in Peninsular Malaysia

ones occur along the more exposed east coast states of Pahang, Terengganu and Kelantan facing the South China sea (Fig. 18.3). The Malaysian Bornean states of Sabah and Sarawak have more mangrove areas, and they are mostly untapped for their socio-economic resources (Table 18.1).

18.2 Mangrove Vegetation

The mangrove vegetation is simple in structure varying from 5 to 25 m in height, depending on the age and evergreen. There are gaps seen usually caused by regular harvestings and lightning strikes in the otherwise closed canopy. The emergent stratum is not obvious except in some areas where the trees were left during harvesting as mother trees, and despite the canopy layer is very clear in most areas, the understorey layer is not well defined, while the ground layer lacks herbaceous and ground flora (Snedaker 1978; Putz and Chan 1986). Many mangrove species are characterized by special roots such as stilt roots and pneumatophores and the viviparous mode of propagation. In spite of being simple in vegetation and community structure, the density of mangrove species has a very high primary production of biomass. However, only in the states of Perak and Johor it is exploited for energy production; those in other states are not fully utilized.

Table 18.1 Extent of mangrove forest reserves (in ha) in Malaysia

State	Total area (ha)	Notes
Johor	25,619	In 1994, it is reported that only 16,659 ha left in the state. Lately more mangroves have been felled in Kukup area for development. A 20-year cycle has been practiced
Kedah	9036	In 1994, it is reported that only 8034 ha left, some have been converted to prawn ponds, while that at Malut has been totally lost to other land use. Much of the mangroves in Langkawi Archipelago has been protected for eco-tourism purposes and those in Merbuk area has been proposed for protection
Perlis	42.9	There are patches of mangrove forests in the area of Kuala Perlis which are important nurseries for the state's economic fisheries activities. All are statelands. Proposed for conversion to a port
Negeri Sembilan	1269	In 1994, it is reported that only 879 ha left; much of the mangroves in the vicinity of Port Dickson have been developed. The poor mangroves at Sungai Linggi are still quite pristine
Pahang	2141	The mangroves are found in the sheltered estuaries and also along the rivers of Sungai Kuantan, Sungai Pahang, Sungai Endau and Sungai Rompin
Perak	40,683	Most are quite intact especially those in the Matang area which are managed sustainably. However, elsewhere in the state, they are not protected and under the statelands
Pulau Pinang	406	Both the mangroves in Penang and Seberang Prai are affected by water pollution. That of Pantai Acheh has been protected
Selangor	26,381	In 1994, it is reported that only 15,090 ha left; that of Jugra and Pulau Ketam have been badly affected by development, while those around Sungai Selangor are pristine, and they are fully protected
Kelantan	Not available	There are patches of mangrove forests at estuaries and river banks in Tumpat and Bachok areas. These are under the statelands
Terengganu	1295	There are patches of mangrove forests at estuaries and river banks, especially in the areas of Sungai Chukai and Kemaman. Those at the Sungai Kemaman are protected as Virgin Jungle Reserve
Melaka	338	There are patches of mangrove forests at estuaries and river banks, and they are not economical
Total for Peninsular Malaysia	105,537	In 1994, it is reported that only 88,731 ha left as pristine areas
Sabah	340,689	Of the total in the state, 23,266 ha are statelands, hence not protected. Much of the mangroves are yet to be exploited
Sarawak	126,400	Of the total, 93,200 ha are statelands; hence they are not fully protected. Much of the mangroves are yet to be exploited
Grand Total	566,856 + 42.8	

18.3 Taxonomic Composition

Watson (1928) had classified the mangroves in Peninsular Malaysia into five vegetation types based on species composition and dominance. They are *Avicennia-Sonneratia* type, *Bruguiera cylindrica* type, *Bruguiera parviflora* type, *Rhizophora* type and *Bruguiera gymnorhiza* type. While these types were very clear a century ago, today they are not distinctive anymore as they have been systematically harvested and disturbed naturally. Chai (1982) included the inland mangroves which gave a better and more comprehensive classification of the mangroves. As for the specific distribution of Rhizophoraceae in Peninsular Malaysia, it is shown by Wan Juliana et al. (2014).

Several authors including Chai (1982) reported there are about 31 plant species which are exclusively found in the mangrove swamp forest, while a total of 51 species are considered non-exclusive or associate species. Worldwide, there are 114 species of mangrove species (Tomlinson 1986), while there are 104 species in Malaysia with only 38 species being exclusive (Japar 1994). Recently, Wan Juliana et al. (2017) reported that there are a total of 119 species of mangrove plants, 105 are exclusive, 65 are non-exclusive and 20 are associate mangroves (Figs. 18.4, 18.5, 18.6, 18.7, 18.8 and 18.9). Compared to other forest types, the structure of mangrove forest is much simpler with lower floristic composition (Wan Juliana and Nizam, 2005).

Fig. 18.4 *Rhizophora apiculata* (Rhizophoraceae)

Fig. 18.5 *Rhizophora mucronata* (Rhizophoraceae)

Fig. 18.6 *Bruguiera gymnorrhiza*

There is not much difference in terms of floristic composition, structure, above-ground biomass and net productivity between the east and west coasts of Peninsular Malaysia except that the flora of the east coast mangroves is poorer and zonation being less obvious as they are not sheltered; the east coast mangroves are exposed to bigger and stronger waves of South China Sea.

A survey on the mangroves of Sementa, Selangor, found 32 plant species with *Avicennia alba* and *Sonneratia alba* being dominant in the *Avicennia* zone (Soepadmo and Pandi Mat Zain 1989). The dominant species in the mixed *Rhizophora* zone are *Rhizophora mucronata* and *R. apiculata*, while and in the *Bruguiera* zone, the dominant species are *Bruguiera cylindrica* and *B. parvifolia*. The total number of stems from zone to zone also differs, ranging from 4189 ha^{-1} in *Avicennia* zone to 13,290 ha^{-1} in the *Bruguiera* zone; the above-ground biomass

Fig. 18.7 *Kandelia* (Berus-berus) Rhizophoraceae

Fig. 18.8 Some common mangrove species

ranges from 124.53 t ha^{-1} in the former zone to 150.78 t ha^{-1} in the latter zone. In another study by Soepadmo and Pandi Mat Zain (1989), a total of 24 species were found from the mangroves of Kuala Kemaman and Kg. Pantai Tinggi, Kemaman (Terengganu) with dominance in *Rhizophora apiculata* and *Bruguiera gymnorrhiza*.

Fig. 18.9 *Nypa fruticans* (Nipah)

A total of 5340 stems per ha was enumerated at Kuala Kemaman with an above-ground biomass of 199.13 t ha^{-1}, while that of Kg. Pantai Tinggi was 3281 t ha^{-1} and 163.10 t ha^{-1}, respectively.

18.4 Mangrove Biomass

Many of the biomass estimates are usually restricted to the above-ground biomass. There are only a few studies of estimates of both the above-ground (AG) and below-ground (BG) biomass productions that have been reported in Southeast Asia (Öztürk et al. 2017). The total above-ground and below-ground biomass accumulation of *Ceriops tagal* in southern Thailand was 1798 gm^{-2} Komiyama et al. (2000). The components of biomass accumulation estimated from stems, branches, leaf, prop roots and below-ground roots were 534, 236, 133, 20 and 875 g m^{-2}, respectively. The below-ground biomass was higher than the above-ground biomass with an AB: BG ratio of 1:05. However, Twilley et al. (1992) found that the above-ground was higher than that of the below-ground biomass in their global estimate of mangrove biomass. The above-ground and below-ground accumulation were 1782 and 1463 g m^{-2}, respectively, which gave the AB:BG ratio of 0.82.

