# Chapter 3
# Empirical Values of Halophytes in Agro-ecology and Sustainability

**Tayyaba Hussain and Mudassir Khan**

**Abstract** Salinity is an increasingly urgent problem causing tremendous yield losses on a global scale. The problem is a marked imperative in arid and semiarid regions. To maximize crop productivity, and alleviate environmental stress, these areas require either reduction of salinity or the use of salt-tolerant crops. Halophytes are plants capable of normal growth in saline habitats and are able to thrive on "ordinary" soil, though these plants have a capacity to tolerate concentrations over 0.5% throughout their life cycle. As a consequence of rapid climate change, the proportion of saline areas is increasing daily, providing motivations for development of salt-tolerant crops to cope with the adverse conditions and contribute to long-term sustainability goals.

Research efforts are directed toward studying phytoremediation of saline environments in order to efficiently ameliorate salts from both soil and water. Challenges of attaining sustainable environments need to be addressed through mitigating global climate change while enabling a cooperatively sustained food industry. Many features of halophytes are highlighted in this chapter, easing the improvement of salt tolerance in crops in the future. Genetic and physiological screening of halophytes facilitates the contribution of halophytes with respect to long-term environmental sustainability.

**Keywords** Halophytes · Salt-responsive genes · Salinity · Phytoremediation · Environmental sustainability · Crop modification

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## 3.1 Introduction

The word "halophytes" is derived from the Greek prefixes *halo* meaning salt and *phyte* meaning plants. Halophytes are plants which have the ability to survive in habitats containing salt concentrations over 0.5% (Stocker 1928). These plants acclimated growth in natural saline environments, via different mechanistic approaches, and are thus "salt tolerant." More recently, Greenway and Munns (1980) depicted that these plants have the ability to thrive in salt-rich environments in which soil solutions exhibit a minimum of 3.3 bars, which is equal to the presence of approximately 70 mM monovalent salt in the soil. Plants unable to sustain growth in these conditions are coined as non-halophytes (Dansereau 1957). Although only 2% of the world's flora is represented by halophytes, this figure exhibits a limited knowledge of plant diversity. In the course of evolution, plants develop a plentitude of morphological, structural, and physiological changes to flourish in salt-rich environments (Mishra and Tanna 2017). It has been estimated that salinity has a tremendous effect on overall soil biogeography, 10% of the world's land surface is affected, and indeed fertile texture suffers greatly with almost 50% of irrigated land being contaminated (Shah 2018).

Implementations of bio-saline practices in the agro-industry sector have been instigated by the scientific community to mitigate salinity naturally via plants with high salt tolerance adaptability. Glenn et al. (1999) reported different practices which showed the significant impacts of halophytes on agriculture. Principally, it would be conducive to analyze the mechanistic approach of halophyte growth in saline environments, which may be integrated in normal wild plants to develop salt-tolerant cultivars (Serrano 1996; Rausch et al. 1996; Zhu et al. 1997). Consequently, halophytic plants can be used as a standard for evaluation of plants growing in agronomic settings (Glenn et al. 1999). Metagenomic approaches involving genomic alteration and integration of genetic factors of halophytes into other plants pave the way for domestication of transgenic crops (Llerena 1994; Squires 1994; Ashraf et al. 2010).

### *3.1.1 Why Study Halophytes?*

Increased salinization is a major motivation to develop our knowledge of halophytes. Salinization is the process of excessive accumulation of salts. Primarily, salts are sodium, potassium, calcium, and magnesium. These salts slowly leach into the soil and affect the rhizosphere and overall water table. Poor drainage, improper crop rotation, and inadequate farming practices are significant factors which contribute to salinization. High levels of salts occur in droughted areas, especially in arid and semi-arid regions with low annual rainfall (Jolly et al. 2008). There are two categories of salinization, natural and artificially induced. The former is caused by physical/chemical weathering, acid rain, high temperature, and presence of natural geological salt deposits (Xia et al. 2020). The latter is due to inappropriate man-made practices such as improper crop rotation, poor drainage, and supply of salty water to crops. Waterlogging also induces salinization. Ironically, supply of excessive water to respective areas seems the best practice to ameliorate salt from the rhizosphere and flush the soil. However, this practice ultimately causes the leaching of water-soluble salts from the rhizosphere into the groundwater table, rendering agronomic practices difficult to manage and production of food limited in the face of increasing human populations.

Arable area is decreasing gradually due to progressive soil salinization, which ultimately depletes crop productivity to dangerously low levels (Kefu et al. 2002). Munns and Tester (2008) estimated several crop decreases in dry matter production in response to salinity, revealing 50% decreases at 80 mM NaCl for rice (*Oryza sativa* L.); 100 mM NaCl for durum wheat (*Triticum turgidum* ssp. durum); and 120 mM NaCl for barley (*Hordeum vulgare* L).