The above-ground biomass accumulation for *R. apiculata* in Peninsular Malaysia ranges from 2700 to 4600 g m^{-2} with a mean of 4090 g m^{-2} (Putz and Chan 1986; Mahmood Hosain 2004). For a comparison, Christensen (1978) had estimated the

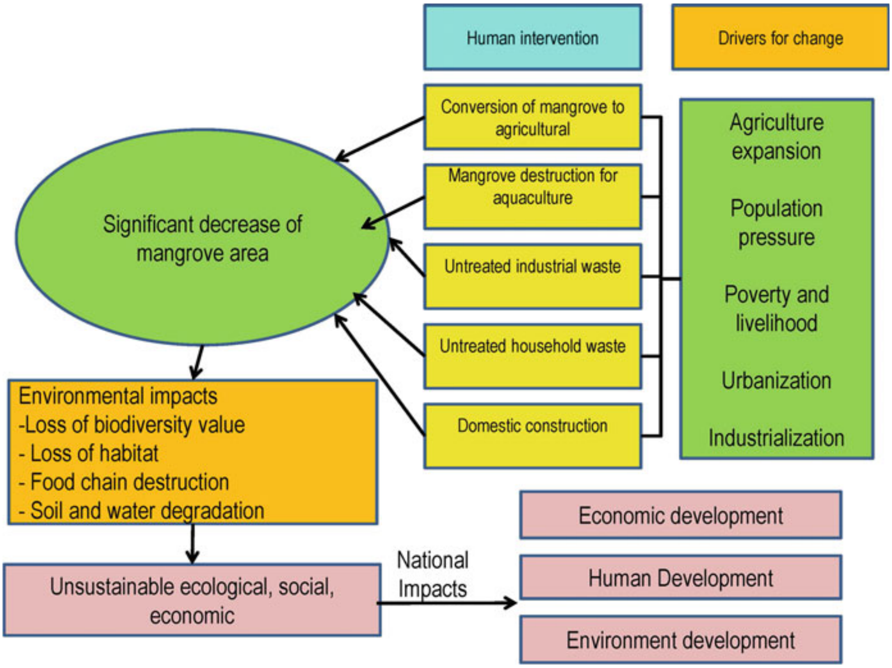

Fig. 18.10 Threats to mangrove and their impacts

primary production of *R. apiculata* in Southern Thailand, as area quite close to Langkawi. Higher values of biomass accumulation occur at lower latitudes throughout the tropical regions (Twilley et al. 1992), This was shown through a model that estimated the distribution of the above-ground biomass of mangrove forests in latitudinal zones where it was fitted to the data resulting in $Y = -7.29(\mathrm{X}) + 298.5$ (R2 = 0.75), where X is latitude and Y is predicted biomass (g m^{-2}).

Mangroves are widely recognized as productive sources of plant debris (Clough 1993). The total above-ground biomass at the Ayer Hangat Forest Reserve and the Kisap Forest Reserve (Langkawi, Kedah) was estimated at 112.3 t ha^{-1} and 117.85 t ha^{-1}, respectively, whereby *R. mucronata* was the main contributor with biomass estimate of 72.65 t ha^{-1} and 68.77 t ha^{-1} at the former and the latter areas, respectively. In other studies, the above-ground biomass were estimated at 115.6 t ha^{-1}, 208.2 t ha^{-1} and 237.7 t ha^{-1} in Langkawi Island, Cape Rachado and Santi Forest Reserve, respectively (Norhayati and Latiff 2001; Norhayati et al. 2005; Wan Juliana et al. 2017). Mangrove forest is a dynamic ecosystem that is sensitive to changes brought about by natural events and anthropogenic activities. Mangrove forests are currently under threat through conversion to other land use especially aquaculture activities, industrial and housing development. Other threats are shown in Figs. 18.10 and 18.11. Therefore, an inventory on mangrove flora, mangrove tree species composition and estimation of above-ground biomass was conducted in Langkawi Island in Kedah, Cape Rachado in Malacca and Santi Forest Reserve in

Fig. 18.11 Example of development seeping into mangroves in Perlis, Peninsular Malaysia

Johor. Sample plots were established to determine the tree species dominance and above-ground biomass estimation (Clough and Scott 1989; Clough et al. 1997). A total of 57, 50 and 26 mangrove plant species were recorded in Langkawi, Cape Rachado and Santi Forest Reserve, respectively. Mangrove plants in the Langkawi Island represented 55% taxa of Malaysia's mangrove species and about 50% of the global total (Wan Juliana et al. 2010). The most dominant species based on Importance Value Index, IV_i was *Rhizophora apiculata* in Langkawi and Cape Rachado, whereas in the Santi Forest Reserve, the *R. mucronata* had the highest IV_i. The most striking findings from all three study sites combined were the occurrence of *Avicennia rumphiana*, *Ceriops decandra*, *Bruguiera hainessi*, *Rhizophora stylosa*, *R.* × *lamarckii* (*R. apiculata* × *R. stylosa*) and *Xylocarpus mekongensis*. All of the species listed were among the rare mangrove species in Peninsular Malaysia.

Basically there are three types of mangrove forests in Malaysia with respect to their socio-economic development, namely, the production forests, the protected forest and the stateland mangroves. Mangroves in the production forests are meant for product harvesting, namely, of the poles for charcoal production, poles for construction and other minor products. The production forests are to be found in the states of Perak, Johor, Sabah and Sarawak. The protected forests are totally protected for biodiversity conservation and erosion protection, and they are found in Kedah, Perak, Selangor, Terengganu, Pahang, Sabah and Sarawak. In fact almost all the mangrove forests in Selangor are under protective forests, and since the last decade, there was no harvesting. In Terenganu five compartments of Sungai Kemaman mangrove forests have been converted to Virgin Jungle Reserves, which augurs very well for biodiversity conservation (Hussain and Ibrahim 2001). The stateland forests are within the jurisdiction of every state to do what they want,

Fig. 18.12 From trees to timber and charcoal

and in many cases they are exploited for aquaculture and agriculture. Normally the stateland mangroves are small in size and not productive at all, as in Perlis, Kelantan, Malacca and Negeri Sembilan.

For the purpose of quantifying the benefits of mangrove forests' biomass in charcoal production and indirectly for socio-economic development, the production forests in Matang Forest Reserves, Perak, are taken as an example (Fig. 18.12). In Matang there are three main production forests, namely, in Kuala Sepetang, Kuala Trong and Sungai Kerang (Table 18.2). The other three localities, namely, Pulau Langkawi, Sementa and Kuala Kemaman, are taken for comparison. From Table 18.2, Matang Forest Reserves alone could produce a total of 5,155,810.74 tonnes of biomass per harvest.

However, in the current practice of mangrove harvesting, only stems and poles from two dominant species, *Rhizophora apiculata* and *R. mucronata*, have been utilized at Matang. Studies at Matang showed that the two species yield 392.61 t ha^{-1} and 211.79 t ha^{-1}, respectively, but the contribution of stems is 223.78 t ha^{-1} and 117.07 t ha^{-1}, respectively. For comparison the mangroves in Compartment 46 of the same forest reserve yielded higher biomass (Table 18.3). For comparison, Sukardjo and Yamada (1992) showed the potential of utilizing biomass and the similar primary production of *R. mucronata* in Java.

In Matang Forest Reserve, the average annual allocation for charcoal production was only between 812 - 835 ha totalling 8289 ha for a duration of 10 years. Awang

Table 18.2 Estimates of mangrove productive forest for energy production in Peninsular Malaysia

Locality	Productive forest (ha)	Extrapolated primary production (tonnes)
Kuala Sepetang, Matang, Perak	15,472	1,943,764.36
Kuala Trong, Matang, Perak	10,139	1,322,644.82
Sungai Kerang, Matang, Perak	7133	905,534.35
Total for the three areas above	**32,744**	**4,171,943.53**
Total for Matang	**40,466**	**5,155,810.74**
Pulau Langkawi, Kedah	3270	376,278.90
Sementa, Selangor	323	40,223.19
Kuala Kemaman, Terengganu	433	7,062.23
Total	44,492	5,579,375.06

Table 18.3 Above-ground biomass of dominant species in mangrove forest harvested for charcoal production

Species	Above-ground biomass (t ha^{-1})	Contribution of stems (t ha^{-1})	Percentage
Rhizophora apiculata at Pulau Kalumpang, Matang, Perak	392.61	223.78	57
Rhizophora mucronata at Pulau Kalumpang, Perak	211.79	117.07	55.28
Rhizophora apiculata at ompartment 46, Matang, Perak	558.00	312.48	56

Noor (2005) had analysed the socio-economic benefits of mangrove biomass in Matang using the existing best practice of production forest. On average the yield of greenwood per ha in an allocated forest is 170 tonnes, and taking into the conversion efficiency of 0.27 (1 tonne of greenwood can produce 0.27 tonne of charcoal), the average yield per ha would be about 212 tonnes, and the average stumpage value per tonne is $2535.00. Taking the total area of 40,466 ha, the possible yield would be 8,578,792 tonnes, and the stumpage value would be $4.5 million per harvest.

To ensure the harvest of mangrove resources remains sustainable or even better, the state Forestry Departments adopt established forestry silvicultural practices. In Malaysia, the Matang mangrove Forest Reserve adopts sustainable harvesting under a formal management regime that has been in operation for over a century in what may be the best example of sustainable tropical forestry silviculture in the world (Gong and Ong 1990). In Matang, mangroves have long been embedded as an industry with high commercial value besides generating wealth and securing long-term employment for the local communities. Thus, for commercial scales, it is deemed important and crucial that relatively large tracts of mangroves are properly managed to comply with the harvest cycles of 30 years old. The current planting and harvesting regimes could be easily adopted based on local conditions where in many cases regeneration is at least partly natural, with no need for nurseries or planting (Janssen and Padilla 1999; Kathiresan and Bingham 2001).

The other states that produce charcoals are Johor, Sabah and Sarawak, whose data on charcoal production are not available for Sabah. Che Hashim Hassan et al. (2005) reported the state of Johor had collected revenue from the mangroves at an average of $3202 per year for the year 1994–2004. Assuming if Johor were to put aside 10,000 ha of its mangrove for charcoal production, the state would generate about 2 million tonnes of greenwood and a revenue of about $5 million. In the early 1970s, Sabah had attempted in the production of chipwood, but at the end it proved uneconomical and disastrous for the mangrove ecosystem and the environment (Ashton and Macintosh 2002; Tangah 2005). For Sarawak, Marajan (2005) had reported in the year 1999–2003 it had produced 2616 tonnes of charcoal. Considering the state has about 126,400 ha of mangroves of which most are within the production forests, the amount of charcoal produced and the revenue generated would be tremendous.

The Matang Mangrove in Malaysia demonstrates an effective balance between harvesting of biomass for charcoal production and conservation. This balance is achieved by adopting a management plan that regulates forestry, fishing and other aquaculture activities. Harvesting of mangrove biomass for poles, firewood and charcoal production occurs on a 30-year rotation cycle, with selective fellings done at year 15 and year 20 and finally clear felled at year 30. Replanting programmes begin 2 years after. It is imperative for the three states above (Johor, Sabah and Sarawak) to follow the practice of sustainable mangrove management for charcoal production like the Matang Mangroves. This way, mangrove forests not only can be conserved but also can provide long-term benefits to the local communities and high economic return to the states.

18.5 Threats and Conservation

The case of the mangroves in the Langkawi Archipelago illustrates the threats and conservation in Malaysia. Over the years, there were many activities that coincided with the declaration of Pulau Langkawi as a free-trade zone in 1985 that demanded the conversion of so-called unproductive forests of mangroves to other more economic enterprises. Among these significant and detrimental activities were the conversion of Malut Forest Reserve to fishing landing port, the development of eco-tourism facilities at Kisap and Kilim areas, the conversion of mangrove areas at Tanjung Rhu for hotels and also that of Pasir Tengkorak for some tourism facilities. With the conversion to other land uses, there was a declining trend in the size of mangroves in Pulau Langkawi; it decreased from a total of 4,165.29 ha in 1988 to 3,902.85 ha in 1993 and 3,764.97 ha in 1999. In total, Pulau Langkawi lost 400.32 ha or 36.39 ha per year of mangroves in just over a decade. A 5-year interval studies (1988–1993) showed some 6.3% of the total mangrove areas were deforested, and in the next interval (1993–1999), another 3.53% was further deforested. With all the activities and threats to the mangrove forests on Pulau Langkawi, it was appropriate that a certain area of mangroves be set aside for conservation, and in 2004 the Kisap-Kilim area which represented mangrove vegetation on shallow limestone substratum, a unique feature in Malaysia, and perhaps in South-East Asia, was proposed as a State Park. However, the idea was surpassed by declaring the area as Kilim-Kisap Geoforest Park under the auspices of UNESCO Global Geopark. Worldwide, Valiela et al. (2001) had argued that mangrove forests is one of the most threatened major tropical environments, and this phenomenon had been demonstrated in tropical Asia (Wolanski 1995; Faridah-Hanum et al. 2014).

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Chapter 19
Halophytic Plant Diversity of Duzdag Area in Nakhchivan Autonomous Republic: Azerbaijan

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Contents

Abstract Based on the typological classification and characteristics of the landscape of the Nakhchivan, the Duzdag lands are characterized by saline soils distributed on some slopes. Salts are accumulated intensively beneath the top soil on the slopes of Duzdag. These play a special role in the establishment of halophytes. In view of this, the flora of Duzdag area of Nakhchivan Autonomous Republic was studied. The phytocoenosis generated by the halophytes in the arid and semiarid desert and heath and among the mountainous xerophytic plants was evaluated. In all 287 species of vascular plants are distributed in the area. The families are dominated by Chenopodiaceae (43 species), Asteraceae (34 species), Fabaceae (18 species), Brassicaceae (17 species), Poaceae (16 species), Apiaceae (14 species), and Lamiaceae (11 species). The ecobiomorphological analysis of the plant diversity has revealed that xerophytes (172 species) dominate the area among the ecological groups. The populations of the species of plants such as *Capparis herbacea*, *Salvia limbata*, and *Daucus carota*, which are spread throughout the main phytocenological complexes of natural plants and used for medicinal purposes, are distributed here. The dynamics of annual productivity has been determined. The ecophytocenotic characteristics and ontogenetic features of every species forming the genetic spectrum were noted together with the state of cenopopulations. The *Daucus carota* topsoil is 313 ha/kg, and underground portion is 45.5 ha/kg; young fruits in *Capparis herbacea* are 310.1 ha/kg, and mature fruits are 421.1 ha/kg; and topsoil

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of g2 and g3 phases in *Salvia limbata* ranges from 13.158–101.979 ha/kg to 18.641–94.303 ha/kg. The carrying capacity of pastures has been calculated for the area, and ephemeral wormwood groups (overall capacity of phytocoenosis – 375 heads of small cattle, 128 heads of big cattle) of spring associations and phytocoenoses of wormwood formation as winter grazing (capacity – 244 heads of small cattle, 81 heads of big cattle) have accordingly been referred to a group of good-quality pastures.

Keywords The Duzdag lands · Halophytes · Phytocenosis · Fodder and medicinal plants

19.1 Introduction

The protection of nature and effective use of natural resources are one of the most pressing challenges in the world. In order to protect and use plant biodiversity more efficiently, such issues as the study of various ecosystems, gene bank collections, and revealing of innovative routes to the use of helpful plants, shortly biodiversity conservation and reproduction are relevant in capturing attention (Aliyev et al. 2008; Mayer and Tikka 2006). The Nakhchivan has always been of particular interest for the plant diversity richness, with clear distinctions from both Azerbaijan's and other Caucasian botanical-geographical regions (Ibadullayeva 2004; Movsumova 1999; Ibrahimov 2005; Öztürk et al. 2018a, b). Being mainly a mountainous country, vegetation cover in the Nakhchivan area is divided into zones (Hajiyev et al. 2009; Ibrachimov 2007). One of these zones is the Duzdag range, which differs sharply from the soil and vegetation cover and from other places. The Duzdag area is characterized by light-colored (red, grayish, gray-greenish, light-brown, brown), gypsum-rich, clay soils, and these are included in the list of carbonate-sulfate saline soils. Intensive salt layers are spread in the lower layers of the soil, which play a special role in the formation of halophytic plant diversity. Due to inefficient use of the Duzdag lands, which is important for winter grazing, productivity, quality, and capacity of fodder have significantly decreased. There is a need to work out a plan for the restoration of vegetation and soil cover, improvement of pasture productivity, and maintenance of useful fodder species. It is important to record the plant diversity of Duzdag, make phytocenological evaluations of the ecosystems at the population level, and study productivity of pastures and quality of the fodder.

19.2 Physio-geographical Conditions of the Study Area

The Nakhchivan differs from other physical-geographical regions of Azerbaijan by its sharp continental climate. The main factors responsible for such climate in the area are abundant solar energy, complexity in atmospheric circulation, and relief diversity. It should be noted that relief plays a key role in the generation of a modern climate in Nakhchivan, a typical mountainous country. Zangazur and Daralayaz mountains from the east, northeast, and north form borders with the plateaus of Armenia and Iran. The significant distance from the large water basins leads to special climatic conditions in the State. Vertical zonality of almost all physical and geographical elements is observed in the territory. Considering the current relationship between the landscape and climatic zones, the study of the various elements of climate was conducted in accordance with the vertical zonality. There are five climate types in the Nakhchivan area: (1) cold semiarid and steppe climate of dry summers, (2) cold climate of dry and warm summers, (3) dry summers and cool climate, (4) dry summers and cooler climate, and (5) tundras (Babayev 1999).

Cold arid and semiarid climate with dry summers dominates the sloping plains and somewhat low mountainous areas (600–1200 m) along the Araz River. The same condition is observed in the Duzdag lands. Average annual temperature is 10–14 °C, average annual rainfall ranges from less than 300 mm, and the possible evaporation rate is 1200–1400 mm. July is typically the hottest month of the year, with averages reaching 29 °C, January is the coldest month with minus 3–6 °C. The snow cover in the year lasts for 20–40 days.