In northern China salinity poses a serious soil problem, affecting cultivated and native plants (Liu et al. 2002); a widely distributed halophytic species, seepweed (*Suaeda salsa* L.), alleviates salinization. Seeds of seepweed have 30–40% edible oil content, which is considered an ideal source of unsaturated fatty acids. Fresh branches of seepweed are edible as a healthy and fresh vegetable (Kefu et al. 2002; Wang et al. 2001). Hence, environmentally degraded soil may be remediated to an extent through halophyte growth. It is important to cultivate a large number of halophytes to improve environments:in areas of concern. Further, kallar grass (*Leptochloa fusca* L.), a "salt grass," is able to accumulate an average of 20 t $ha^{-1}$ dry matter after 4–5 cuts per year and is considered a useful plant in improving saline-sodic soil conditions to successfully sustain vegetation growth after 5-year periods (Mahmood et al. 1994). Correspondingly, quinoa (*Chenopodium quinoa* L.), grown in Bolivia under suboptimal soil conditions, exhibits low yield potential ($< 0.5$ t $ha^{-1}$), but under optimal conditions its yielding potential can be substantially increased up to 3–4 t $ha^{-1}$ (Adolf et al. 2013). Overall natural and artificially induced salinization compound and endanger the environment. The introduction of salt-tolerant crops provides hope as these plants can take up excess salts from the soil and assist soil rehabilitation. Using halophytes in remediation approaches may also be complemented with production of transgenic salt-tolerant cultivars (Aslam et al. 2011).

The remaining sections of the chapter consider the future prospects and goals of halophytic integration. In Sect. 3.2 objectives of halophytic research are succinctly stated. Strategies implementing salinity treatment are detailed in Sect. 3.3. Section 3.4 discusses distribution of halophytes. Section 3.5 proposes the use of halophyte habitats as natural "laboratories." In Sect. 3.6 adaptation mechanisms and the physiology of salinity avoidance are covered. In Sect. 3.7, ion compartmentalization is detailed. In Sect. 3.8 halophyte screening methods are given. In Sect. 3.9 salt tolerance mechanisms are summarized. Section 3.10 discusses salt tolerance genes. Section 3.11 outlays effective treatment of salinity by halophytes. Section 3.12 mentions the contributions of halophytes in environmental sustainability. Section 3.13 indicates future prospects and functions for halophyte species. Potential techniques for genetic integration of halophytes are covered in Sect. 3.14 and concluding remarks are given in Sect. 3.15.

## 3.2 Mitigation of Salinization

The principle objective of future halophyte research is to introduce salt-resistant cultivars to mitigate salinization. To understand and realize this goal, two research directions are proposed. Firstly, to breed salt-tolerant relatives with wild varieties to induce salt resistance via conventional breeding principles (Flowers 1989); secondly, naturally salt-tolerant plants may be cultivated at domestic levels to ameliorate salinity. Using both of these means, physiological traits and responsible gene functioning against salinity can be identified, which assists in the development of transgenic crops (Epstein et al. 1980).

## 3.3 Strategies of Salinity Treatment Implementing Technological Applications

Treatment of highly saline soils involves different approaches and techniques, which can mainly be separated into two basic categories. Ex situ techniques remediate excavated contaminated soil by different means and potentially includes chemical extraction, thermal treatment, and solidification. In situ techniques are preferred where remediation is carried out with exception of excavation of the contaminated soil. However, ex situ treatment of the soil is more expensive as it requires returning the soil to the restored site after treatment. In situ techniques are favored over ex situ with low cost benefits and minimum impact on the ecosystem (Sauer et al. 1996).

South-west Haryana in India, parts of Rajasthan, and other adjacent areas that comprise the "Thar Desert" found at 27.4695° N, 70.6217° E, in predominantly an arid zone interspersed with saline domains, will benefit from in situ techniques. Saline soil and its native flora have unique biology, enlisted in Table 3.1.

Saline stress is relieved via phytoremediation, which remediates the soil with the use of beneficial microbes and potential halophytes. Biotechnological interventions which enhance phytoremediation play a key role in crop sustainability; among these marker-assisted technology, quantitative trait loci (QTL) mapping, and gene tagging techniques are being adopted in screening and selection of desirable traits in plant genomes (Vera-Estrella et al. 2005; Devi et al. 2017).

**Table 3.1** The native flora of Thar Desert

| Plant | Common name | Family | References |
|---|---|---|---|
| *Salsola baryosma* | Dandy | Amaranthaceae | Sharma and Ramawat (2014) |
| *Zygophyllum simplex* | Zygophyllum | Zygophyllaceae | |
| *Trianthema triquetra* | Horse-Purslane | Aizoaceae | |
| *Tamarix aphylla* | Athel tree | Tamaricaceae | Charan and Sharma (2016) |
| *Portulaca meridiana* | Chickenweed | Portulacaceae | |
| *Zygophyllum simplex* | Zygophyllum | Zygophyllaceae | |
| *Haloxylon recurvum* | Saxaul | Amaranthaceae | |
| *Haloxylon salicornicum* | Rimth saltbush | Amaranthaceae | |
| *Suaeda fruticosa* | Shrubby seablite | Amaranthaceae | |
| *Salsola baryosma,* | Dandy | Chenopodiaceae | |
| *Sesuvium sesuvioides* | Desert pink | Aizoaceae | |
| *Chenopodium murale* | Goosefoot | Amaranthaceae | Rajaram et al. (2006) |

## 3.4 Halophyte Distribution

Diverse halophyte distribution covers 1% of the world's flora, enabling responses to abiotic stress, such as drought stress, saline stress, osmotic stress, habitat, and even stress distribution among taxa of flowering plants (Flowers et al. 2010). Plants which can complete their life cycle at 200 mM NaCl are categorized as halophytes (Flowers and Colmer 2008).

Most Cyperaceae, Poaceae, and Brassicaceae species and also a large number of dicotyledons such as *Aster tripolium*, *Glaux maritima*, and *Plantago maritima* are halophytic. These plants can cope with salty soils in nature when required, though may be indifferent to their habitat in their patterns of distribution. Examples of highly adaptive species are *Myosurus minimus*, *Potentilla anserina*, and *Chenopodium glaucum*, which can grow in any habitat. Many species, such as *Agrostis stolonifera*, *Festuca rubra*, and *Juncus bufonius* populations, live on salty soils with those on salt-free soils varying genetically. The latter indicates that strategically grouped competitive stress-tolerant species have highly adaptable genetic factors which are differentially triggered according to their suitability with the habitat. Halophytes can be classified in terms of ecological factors. Classifications of halophytes are obligate, facultative, habitat-indifferent, and glycophytic (Von Sengbusch 2003) and are shown and defined in Table 3.2.

Saline conditions alter growth patterns. Obligate halophytes require a continuous supply of salt for optimum growth, while facultative halophytes have no such issue and can grow in saline as well as in non-saline condition. Quinoa is a potential facultative halophyte and is able to survive in extreme saline stress. Indeed the species tolerates soil electrical conductivity greater than 40 dS $m^{-1}$. This species has been cultivated since around 3500 years ago for a dietary source (Jacobsen et al. 2003; Razzaghi et al. 2011; Bonales-Alatorre et al. 2013). Obligate halophytes grow in salty habitats only.

**Table 3.2** Types of halophytes and their habitats

| Types of halophyte | Habitat | Examples |
|---|---|---|
| Obligate | Growth in high saline environment<br>Salt concentration greater than 200 mM NaCl | *Arthrocnemum macrostachyum*<br>*Frankenia salina* |
| Facultative | Moderate saline environment, salt concentration approximately less than 200 mM NaCl | *Aster tripolium* L.<br>*Plantago lanceolata* |
| Habitat-indifferent | Can grow in salt-free environment but can grow better as compare to glycophytes | *Salsola imbricate*<br>*Agrostis stolonifera* |
| Glycophyte | Preferably grow in low salt concentrations, less than 100 mM NaCl | *Zea mays*<br>*Vicia faba*<br>*Oryza sativa* |

Domestication of halophytes will inevitably lead to establishment of completely new and artificial agro-ecosystems with cooperative benefits such as the production of highly productive yields of food, fodder, fiber, and fuel while also giving phytoremediation impact, for example, *Vetiveria zizanioides* (Chen et al. 2004). Such an approach may fulfill the needs of rapidly increasing human populations. The major factor behind soil salinization are anthropogenic activities and climatic changes. Halophytes are preferred by governmental bodies to remediate damage caused by salinization of soil and fresh water (Seydehmet et al. 2018; Parnian and Furze 2021).

## 3.5 Habitats of Halophytes as Natural Laboratories

Saline ecosystems remain a research spotlight and their consideration is of ongoing importance for humans. Indeed, many archeologists theorize that the first colonization of the new world was due to pre-Aleut fisher-gatherers swimming along the Pacific “kelp highway” during the last ice age (Pringle 2008). Studies of brown algae beds and its ecology aided our understanding of the key mechanisms of food webs and top-down trophic processes of regulation mechanisms (Welch and Graham 2004).

Bottom-up regulation has been studied in salt deserts in ephemeral alkaline lakes. Allelopathy, its traditional breeding and biotechnological integration, leads us toward understanding of the salinization and desalinization process. It is basically a chemical interaction between living organisms like plants. To exploit allelopathy, we need to study the ecology of competitive bushes in salt semi-desert areas (Woodell et al. 1969; Charley and West 1975). Manipulations of allelochemicals can be managed by root exudation. High concentrations of chemicals are leached out by well-structured irrigation systems (Jabran et al. 2015).

## 3.6 Adaptation of Halophytes to Resist Salinity

Different mechanisms of adaptation have been recognized by studies relating to plant salt tolerance. Adaptations include compartmentalization of ions, production of osmolytes, responses of germination, osmotic adaptation, succulence, enzyme responses, salt excretion, and genetic control (Koyro et al. 2011). Halophytes adapt themselves by establishment of compartments at a cellular level, specifically in vacuoles, where sodium and chloride ions play key role in osmotic adjustment (Flowers et al. 1986). Halophytes secrete a myriad of osmotically compatible solutions which are responsible for osmotic adjustments. Likewise, production of monosaccharides and disaccharides assists halophytes to absorb more water under saline stress conditions (Weber 2009). Potential xerophytic halophytes such as *Haloxylon ammodendron* and *Zygophyllum xanthoxylum* are reported to absorb of high quantities of ions and retain a great amount of water (Wang et al. 2004). Abiotic stress directly interacts with the soil and affects germination rates, which ultimately determine the fate of seed to germinate and the health of the plants. Further rainfall significantly assists in triggering the growth of seedlings through dilution of soil salinity (El-Keblawy et al. 2020). Plant systemic immune systems develop regulatory networks to mitigate salinity stress, seen in ROS production in response to cytotoxicity. In defense processes plants synthesize vital enzymes such as peroxidase, superoxide dismutase, and catalase in turn regulating ROS signaling pathways (Brito et al. 2021). Salt excretion is well adapted by halophytes to balance salinity stress. Similarly, halophytes prefer to excrete salts by glandular tissues present on green leaf. These glands excrete excessive sodium and chloride ions and heavy metals (Wang et al. 2014). Many genes are activated by the influence of salinity stress resulting in product expression of zeaxanthin oxidase, ABA-aldehyde, and 9-cis-epoxycarotenoid dioxygenase (Gorham 1995).