The second climate type, characteristic for the Duzdag area, is dry and hot. This climate type covers the upper parts of the low mountainous zone and lower parts (1200–1600 m) of the moderate mountainous zone. Average annual temperature is between 8 and 10 °C, average annual rainfall is 300–350 mm, and the possible evaporation rate is 800–1100 mm. July is typically the hottest month of the year, with averages reaching 21–26 °C, and January is the coldest month with minus 5–6 °C. The solar radiation also plays an important role. It is mainly calculated by the number of sunshine hours in the plains and somewhat low mountainous areas of the studied area (average annual values are around 2800 h). It is higher than other regions of Azerbaijan. Annual average sunshine hours observed in the middle mountainous zone of the area (2600 h) is detected only in the plains (the Kura-Aras Lowland, Absheron Peninsula, southeastern Gobustan, Jeyranchol, etc.) and partially low mountainous areas of the country's territory. In the high mountainous zone, it is about 2600 h. Radiation balance, depending on the period and seasons of the year, is maximum with a value of 44–45 in the plains along the Araz, including the Duzdag area, 35–40 in the middle mountain zone, and 20 kcal/m^2 in the highlands. About 50% of annual radiation balance is only for the summer months.

Duzdag region is characterized by light-colored (red, grayish, gray-greenish, light-brown, brown), gypsum-rich clay soils, and these lands are included in the list of carbonate-sulfate saline soils (Zacharov 1939). There a certain amount of gypsum is ongoing on the surface, as well as calcium carbonate accumulation in the process of soil formation and abrasion, which partly emerges from gypsum splitting by the plants. The amount of water-soluble salts in the area has increased in the upper layers relative to the lower layers, and chlorides are completely removed from the upper layers and increasingly observed in the inland.

According to the typological classification and characteristic of the Nakhchivan landscape, it has less splitted sloping plains. Duzdag region belongs to the developed saline soils (Salayev and Aliyev 1991). The northern part of the area is dominated by gray primordial saline soils, and the central and southern parts are fully saline in nature. In the south of the area, salinization is more severe.

Geological and tectonic structure of the Nakhchivan is of great importance in the complexity of the diversity of the landscape. The region covers three primary structures: Sharur-Julfa Anticlinorium, Ordubad Sinclinorium, and Zangezur Anticlinorium. Sharur-Julfa Anticlinorium splits into two secondary anticlinoriums – the Sharur and Julfa – separated by the Nakhchivan pit. Devon, Carbon, Perm, and Triassic sediments are found in the formations of Sharur-Julfa Anticlinorium. In the Nakhchivan pit, the Great Plain, Khock, and Givrag anticlinal folds are noted. These are separated by Duzdag, Taziuchan, and Khinjab sinclinals and are composed of gypsum-saline-terrigenous sediments of the Miocene, mainly involved in the construction of lower mountainous areas (Hajiyev 2009).

Duzdag area is well-known from the early nineteenth century due to its significant deposits of rock and salt. Salt mining area has been explored by geologists since 1830. A total of five stone salt layers have been found, of which only two layers are of industrial importance. These are located in the upper part. The first layer is located between 105 and 178 m below the ground surface, and average thickness of salt is 6 m. The second layer is separated from the first layer by a 6–9-m-thick clay layer, and an average thickness of the salt is 8.6 m. The NaCl content in these deposits is 92.0–98.5%. At present, a sewage sludge with a depth of 100 m and a length of 300 m has been opened, where a sanatorium for the treatment of asthmatic patients has been organized. Salt sprays, which are intensively spread on the bottom of the soil in the slopes of Duzdag, play a special role in the formation of halophytes.

Typical saline soils are visible on the slopes of Duzdag plateau due to the rise of ground water levels and occurrence of salt rocks (Guliyev 2008). Areas exposed to desertification and land degradation have increased from 32% to 41% during the last 30 years. According to 2008 data, more than 10,000 ha of land in these areas are exposed to salinity (Hajiyev and Malikov 1999).

In Duzdag sloping plains (lowlands, plains, hills, etc.) in various relief forms, salt rocks play a key role in the formation of saline habitats along with salt water rich in salt-soluble solutions. Territories of Duzdag are attributed to a typical saline subtype of largely automorphic genetic type. In areas with salinization, clay coating is formed that is characterized by weak vegetation in these zones. Chemical composition is divided into chloride-sulfate and sulfate-chloride sections. In hot, dry climates, salts quickly dissolve. NaCl does not reach deep layers and collects in the top layer. On top of this soil, the salt content is 3.885–6.857%. Groundwater is at a depth of 10–15 m. Desertification in Azerbaijan, including the Nakhchivan, shows different agroecological balance, degradation of lands, and severe erosion of ecosystems in mountainous areas. From the bio-indicators of the area, there is a great potential for land degradation in the desertification process in the area (Ibadullayeva and Nabiyeva 2012).

The absolute altitudes of the poorly fragmented plains of the Duzdag Gorge are between 850 and 900 m. The plains form river cones in the narrow strip of the southwest part, reaching Araz River 5 km long. Depending on the ecological conditions of the area, the clay-saline rocks in the northern part are gray, primitive gray, saline soils, the brown soils observed in the stony eastern part, in the central and southern parts are brown clayey soils. Wormwood-ephemeral groupings and saline plants are spread on these lands. In Duzdag area, between elevations of 800 and 1200 m among the fragmented mountainous and slopy plains, the pebbles are light gray and gray, and it has light chestnut soils. Wormwood and other plants are widespread on these lands. On the slopes of the Duzdag plateau, at altitudes of 1000–1200 m, intensive fragmented arid-denudation low mountainous relief forms are spread. In these areas, gray and saline soils are more commonly found where wormwood and saline plantations are observed.

19.3 Data Analysis

The floristic, phytoecological, and other data published by Hajiyev and Malikov (1999), Movsumova (1999), Ibadullayeva (2004), Güvensen et al. (2006), Ibrachimov (2007), Ibrahimov (2005), Aliyev et al. (2008), Hajiyev et al. (2009), Ghazanfar et al. (2014), Altay and Öztürk (2012), and Öztürk et al. (2008a, b, 2014, 2016, 2017, 2018a, b, c) has been evaluated in this chapter, together with other published records on halophyte diversity.

19.4 Plant Diversity in the Study Area

The total number of vascular plants growing in the study area includes 287 taxa. Two hundred forty-nine are a Dicotyledonous group, 36 belong to the monocotyledonous group. The following families are represented by the largest number of taxa: Chenopodiaceae (43 species, 18%), Asteraceae (34 species, 14.47%), Fabaceae (18 species, 7.66%), Brassicaceae (17 species, 7.23%), Poaceae (16 species, 6.81%), Apiaceae (14 species, 5.96%), and Lamiaceae (11 species, 4.68%). As for the bioecological features of plant cover, there are 32.7% annuals, 3.5% biennials, 49.97% perennial grasses, 1.6% hemi-shrubs, 3.5% dwarf shrubs, 3.8% hemi-shrubs, and 5.3% shrubs in the flora.

An analysis of Duzdag sloping plain flora on the basis of ecological groups mainly, plants with different humidification rates, has been considered, together with season and change of light, heat, and humidity within a day. According to the distribution dynamics on ecological groups of the territorial flora, 172 species are xerophytes (54%). These predominate in the regional flora (Shennikov 1964). There are 26.5% of mesoxerophytes, 11.6% of xeromesophytes, and 7.9% of mesophytes. The geographical analysis was conducted in order to determine the distribution and formation centers of genesis. Genetic origin of species was determined on the basis of geographical elements and the areal types they belong to. There are four species of relict plants in the ancient areal type in the area – *Suaeda dendroides*, *S. salsa*, *Salsola nodulosa*, and *Climacoptera crassa*. Eight main and 27 transition groups are concentrated in 3 classes (Mediterranian, West Asian, and Central Asian) of xerophillic areal type represented by more species (195 species). Most species are distributed on Atropatene (41 species), Irano-Turanian (21 species), Mediterranean Irano-Turanian (22 species), Iran (21 species), and Western Asia (16 species) groups. Turan group of Turan and Saxaro-Iran class of desert areal type is represented by nine species, Eastern Transcaucasia group with two species, and Saxaro-Iran group with one species. *Chenopodium album* includes the cosmopolitan areal type, and *Kochia laniflora* and *Petrosimonia brachiata* include arid areal type. One of the main dominant species in the plant cover of the area is *Artemisia fragrans* which includes adventive areal type. Caucasian areal type includes 28 species like *Callicephalus nitens*, *Xeranthemum longepapposum*, *X. cylindraceum*, *Centaurea behen*, and *Achillea tenuifolia*. *Sisymbrium altissimum* species belongs to heath areal type of the region including Pontic-Sarmat, *Stipa lessingiana* species including Pannon-Sarmat, *Phlomis pungens* including Eastern Mediterranean-Pontic transition group, *Eremopyrum triticeum*, *Catabrosella humilis*, *Ceratocarpus arenarius*, and *Atriplex cana* species including Sarmat group.