Eco-physiological processes used by tissues and cells of halophytes are common in vascular plants. Halophytes' versatility and phylogeny incorporate novel organisms, salt pan-based agriculture, and phytoremediation (Flowers et al. 2010).

Morphological research and genetic analysis enable exploration of “hidden” species diversity of the sub-halophiles, coastal halophytes, and inland grasslands (Hassan et al. 2016). Understanding diversity leads us to make use of specific genetic factors and background. Biotechnological application furthers development of transgenics. Production of transgenic crops has different applications which potentially enhance both human productivity and ecosystem value. Halophytic transgenic species include developed gourmet vegetables while retaining ornamental qualities or even biofuel uses. Agricultural plants are sensitive to a low amount of sodium chloride. Maas and Grattan (1999) showed soil salinity of lower than 2 dS $m^{-1}$ resulted in a reduction of yield of vegetable species productivity, examples of which are enlisted in Table 3.3.

Basic osmotic adjustment has evolved, despite its polyphyletic origins, through inorganic salt accumulation, NaCl in the vacuole, and organic solutes in cell cytoplasm. Glycophytes and halophytes have variable function ion-transport systems.

**Table 3.3** Reduction of vegetable yield in moderately saline environments

| Plant | Yield reduction |
|---|---|
| *Phaseolus vulgaris* L. | 19% |
| *Capsicum annuum* L. | 14% |
| *Zea mays* L. | 12% |
| *Solanum tuberosum* L. | 12% |

Glycophytes evolved under natural selection pressure adapting to retain low sodium concentration in aerial parts of plants (Cheeseman 2015). In halophytes Na/$H^+$ antiporters are required for $Na^+$ and $H^+$ ion uptake; $Na^+$ ion leakage is prevented by specialized lipid vacuoles (Glenn et al. 1999). *Suaeda maritima* exhibit a large vacuole among halophytes, which occupies 77% of mesophyll cells (Hajibagheri et al. 1984). This feature enables tolerance in higher concentrations of salts with up to 500 mM potential accumulation (Dracup and Greenway 1985). *S. maritima* can bear a concentration of the Na+ in the cell sap that is up to 800 mM.

Salt accumulation varies from species to species. However, a prominent feature of halophytes is their capacity of salt accumulation through a range of strategies (Dajic 1996). Based on different adaptive mechanisms, halophytes are classified as salt excluding, salt excreting, and salt accumulating.

Salt stress can be efficiently relieved by salt exclusion. A low uptake of $Na^+$ at root cortex leads to Na+ ion exclusion (Davenport et al. 2005). Ultra-filtration mechanisms are possessed by such plants; likewise, *Bruguiera gymnorrhiza*, *Kandelia candel*, *Ceriops candolleana*, and *Rhizophora mucronata* have specific characteristics to establish exclusion.

Internal salt levels can be regulated by salt-excreting plants through their foliar glands. Examples of salt-excreting species are *Acanthus ilicifolius*, *Avicennia marina*, *Avicennia officinalis*, *Aegiceras corniculatum*, and *Avicennia alba*. Such plants release salts via salt bladders. These modified cells release salt on the surface of leaves in a liquid form which subsequently becomes crystallized.

Salt accumulators accumulate high concentration of salt and hence overcome toxicity of salt by succulence development. Examples of this are shown by *Sonneratia acida*, *Lumnitzera racemosa*, *Salvadora persica*, *Sonneratia apetala*, *Sonneratia alba*, *Suaeda nudiflora*, *Sesuvium portulacastrum*, and *Excoecaria agallocha*.

## 3.7 Halophytes Are Ion Compartmentalization Specialists

Ion compartmentalization mechanisms are used for salt tolerance and have been explored at the sub-cellular level. Fructose-1,6-bisphosphatase is an enzyme confined to chloroplasts which works more effectively in halophytes compared to glycophytes (Bose et al. 2017). Retention of $K^+$ is achieved without plasma membrane activation. Activation of $H^+$ ATPase in mesophyll cells of halophytes has been demonstrated by ion influx studies. This strategy is very energy efficient among halophytes (Percey et al. 2016). $Na^+$ can be extruded effectively via salt overly sensitive (SOS1) $Na^+/H^+$ antiporters present on plasma membranes. Further $Na^+$ compartmentalized inside vacuoles via Na+/H+ exchangers (NHX) assists in the movement of excessive Na+ ions into vacuoles (Tuteja 2007). NHX is an antiporter of $NA^+/H^+$ present on the tonoplast (Yamaguchi et al. 2013).

*Z. xanthoxylum* is a succulent xerophyte in which the AKT1 (*Arabidopsis* $K^+$ transporter 1) gene has been identified, which is responsible for effective $K^+$ uptake in roots. This plant modulates selective uptake of K and $Na^+$ from roots (Ma et al. 2017). Under salt stress halophytes possess specialized transporters for the homeostasis of ions. In glycophytes salt tolerance can be enhanced by integration of these transporter transgenes (SeNHX1 and PutNHX1 from *Salicornia europaea* and *Puccinellia tenuiflora*). Further cytosolic $K^+$ retention occurs; $Na^+$ sequestration takes place in *Arabidopsis thaliana* (Liu et al. 2017).

Halophytes have the ability to tolerate different ionic concentrations of salts. Ionic stress is reduced by the amount of $Na^+$ which accumulates in the cytosol of cells, though this strategy is confined to plants whose leaves are able to carry out transpiration (Woodrow et al. 2011). True halophytes have developed transport systems which facilitate accumulation of salt in their aerial parts (Dajic 2006). In high concentrations of soil salinity, salt exclusion is achieved by lower permeability of roots (Zhu 2001; Flowers and Hajiagheri 2001). Exclusion of sodium is associated with salt tolerance in glycophytes including barley, rice, and wheat (James 2011). There are a range of different factors which account for exclusion of salts or ions. $K^+$ loading is of greater priority to that of $Na^+$ in the xylem, effectively removing salt from upper parts of xylem, leaf sheaths, and stem (Munns 2002).

Sensation of $Na^+$ ions is detected by receptors of membranes extracellularly, while intracellular sensation is either via enzymes in the cytoplasm which are sensitive to $Na^+$ ions or by membrane proteins (Woodrow et al. 2011). Survival of halophytes is based on refined strategies. Accumulation of compatible solutes under high salt stress occurs (Lee et al. 2008). Moreover, leaf tissues of halophytes are adopted to accumulate high levels of salt ions. This adaptation is crucial for the generation of a water gradient potential along roots and shoots for the maintenance of water flux throughout plants (Silveira et al. 2009; Herbst 2001).

## 3.8 Halophyte Screening

Halophyte planting under similar environmental conditions enables effective comparison (Pasternak 1990). Observations screened over 3 sequential years allow visual observations to be made. Hence 78 plant species showed very good growth even when irrigated with 100% seawater, whereas a further 22 species found to have best growth at 15% seawater were identified (Ventura et al. 2015).

A database named HALOPH was initialized and published by Aronson in 1989. HALOPH included around 1560 species of plants based on the capacity of plant to tolerate salt concentrations of 80 mM NaCl with electrical conductivity 7.8 $dSm^{-1}$.

Thus plants whose growth is inhibited by salt concentration more than 80 mM are termed as glycophytes (Aronson 1989). Halophyte species were able to grow when exposed to irrigation water with an electrical conductivity of 7–8 dS $m^{-1}$. HALOPH was dedicated to provide economic uses of different plant species. The database was modified from the code developed by G.E Wickens and coworkers for the survey of economic plants for semi-arid and arid lands (Wickens 2013). Aronson's data was extended (Menzel and Lieth 2003). An interactive version of the HALOPH database has been compiled recently and can be found at http://www.sussex.ac.uk/affiliates/halophytes (accessed 19 September 2019).

Multiple applications of halophytes are enlisted in Table 3.4.

Scientists collaborate in research efforts on cultivation of halophyte crops, from areas of extremities, with ample rainfall or from dry regions, encountering the inland salt pans and salinity problems in coastal areas.

Different research groups around the globe particularly the Rozema group in the Netherlands (Katschnig et al. 2013; de Vos et al. 2013 ; Rozema and Schat 2013; Koyro et al. 2011), Papenbrock in Germany, Abdelly in Tunisia (Buhmann and Papenbrock 2013), Ksouri et al. (2012), and the Khan research group from Pakistan (Gul and Khan 2003) present halophytes as cash crops. New species are presented with novel growing techniques. Ornamental cultivation of halophyte plants for floriculture or landscaping is still in its infancy. Efforts are directed for improved performance toward testing of glycophytes under salt stress (Cassaniti et al. 2013). The explicit use of halophytes in chemical, food, and ornamental plant-growing industries has also been explored (Koyro et al. 2011). Plants are best suited for raw material in industries; the foremost application of halophytes is bioremediation. In context, selection of improved varieties of halophytes is required for agricultural production, though they are barely domesticated.

"COST Action" has played significant role in utilization of halophytes with novel features for forthcoming agricultural growers and documented online at http://www.cost.eu/domains_actions/fa/Actions/FA0901 (accessed 19 September 2019).