Boreal areal type is in the second place for the number of its species. It is represented by 42 species in the area. Holarctic areal elements with 15 species occupy the main place in this areal type. Western Palaearctic is represented by six species, Palaearctic by seven species, and European element by five species. The plants of Duzdag area are formed on the xerophyllous elements of Mediterranean from one side and Iran, Turan, and Western Asia from the other side. The local oborogen species are Atropatan and Caucasian elements. Main plant types in the area are semideserts. The second place is mountain xerophytes representing the half of the areal flora. The elements of this plant type play certain role in semideserts and deserts. Desert plants occupy some locality and a small area here. Heath plants are spread over the mountain zones above 1000 m of Duzdag area. The mesophyte formations in the lowlands near the TV tower called Uchtapa of the Duzdag area have Ephedraceae. These are represented by heath plants. Ephedraceae form an association in pure stands or in mixed ones with xerophytic elements. More than half of the 20–25 components are mixed association including mesophytic elements. There are five plant types: desert, semidesert, mountain, xerophytes, and heath in Duzdag territory.

Desert plants in the region are distributed between 917 and 1000 m altitudes. These are distinguished by plants adapted to harsh environments. Main edificators of phytocenoses in desert plants are shrubs, subshrubs (*Salsola*, *Suaeda*, etc.), and hemi-shrubs. Desert plants in Duzdag territory basically represent dwarf shrub desert formation class. There are two formation groups here (*Salsola dendroides* and *Suaedactum dendroides*). *Salsola dendroides* formation group is formed by *Salsola*, and perennial saline plants inside the desert are represented by *Salsoleta dendroides* and *Alsoletum qemmuscens*.

Salsoleta dendroides formation: It is the main edifactor of the formation in the perennial subshrub reaching up to 170 cm. It is useful species as a fodder plant. During geobotanical studies *Salsoleta dendroides* formation was determined to be represented by the association of *Salsola dendroides*, *Ceratocarpus arenarius*, and horned ephemeral *Salsoleta dendroides* which forms the edifactor and domination of ephemerals. There are also *Anabasis aphylla*, *Halimione verrucifera*, *Atriplex turcomanica*, *Suaeda salsa*, *Petrosimonia glauca*, *Kochia scoparia*, *Poa bulbosa*, *Stipa arabica*, *Bromus scoparius*, *Aristida heymannii*, *Allium atroviolaceum*, *A. rubellum*, and other species in the association. Species composition is very poor, represented by total 20 species. General surface cover of the plant is 25–35%.

Gemmascens dendroides formation: This is the dominant species of formation as dwarf shrub upto 30 m tall, branching from the base. It is a xerophyte plant. Formation in the region is represented by one association – *Girgensohnia Gemmascens dendroides, Girgensohnia oppositiflora*, and *Salsola nodulosa.* The dominant and subdominant species are in the composition of the group. Ephemerals, ephemeroids, and sporadic plants are also involved in the formation of the association. Generally, there are 20–30 species inside the groups that, most of them, are ephemerals and ephemeroids (*Anisantha tectorum*, *Tulipa biflora*, *Gagea bulbifera*, *Eremopyrum distans*, *E. triticeum*, *E. orientale*, *Bromus scoparius*, etc.). The association is represented by a sparse plant. Surface cover of the plant is 30–40%.

Suaedeta dendroides formation group: This formation is represented by *Suaedeta dendroides*. Main dominant species forming the formation are *Suaeda dendroides*, which are grayish-green in color, with many branched dwarf shrubs 25–70 cm high. *Suaeda* plants form groups with ephemerals and ephemeroids in the composition of spring phytocenosis in the winter phytocenosis with *Salsola* plants, not in pure form. One association within the formation of the area is *Suaeda dendroides* + *Anabasis aphylla* + *Petrosimonia brachiata* + *Ephemereta*. The floristic composition of the association is formed by a participation of ephemerals and ephemeroids (*Tulipa biflora*, *Gagea bulbifera*, *Allium* species, *Eremopyrum orientale*, *Bromus scoparius*, *Adonis aestivalis*, *Sisymbrium altissimum*, *Alyssum stapfii*, *Conringia orientalis*, *Agropyron pectinatum*, etc.) except edificators forming the group. The group forms a green cover basically with the participation of ephemerals and ephemeroids in early spring and summer, creating a gloomy background at the expense of sparse saline plant cover toward the end of the summer, in autumn, and in winter. Surface cover of the association has more than 30 species with a cover of 50–60%.

Semidesert plants are spread mainly on foothill zone between 1000 and 1200 m altitude. Wormwood species are found in the form of dwarf shrubs in the formation of semidesert *Juniperus foetidissimum* + *J. polycarpos* + *J. hemispaerica* (various plants, ephemerals, and ephemeroids play the main role in the region). *Artemisia fragrans* is the dominant species in semidesert plant type in the region. It is possible to find this species in all cenoses. *Artemisia fragrans* and *Salsola* plants within the *Artemisieta fragransae* formation have spread in mixed form with ephemerals and ephemeroids. There are four associations dominated by *Artemisia fragrans*: *Artemisia fragrans* + *A. vulgaris* + *Ephemereta*, *Artemisia fragrans* + *Petrosimonia brachiata* + *Climocoptera crassa*, *Artemisia fragrans* + *Salsola nodulosa* + *S. dendroides*, *Artemisietum – Capparosum* association (Fig. 19.1).

Plant cover consisting of ephemerals and ephemeroids in *Artemisia fragrans* + *A. vulgaris* + *Ephemereta* cenosis in spring months predominated by special cover.

Salsoleta dendroides

Artemisia fragrans+ *Petrosimonia brachiata* + *Climocoptera crassa* community

Callicephaleta nitensae

Acantholimon quinquelobum + *Artemisia fragrans community*

Astragalus falcatus + *Achillea tenuifolia* + *Callicephalus nitens community*

Allochrusa versicolor + *Xeranthemum squarrossum community*

Xeranthemum cylindraceae + *Onopordum acanthium community*

Ephedra aurantica + *E. Procera community*

Fig. 19.1 A general look of some plant communities in the study area

Capparis is dominant in the association; *Eremopyrum distans*, *E. triticeum*, *Anisantha tectorum*, *Chamaemelum praecox*, *Roemeria refracta*, *Roemeria hybrida*, and *Adonis aestivalis* are subdominants; and *Geranium tuberosum*, *Gagea bulbifera*, *Iris lycotis*, and *Allium* species are from ephemeroids. Forty-five to 50 plant species are found in this group. General surface cover is 65%.

Artemisia fragrans + *Petrosimonia brachiata* + *Climocoptera crassa* association: The association has spread disorderly as an edifactor. Different species of *Iris caucasica*, *Tulipa biflora*, *Fritillaria gibbosa*, and others are found among them. There are 25 species of plants in the association.

Artemisia fragrans + *Salsola nodulosa* + *S. dendroides* are mainly formed with edifactor of xerophyte plants. Rare species like *Tulipa julia* and *Tulipa biflora* are found in this association, as well as *Climocoptera crassa*, *Halanthium rarifolium*, *Kalidium caspicum*, *Anabasis aphylla*, *Suaeda dendroides*, *S. altissima*, *Halostachys belangeriana*, *Halocnemum strobilaceum*, and *Ceratocarpus arenarius*. The species from *Salsola* plants are also distributed here. *Euphorbia marschalliana*, *E. falcata*, *Peganum harmala*, *Convolvulus arvensis*, *Heliotropium ellipticum*, *Carthamus lanatus*, and *Tribulus terrestris* species are spread disorderly in the association and in mixed form. The composition of association is formed by the participation of more than 50 species.

Capparis herbacea and *Artemisia fragrans* from *Herbacea-Capparis* association formed as an edifactor on open phytocenoses spreading away from each other (a few meters away). *Cousinia macroptera*, *Poa bulbosa*, *P. sinaica*, *Bothriochloa ischaemum*, *Fumaria schleicheri*, and *Stipa* species are also found along with *Salsola* plants among the shrubs. There are more than 20 plant species in the association.

Juniperus foetidissimum + *J. polycarpos* + *J. hemispaerica* (various plants) formation is divided into three sections (*Herbacea*, *Callicephaleta nitensae*, and *Xeranthemumeta cylindraceaes*).

Cappareta herbaceae formation in Duzdag area is found as a combined form with *Capparis herbacea* + *Artemisia fragrans* + *Achillea tenuifolia* and *Artemisia fragrans* + *Capparis herbacea* + *Scorzonera leptophylla* associations.

Herbacea shrubs form open cenosis lying on the ground in the *Capparosum herbacetum* association. There are also *Atraphaxis spinosa*, *Senecio vernalis*, *Lepidium vesicarium*, *Onobrychis subacaulis*, *Koelpinia linearis*, *Chenopodium album*, and *Allium dictyoprasum* species in this group. The group with *Capparis herbacea* + *Artemisia fragrans* + *Achillea tenuifolia* also includes *Artemisia fragrans* + *Capparis herbacea* + *Scorzonera leptophylla* association: structure of this phytocenosis was formed with the participation of *Capparis herbacea* and *Artemisia fragrans* as well as ephemerals and ephemeroids.

Callicephaleta nitensae formation is divided into *Callicephalus nitens* (Fig. 19.1), *Callicephalus nitens* + *Achillea tenuifolia* + *Astragalus falcatus* (Fig. 19.1), *Callicephalus nitens* + *Salvia limbata*, *Callicephalus nitens* + *Szovitsia callicarpa* + *Camphorosma lessingi*, and *Callicephalus nitens* + *Salvia limbata* + *Atriplex turcomanica* + *A. tatarica* associations. General surface cover of groups has participation of 30–50 plant species with 60–70%. Structures of *Callicephalus nitens*

+ *Achillea tenuifolia* + *Astragalus falcatus*, except *Callicephalus nitens* species, are distinguished by bright yellow flowers as an edificator. There are also *Achillea tenuifolia* and *Astragalus falcatus* species observed as second-degree companions, as well as *Chenopodium*, *Atriplex*, *Capparis*, *Carthamus*, *Centaurea*, and *Cephalaria* species dominant in the group.

Other associations are formed by primary or secondary participation of *Salvia limbata*, *Szovitsia callicarpa*, *Camphorosma lessingi*, *Atriplex turcomanica*, and *A. tatarica* species. There are also *Sisymbrium altissimum*, *S. septulatum*, *Conringia orientalis*, *Campyloptera carnea*, *Centaurea behen*, *Astragalus commixtus*, *A. falcatus*, and *Alhagi persarum* species in these groups.

In the *Xeranthemumeta cylindraceaes* formation, the structure of this phytocenosis is divided into *Xeranthemum cylindraceae* + *Onopordum acanthium*, *Xeranthemum cylindraceae* + *Alhagi pseudalhagi* + *Onopordum acanthium*, and *Xeranthemum cylindraceae* + *Salvia limbata* + *Cousinia macroptrea* associations.

Xeranthemumeta species are one of the most commonly encountered species in the region, but its mixed cenosis with other flowers are not in pure form. There are also *Allium rubellum*, *A. materculae*, *A. persarum*, *Alhagi pseudalhagi*, *Carthamus lanatus*, and *C. oxyacanthus*. The species except for *Onopordum acanthium*, *Alhagi pseudalhagi*, *Cousinia macroptrea*, *Salvia limbata*, and *Onopordum acanthium* (Fig. 19.1) form the structure of these groups as an edificator by the domination of *Xeranthemum cylindraceae* species.

Petrosimonieta brachiatae formation includes *Petrosimonia brachiata* + *Atriplex turcomanica* and *Petrosimonia brachiata* + *Climacoptera crassa* + *Seidlitzia florida* + *Gamantus pilosus* associations found in the region. Twenty types of plants are found in the phytocenosis, and most of them are *Salsola* plants.

Gamma plant types are spread between 1000 and 1100 m altitudes in the region. Desert and friganoid elements are found in gamma plant. Unlike phytocenosis of semideserts, there is a phytolandscape formed by dwarf shrubs in the composition of this plant. Taking into account the instability of the plant cover in the region, there are clear differences in the structure of plant groups depending on sloping of mountain downhills as well as land structure.

One formation class, two formation groups, and four associations are present in the formation of gamma plant. *Acantholimon quinquelobum*, *Halothamnus glaucus*, *Amblyopogon xanthocephalus*, and *Leontice minor* are dominant species here.

Pillowy shrubs in gamma plant formation group are divided into *Acantholimoneta quinquelobae* and *Amblyopogoneta xanthocephalae* formations. Pillowy groups form the edifactor of dwarf shrub *Acantholimon quinquelobum* in *Acantholimon quinquelobum* + *Artemisia fragrans* (Fig. 19.1) association; the *Capparis* species is a subdominant species found here.

Amblyopogon xanthocephalus + *Artemisia fragrans* + *Leontice minor* association is a pillowy group spread on stone-gravel mountain foothills. Surface cover of the group main characterization poor floristic structure, that forms half-open cenosis by organizing 35–40%.

Ephemeral formation group is represented by *Iriseta lycotae* and *Fritillarieta gibbosae* formation. *Iriseta lycotae* is found in Duzdag area as a rare species spread in the desert and semidesert cenosis. Small location (*Iris lycotis* + *Tulipa biflora* + *Bieberstenia multifida* association) is formed by the species domination within *Iriseta lycotae* formation in qammada plant. Structure of phytocenosis formed with the priority of ephemeroids includes *Iris lycotis*, *Tulipa biflora*, *Bieberstenia multifida*, *Iris caucasica*, *Spinacia tetrandra*, *Geranium tuberosum*, *Matricaria recutita*, and *Artemisia vulgaris*. Structure of the group is very poor with 15–20 species.

In *Fritillaria gibbosa* + *Iris lycotis* + *Bellevalia zygomorpha* association within the *Fritillarieta gibbosae* formation, *Iris caucasica*, *Bellevalia montana*, *Leontice minor*, *Scabiosa rotata*, *Bromus scoparius*, *Koelpinia linearis*, *Senecio vernalis*, and *Ziziphora tenuior* species form ephemeroids spread in the structure of phytocenosis.

Mountainous zone in Nakhchivan forms an independent mountainous halophytic plant zone with mixed transition type of *Capparis* semidesert. Halophytic plants are organized from the open cenosis growing away from each other in vegetation period. These cenoses are formed among the halophytic formations consisting of drought-resistant, thorny shrubs, semishrubs, and perennial grasses which are usally spread on dry, stony slopes.

Mountain xerophyte (phryganon) plants have zonal characters and are spread between 1100 and 1200 m altitudes in the region. Perennial grasses and shrubs are on dry, stony, weakly developed soil-coated friganoids of the region and form 2 formation classes, 3 formation groups, 8 formations, and 12 associations. *Zygophyllum fabago*, *Amblyopogon xanthocephalus*, *Hedysarum formosum*, *Stachys fruticulosa*, and *Astragalus* are seen as main species formed in this type. Except dominants mentioned in all variants of groups, *Euphorbia*, *Achillea*, and *Cousinia* species are widespread.

In frignoid plant, the *Fabago-falcatae* formation group is represented by two formations, *Zygophylleta fabago* and *Astragaleta falcatae.*

In *Zygophylleta fabago* formations, *Zygophylleta fabago* species is an edifactor forming the *Reanmuria-spinosa-fabago* association together with usual *fabago* species *Reaumuria persica* and *Atraphaxis spinosa* in the structure of frignoid plant. *Zygophyllum atriplicoides*, *Thymus kotschyanus*, *Caragana grandiflora*, and *Atraphaxis angustifolia* species are found in the structure of phytocenosis. General cover is 35–50%.

Astragaleta falcatae formation is formed with *Astragalus falcatus* domination divided into *Astragalus falcatus* + *Festuca sclerophylla* and *Astragalus falcatus* + *Acantholimon karelinii* associations. *Crambe armena*, *Ferula oopoda*, *Prangos ferulaceae*, *Salvia limbata*, *Camphorsma lessingi*, *Caragana grandifolia*, *Kochia prostrata*, *Atraphaxis spinosa*, and other species are spread in the cenosis. *Caloplaca cerina*, *Candelariella aurella*, *Fulgensia fulgens*, *Funaria convexa*, *Campylium chrysophyllum*, and *Lecidea subconcava* covers are found in the group.

Salvieta, *Thymus kotschyanus*, and *Stachyeta inflatae* formations are combined in the plant formation group with bushy-grainy features.