**Table 3.4** Halophytic plant species and their uses

| Scientific name | Uses | References |
|---|---|---|
| *Crithmum maritimum* | Vegetable | Meot-Duros and Magne (2009) |
| | Edible seed oil | Zarrouk et al. (2003) |
| *Inula crithmoides* | Food and fodder | Zurayk and Baalbaki (1996) |
| | Ornamental | Franke (1982) |
| *Atriplex hortensis* | Vegetable | Wilson et al. (2000) |
| *Salicornia*<br>*Sarcocornia* spp. | Biofuel/oilseed crop | Glenn et al. (1991) |
| | Bioremediation | Webb et al. (2013) and Shpigel et al. (2013) |
| | Forage | Glenn et al. (1992) and Imai et al. (2004) |
| | Vegetable | Ventura and Sagi (2013) |
| | Probiotics | Sarker et al. (2010) |
| | Ornamental | Ventura and Sagi (2013) |
| *Pennisetum clandestinum* | Biomass | Muscolo et al. (2013) |

## 3.9 Salt Tolerance Mechanism in Halophytes

Halophytes are well adopted to high stress and have developed a myriad of anatomical and morphological features which assist their survival in saline environments (Grigore et al. 2014). Mechanistic approaches including osmolyte regulation, succulence development, antioxidant responses, and transport of ions via selective permeability to regulate redox reactions play pivotal roles in salinity tolerance. Moreover, signal transduction, ROS generation, and detoxification pathways are coordinately linked with salt tolerance mechanisms. Ion homeostasis (influx and efflux) includes salt tolerance in defense mechanisms. Secretion of osmoprotectants such as glycine, betaine, proline, sugars, polyphenol, and inorganic ions plays an essential role in defense mechanisms in halophytes (Patel et al. 2016; Lokhande and Suprasanna 2012). Defensive approaches against salt stress are often accompanied by salt bladders/glands, cross-talk activating genes, and antioxidant induction. The latter often results in antimicrobial activity (Himabindu et al. 2016; Shabala et al. 2014; Khan et al. 2018). Antioxidative enzymes responsible for ROS detoxification assist in deterioration of toxic radicals (Das and Strasser 2013). Furthermore, halophytes are adapted to secrete excess amounts of salt in the form of liquids, which become solid after exposure to external atmosphere and are subsequently visible to the naked eye on the leaf surface in the form of crystals. Cytosol of halophytes has great potential in managing a high ratio of Na+/K+ ions by initiating the transport of excessive salt into vacuoles (Sreeshan et al. 2014; Kronzucker and Britto 2011).

Figure 3.1 shows a breakdown of salt glands within upper layer of epidermal cells along with modified epidermal cells. With plasmodesmata, these modified epidermal cells accumulate salt from surrounding mesophyll cells and secrete salts onto the aerial surface of leaves.

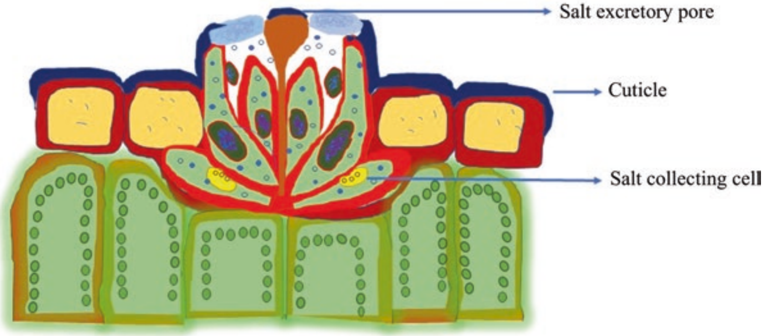

**Fig. 3.1** Longitudinal view of salt glands in salt-tolerant plants

## 3.10 Salt-Responsive Genes and Halophytes

*Salicornia brachiate* is reported as a hyper-accumulator halophyte native to salt marshes and also copes with various abiotic stresses. This species is well known for having stress-responsive promoters and genes which have unique properties and operate in adverse conditions such as salinity and drought stress (Singh et al. 2014; Jha et al. 2011; Chaturvedi et al. 2012; Udawat et al. 2016; Tiwari et al. 2016). Salt-responsive genes are manipulated as transgenes in plants to combat salinity, for example, in cumin, jatropha, castor, and peanuts (Pandey et al. 2016; Joshi et al. 2011). Additionally, *S. bigelovii* is a functional food due to the presence of nutritious metabolites, sugars, and seeds rich in protein and sulfur content. Moreover non-targeting metabolomics, antioxidant, and scavenging properties of *S. bigelovii* enhance its nutritional value (Mishra et al. 2013; Jha et al. 2011). *Porteresia coarctata* has a polyphyletic linkage with wild rice; the former has been reported to have high adaptability against high salt stress. This species has reserved 15,158 genes to control unraveling key metabolic pathways in the context of saline stress and submergence tolerance (Garg et al. 2014; Jha et al. 2012).

Potential uses of halophytes are summarized in Fig. 3.2.

Figure 3.2 shows potential uses of halophytes and their vital role and versatility in environmental sustainability.