Salvieta formation is formed with the domination of *Salvieta* species divided into pure sagy and *Salvia* associations in the region. *Salvia limbata*, *S. hydrangea*, *Bothriochloa ischaemum*, *Stipa caucasica*, *Dracocephalum botryoides*, *Veronica* *microcarpa*, *Bungea trifida*, *Lappula patula*, *Cynanchum acutum*, and other species are spread in the *Juniperus foetidissimum* + *J. polycarpos* + *J. hemispaerica*.

Thymeta kotschyanus formation forms the *Thymus kotschyanus* + *Stipa capillata* and *Thymus collinus* + *Astragalus falcatus* + *Acantholimon karelinii* associations on stony-gravelly mountain foothills. *Stipa*, *Thymus*, *Astragalus*, *Achillea*, and *Allium* species are found in the composition of rare plant-covered phytocenoses. The primitive plants (*Psora decipiens*, *Cladonia turgida*, *C. rangiformis*, and *C. pleurota*) form the sublayer of the group.

Stachyeta inflatae is represented by *Stachys inflata* + *Thymus collinus* + *Th. kotschyanus* + *Acantholimon karelinii* and *Stachys inflata* + *Capparis herbacea* associations.

Woody forms and perennial grass formation group are divided into three formations – *Euphorbieta marschallianae*, *Eryngieta billardieri*, and *Prangoeta ferulaceae*.

Euphorbieta marschallianae formation in the friganoid plant domination of *Euphorbieta marschallianae* group is spread in small area, together with *Euphorbia falcata*. *Euphorbieta marschallianae* is one of the rare species spread in the region found in the semidesert phytocenoses.

Eryngieta billardieri is represented by *Eryngium billardieri* + *Phlomis pungens* + *Herbosa* association. Except the dominant and subdominant species, *Scorzonera papposa*, *S. leptophylla*, *Catabrosella humilis*, *Poa sinaica*, *Matthiola boisseri*, and other species are found in *Eryngium billardieri* + *Phlomis pungens* + *Herbosa*.

Prangos ferulacea + *P. acaulis* + *Dorema glabra* association develops within the *Prangoeta ferulaceae* formation. Small groups with *Prangos acaulis* and *Dorema glabra* species as edificators are formed on the sloping mountain foothills.

Heath plants in Duzdag area are found above 1000 m. *Salsola* plants are found here in two formation classes, four formation groups, four formations, and ten associations. Perennial halophyte plants include *Anabasis aphylla*, *Atraphaxis angustifolia*, *Kochia prostrata*, *Gamanthus pilosus*, and *Salicornia europaea*. Others are found separately or together with *Salsola* plants. *Campylium chrysophyllum*, *Polytrichum commune*, and other species are separately found around the heath mountain foothills with poor plant cover.

In *Stipa* formation group, *Stipa cappilata* constitutes 60% of the cover as pure or spreading form mixed with different grasses with a domination of hairy *Stipa*. *Teucrium polium*, *Agropyron pectinatum*, *Atraphaxis spinosa*, *Stipa capillata*, *S. lessingiana*, *Stachys atherocalyx*, *Thymus kotschyanus*, *Kochia prostrata*, *Verbascum pyramidatum*, *Allium*, *Achillea*, *Lappula*, and *Helichrysum* species are found here. These areas are also used as a winter pasture.

Allochruseta versicolorae formation is represented by *Allochrusa versicolor* and *Allochrusa versicolor* + *Xeranthemum squarrosa associations*, found in *Allochrusa versicolor* formation (Fig. 19.1). *Carthamus lanatus* and *C. oxyacanthus* types and *Artemisia*, *Achillea*, *Allium*, *Verbascum*, and *Xeranthemum* species are more spread in the group. Surface cover of phytocenosis is 60–70%. Garig-type heath formation class is divided into *Atraphaxeta spinosae* and *Ephedreta* formation groups.

Atraphaxeta spinosae formation group is represented by *Atraphaxeta spinosae* formation consisting of *Atraphaxis spinosa* and *Atraphaxis spinosa* + *Caragana grandiflora* associations.

Ephedra aurantica + *E. procera* is defined in *Ephedretaauranticae* formation within the *Ephedreta* formation group (Fig. 19.1).

Generally, as a result of geobotanical studies in Duzdag area, 5 plant types have been defined with a participation of 7 formation classes, 13 formation groups, 24 formations, 46 associations: desert, semidesert, gamma, mountain xerophytes, and heath. Two formation groups: *Zygophylleta-falcatae, Allochruseta;* three formations: *Allochruseta versicolorae, Xeranthemumeta cylindraceaes, Salvieta*; and eight associations: *Salvia limbata-Callicephalus nitens, Xeranthemum cylindraceae* + *Onopordum acanthium, Xeranthemum cylindraceae* + *Alhagi pseudalhagi* + *Onopordum acanthium, Xeranthemum cylindraceae* + *Salvia limbata* + *Cousinia macroptrea, Camphorosma lessingi-Salvia limbata, Salvietum, Allochrusetum versicolorae, Allochrusa versicolor* + *Xeranthemum squarrosa* are recorded from the region by us for the first time.

19.5 Fodder Evaluation

Ephemerous and ephemeroid formations are the main elements in the summer season in the rugged vegetation. These plants are not found in the spring season, also in desert and semideserts, as well as mountain xerophytes, frigate, and steppe vegetation. Pastures observed on the low-sloping slopes with gray brown soils. The fodder crops form the main component of both desert and semidesert cover, as well as mountain xerophyte and steppe vegetation. The average annual productivity in rich cenosis *Suaeda dendroides* + *Anabasis aphylla* + *Petrosimonia brachiata* + *Ephemereta, Artemisia fragrans* + *A.vulgaris* + *Ephemereta, Stipetum*, were studied according to dry mass.

The main dominant ephemerals and ephemeroids in Duzdag area are *Anisantha tectorum*, *Tulipa biflora*, *Gagea bulbifera*, *Eremopyrum distans*, *E. triticeum*, *E. orientale*, *Sisymbrium altissimum*, *Agropyron pectinatum*, *Bromus scoparius*, and *Allium* species. Associations are represented by a sparse vegetation. Ephemerals and ephemeroids play an important role in the summer pastures. *Stipa arabica*, *S. caucasica*, *S. holosericea*, *S. lessingiana*, *Bothriochloa ischaemum* (*Poaceae*), *Alhagi persarum*, and *A. pseudalhagi* (*Fabaceae*) associations play a dominant role. Nearly 34 species of fodder crops, including grains, legumes, and cereals, are also spread in the area. Wormwood, scratch, and watercress are used as a partial or whole feed by animals throughout the year.

The composition of wormwood, salinity, and other formations were analyzed for winter grazing. In the semidesert herbage, the highest rate of differentiation of productivity was observed in the autumn seasons in the diversion-shaped class of flavors developing in the same area. Overall productivity of the formulation was 10.63 s/h. in dry mass (with a coefficient of 1.3–1.6). The productivity of selected wormwood-hawthorn, hawthorn-wormwood, and brown-brown-wormwood associations has been identified within these groups. As a result of our studies on the biochemical composition, productivity, and feed reserve of the vegetation cover areas, the capacity of the pastures was determined. The area of the pastures was calculated as total phytocenosis capacity for 375 small cattle and 128 big cattle and winter grazing capacity for 244 small cattle and 81 big cattle.

19.6 Status of Some Populations as Herbal Drugs

Populations of *Capparis herbacea*, *Salvia limbata*, and *Daucus carota* species are spread throughout the main phytocenological complexes of natural plants and are used for medicinal purposes. Eco-phytocenosis characteristics and ontogenetic properties of each selected species were compiled, and ontogenetic spectrum was studied together with investigating the dynamics of annual productivity by evaluating the status of cenopopulations.

The underground part of the wild carrot *Daucus carota* is raw material for pharmacoseptic processing. Drugs from seeds of wild carrot are used in the treatment of kidney stones diseases, kidney colitis pains, in spasms of the heart (Medicinal plants and their using 1976).

Table 19.1 *Daucus carota* mass on the basis of age (dry weight, gr)

Age	Aboveground mass	Underground mass
im	15.5 ± 1.60	4.97 ± 0.37
v	27.89 ± 4.2	6.55 ± 2.10
g_1	310.1 ± 40.9	13.6 ± 1.33
g_2	568.3 ± 50.3	24.6 ± 2.45
g_3	421.1 ± 40.2	15.78 ± 1.60
ss	67.5 ± 21.5	6.45 ± 0.9
s	62.1 ± 18.9	6.12 ± 0.8

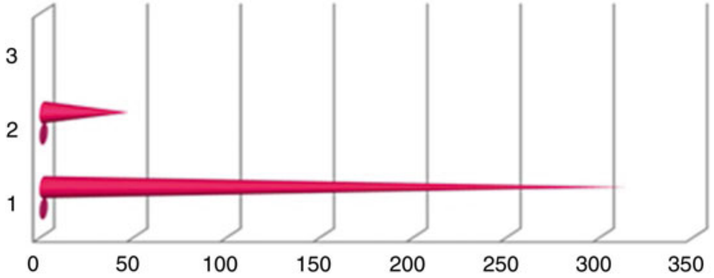

Fig. 19.2 Reserves of *Daucus carota* (dry weight, kg/ha). (1) Aboveground mass, (2) underground mass

Table 19.2 Phytocenological structure of *Capparis herbacea*

Vegetation type	Structure of associations	Cover (%)
Mountain xerophytes	1. *Stachys inflata* + *Capparis herbacea*	35
Semidesert	2. *Capparis herbacea* + *Artemisia fragrans* + *Scorzonera leptophylla*	45
	3. *Capparosum herbacetum*	60
	4. *Artemisia fragrans* + *Capparis herbacea*	30
	5. *Capparis herbacea* + *Artemisia fragrans* + *Achillea tenuifolia*	50

Daucarin extract is spasmolytically effective found in the seeds. Plant brew is used in jaundice, heart attacks, and liver diseases, and root is used in gastritis. Boiled water of the plant is used for bathing children (Nikolaeva 1964). The productivity of the wild carrot in Duzdag area was studied in younger types of first population (Table 19.1). Underground and surface phytomass was calculated at different age periods (Fig. 19.2). It was found that productivity of the species is high in the selected population, according to surface and underground phytomass.

Capparis herbacea is a perennial, semi-aromatic plant, both a medicinal and a valuable wild food plant. Flower buds are used as spice if marinated. In many regions like Caucasus and Dagestan, the local population collects young trees, fruits, and buds for marination. In Turkey only fruits are collected and marinated. In some regions it is harvested for winter, and seeds are also used (Report of working group on medicinal and aromatic plant 2007). The red food color is derived from its fruits. It has 18% protein and 30% fat (Hong-Yen et al. 1982). It is more commonly used in herbal medicine for spleen illnesses. The studied species grows on gray soils, on clay-gravel-salt plains, on the slopes of low mountains, mainly in the steppe, on grassland, and on semidesert vegetation (Table 19.2).

The buds and fruits are very important. However, full-grown fruits are important for medicinal purposes. Abundance in budding and fruiting and full maturation phase in the third population have been studied. The productivity is 310.1 ha/kg, while the adult fruits are 421.1 ha/kg (with age).

Salvia limbata is more interesting as medicinal and essential oil plant. The spasmolytic, bacteriostatic, chill, and anti-inflammatory effects of the plant are due to its flavonoids, organic acids, terpenoids, and other biologically active substances (Ogutcu et al. 2008). The results of the study of phytocenological structure of *S. limbata* species is shown in Table 19.3.

An analysis of phytocenological structure of *S. limbata* species in various populations shows that it is one of the elements of the steppe, grass, semidesert, and mountain xerophyte communities, which are included in the xerophytic ecological group. The surface area of the plant is important as a herbaceous plant; ontogenesis in the g1, g2, and g3 phases has been studied (Table 19.4). In g1, g2, and g3 phases of ontogenesis, high productivity was achieved in the sixth population (94.303–101.979 ha/kg), and in the 1, 8, and 9, the productivity was weak

Table 19.3 Phytocenological structure of *S. limbata* in different populations

Vegetation type and formations	Structure of associations (the main species)	Cover (%)
Semidesert		
1. *Callicephaleta nitensae*	1 cp: *Callicephalus nitens* + *Salvia limbata* + *Atriplex turcomanica*	30
	2 cp: *Callicephalus nitens* + *Salvia limbata*	30
2. *Xeranthemumeta cylindraceaes*	3 cp: *Xeranthemum cylindraceae* + *Salvia limbata* + *Cousinia macroptera*	40
Mountain xerophytes		
3. *Salvieta*	4 cp: *Salvia limbata* + *Camphorosma lessingi*	30
	5 cp: *Salvia limbata* + *Salvia ceratophylla*	40
4. *Zygophylleta fabago*	6 cp: *Zygophyllum fabago* + *Reaumuria persica* + *Atraphaxis spinosa*	50
5. *Stachyeta inflatae*	7 cp: *Stachys inflata* + *Thymus collinus* + *Th. kotschyanus* + *Acantholimon karelinii*	35
Steppe		
6. *Stipeta capillatae*	8 cp: *Stipa capillatae* + *Atraphaxis spinosa* + *Herbosa*	25
7. *Atraphaxeta spinosae*	9 cp: *Atraphaxis spinosa* + *Caragana grandiflora*	20

Table 19.4 Reserves of *S. limbata* in different years (wet weight, ha/kg)

Years	2009		2010	
CP	The number of individuals	Biological reserve	The number of individuals	Biological reserve
1.	45	44.958 ± 4.12	41	51.550 ± 5.14
2.	55	62.503 ± 5.76	57	60.325 ± 6.31
3.	53	55.924 ± 5.23	51	58.117 ± 5.92
4.	52	53.730 ± 5.12	49	57.020 ± 5.56
5.	51	49.344 ± 4.89	45	55.924 ± 5.23
6.	86	101.979 ± 8.45	93	94.303 ± 7.89
7.	41	49.344 ± 4.51	45	44.958 ± 4,23
8.	20	29.606 ± 2,45	27	21.931 ± 2.17
9.	17	13.158 ± 1.57	12	18.641 ± 1.91
Total	420	411.624 ± 40.89	431	462.849 ± 46.67

(13.158–44.958 ha/kg). Some years back (462.849 ha/kg) biological reserves of the plant were very high (411.624 ha/kg).

19.7 Conclusions

The Arazboyu plains of Nakhchivan include the slopes of Duzdag. This is subjected to desertification. The developmental peculiarities, modern status, criteria, and determination of ways to prevent desertification are regularly investigated (Nabiyeva and Ibadullayeva 2012). The studies have revealed that for solving problems, one of the key indicators in low and middle mountain slopes of Duzdag sloping plain is specific areas with synodial manifestation conditions. The structure of plants, vegetation regime, development, and other factors of plant cover should be taken into account for combating desertification. Basically, in desertification areas it is necessary to explore the ecological changes (monitoring), determine the intensity of desertification, and prepare a control measure. To solve the problem, first of all, it is necessary to identify natural and anthropogenic factors of desertification, justify their ecological reasons, the current situation, prediction, and diagnosis of desertification in different ecosystems.

Xerophytes are the main elements of the area's vegetation. It has helped to maintain the floral cover in this area. However, as a result of extreme exploitation, collapse of the soil cover, destruction of natural plants, and overgrazing by cattle pasturing, it has ended up with poor productivity areas, deterioration of hydrological systems, and recirculation of the soil due to drainage irrigation leading to desertification. In the Duzdag area, especially around salt mines, the surroundings are complex, and currently, a hotel is operating it. There is an increased tendency to organize recycling of irrigation. Plants are cultivated here for greenery, but their life is shorter, and these plants dry up quickly.

Factors causing desertification in the slopes of the Duzdag can be grouped as follows: destruction of vegetation and the soil covering as a result of the construction of communals and irrigation, degradation of indigenous vegetation as a result of excessive pasturing, repeated salinization in the case of dryland agriculture, increase of shrub, and salinity in mountainous plains and uninhabited sediments, primarily in the field of mining and ventilation in the mining zone and the variability in climate factors. Every single step of the evolutionary process is characterized by the speed and effectiveness of its consequences, and consequently, it can cause great difficulty. The area of winter pasturing in Duzdag sloping plain has dropped more than half due to several human impacts.

In Duzdag flora, the species of *Chenopodiaceae*, *Asteraceae*, *Fabaceae*, *Brassicaceae*, *Poaceae*, *Apiaceae*, and *Lamiaceae* dominate the area. Ecobiomorphological analysis has shown that phytocenosis, which has been created by the advantage of ecosystems with salinity and drought-resistant Xerophytes (172 species), is spread in the desert, semidesert, gamma, mountain xerophyte, and steppe plants. Populations of species of *Daucus carota*, *Capparis herbacea*, and *Salvia limbata* form useful vegetation in the region. These have been evaluated, and reserves have been calculated. The areas of weeding have been calculated, and ephemerochemical groupings of summer associations (total phytocenosis capacity – 375 small cattles, 128 big cattle) and phytocoenosis such as winter grazing (capacity of 244 small cattle, 81 big cattle) have been attributed to a good-quality group.

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This book was inadvertently published with an incorrect affiliation of Dr. Pooja in chapters 2, 5 and 9. The correction affiliation should read as

Regional Center,
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