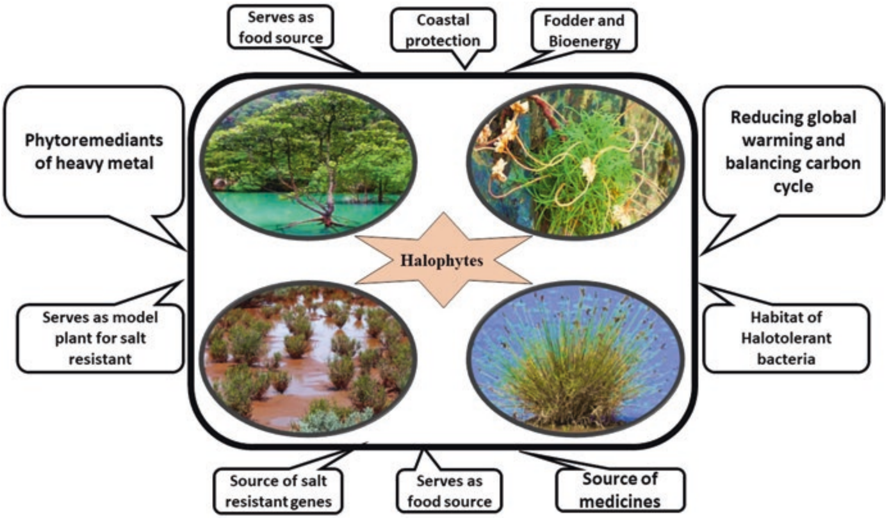

**Fig. 3.2** Potential uses of halophytes

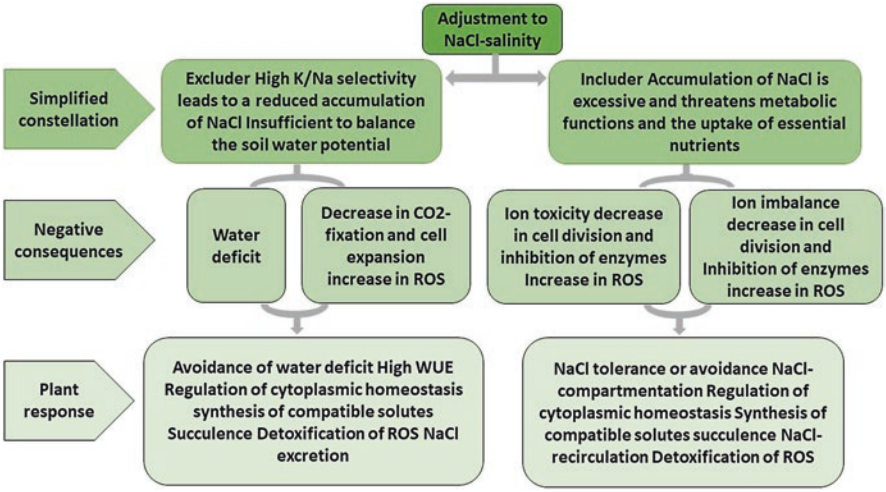

**Fig. 3.3** Adaptation of resistance against NaCl salinity

## 3.11 Treatment of Salinity by Halophytes

In high salt conditions, halophytes are of great importance because of their yield productivity. Satisfactory yield is shown by halophytes under different degrees of salinity (Simpson et al. 2018). The most productive species yield 10–20 t ha biomass after irrigation of seawater; under high salt conditions, oil seed of *S. bigelovii* yields 2 t ha$^{-1}$ of seed containing 31% protein and 28% oil similar to soybean seed oil quality (Glenn et al. 1995).

Figure 3.3 shows a schematic flow of how plants develop resistance to high concentrations of salt/ions and shows us how salinity is regulated going through different stages of simplified constellation, negative consequences, and plant response.

Nutritional barriers may be caused by some halophytes due to partially high antinutritional compounds and high salt contents (Khan et al. 2009). Mechanisms of salinity stress tolerance are detailed in Fig. 3.4.

Figure 3.4 represents a schematic flow of how salt tolerance is established by halophytes; osmotic and ionic imbalance is sensed by receptors which activate different genes in plants.

## 3.12 Halophyte Contribution to Sustaining Environmental Stability

Halophytes possess various mechanisms in order to survive in saline environments as shown in Fig. 3.4. Further, the development of a salt bladder has been reported in approximately 50% species of halophytes (Flowers and Colmer 2008). The salt

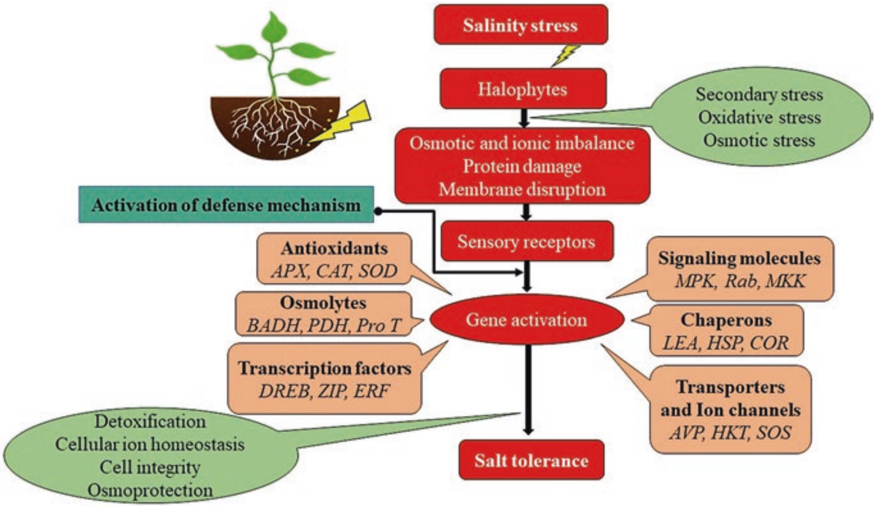

**Fig. 3.4** A generalized schematic representation of salinity stress tolerance mechanism in plants

bladder is derived from epidermal glandular hairs or trichomes. These are characteristics of halophytes with the exception of those in the Pooideae family (Amarasinghe and Watson 1988; Ramadan and Flowers 2004). Findings of Shabala and Mackay (2011) depicted that epidermal bladder cells (EBCs) have a salient impact in sodium ion uptake. This process is aided by a larger size of EBCs ten times greater in size than the normal epidermal and mesophyll cells; these bladder cells assist in desalinization by sequestering 1000 times more sodium ions through each EBC channel. Bladder development is conducive to mitigate salinity issues along with water loss reduction (Adams et al. 1998).

Phytoremediation is considered as an effective amelioration strategy by several researchers for calcareous saline-sodic soils against the use of chemical amendments with comparable performance (Singh et al. 1989; Qadir et al. 1996; Ahmad et al. 1990). Besides their positive impact on salt-affected soils, some halophytes can be potentially used as oil seed crops and forages (Qadir et al. 2007). Halophytic plants can also be used to desalinate water and soil, as was firstly suggested by Boyko (1966).

## 3.13 Future Prospects

Phytoremediation is an environmentally sound technology and is cost-effective for remediation of saline soil, given it is properly developed. In the wake of this issue, applications of halophytes best practice are seen in not only desalinization/remediation but also in the agriculture/agroecological sector as in the forage industry (Erakhrumen and Agbontalor 2007). It is imperative to select plants which have ability to reduce salt concentration from the soil with high biomass yield depicted in Table 3.2. Such plants are selected for phytoremediation ability and tolerate high saline environments. Molecular knowledge of tolerance mechanisms and responses will pave the way for engineered plants that could be the foundation for salt-resistant crop cultivars. This would provide resilience to maintain economic (and ecological) stability. Hence, molecular and physiological studies are essential to reveal underlying mechanisms of stress and resilience processes. Signaling pathways and identification of novel genes responsible for high biomass yield require attention in halophytic species. Producing protocols toward introducing halophytic genes into transgenic crops requires further study and suitable conditions. To date, only a small number of investigations have evaluated potential genetic material in salt-tolerant plants. To combat the economic and food crises, halophyte production must be enhanced.

## 3.14 Encouraging a Scientific Revolution Integrating Genetic Factors of Halophytes

Genes responsible for salt-tolerant features in halophytes can be introduced into wild plant species by following cutting-edge technique like Crispr-Cas9-mediated transformation technology. Parallel complications, such as genetic misalignments, may be solved with use of computational modeling using R/MATLAB software platforms.

Halophytes not only provide aid in desalinization but can also be of use as the best indicator of natural geological salt deposits. In this regard, indication of wild halophytes provides value for the mining industry. Further mapping studies of these species are encouraged. Moreover, microbial communities associated with halophytes can be used as an alternative source of soil reclamation on one hand and for the agriculture industry on the other hand (Sáenz-Mata et al. 2016). Rhizosperic interaction studies are urgently required to assist this area. The urgency of halophytic research is underlined in that by the year 2050, population of the world is projected to stabilize at around 9.5 billion people (http://faostat3.fao.org/home/E) (accessed 17 October 2019).

## 3.15 Conclusion

Halophytes are "salt lovers" and are well organized in saline environments. However, there are enormous variations in the adaptability of halophytes toward salinization. Thus, a selection of halophytes adorning hyper-accumulation features, yielding high biomass and greater rates of salt amelioration from the soil, should be preferred. Application of halophytes is greatly required in the locality of arid and semi-arid regions where other measures of soil reclamation and desalination are not economically possible. Scientific revolution is still needed to introduce halophytes on a commercial scale. This will aid in removing barriers in the availability of fresh water and proper economic growth as well (Parnian et al. 2020). Parallel to this, halophytes are considered as the best source of biofuel production. Many plants are reported to have antioxidant and oil content; however more research is needed to detail quantitative and synergistic relations of salts and halophytic oil producers. Development of transgenic plants is the ultimate solution to avoid salinization, water scarcity, and global food insecurity. Research on a selection of desired genes responsible for salt-tolerant mechanism is taking place through RNA sequencing and protein expression. Despite such developments, ascertaining the correct breeding lines is hindered by lethal side effects such as sterility, which cannot be ignored in engineering transgenic cultivars.

Global agriculture must double its productivity in order to feed our population in the future; indeed this is the principal goal of sustainable development. The challenges of attaining sustainable and accelerated growth and food security have been exacerbated by global climate change and extreme weather fluctuations. The main impact of climate change is the highly variable and increasing temperature which will bring changes in precipitation patterns and ultimately increase soil salinity.

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