Halophytes of Semi-Arid Areas: Resources for Mitigation of Climate Change

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Abstract Halophytes grow in coastal areas of the semi-arid regions are often exposed to intense and varying environmental stresses (especially salinity). India has a total coastline of 7516.6 km and Gujarat enjoys the distinction of having the longest coastline (more than 1650 km) in India. The vast coastal area of Gujarat falls under semi-arid climatic zone and is mostly made up of mudflats and sandy loam soil. The impact of tides that ranges from about 3 m to a maximum of 10 m is quite high along the coast. The coastal area of Gujarat consists of different halophytes (*Salicornia*, *Arthrocnemum*, *Haloxylon*, *Sesuvium*, *Suaeda*, *Aeluropus*, *Heleochloa*, *Atriplex*, and *Salvadoraetc*), which have potential economic importance (food, fodder and natural products) along with environmental and ecological benefits. The rise in sea levels, increasing salinity and droughts are the main effects of climate change in many parts of the world. Halophytes are extraordinary plants to tolerate the salinity that other species cannot survive. Halophytic plants have different physiological and molecular mechanisms (salt excretion, accumulation and avoidance) to survive under extreme salinity. Succulent halophytes have a higher Na^+/K^+ ratio (accumulator) in the shoot and root which are potential plants to be used for bioremediation of salt-affected soils. The rhizosphere of halophytes is a potential source of plant growth-promoting bacteria which can be used for the development of salinity tolerance in the crop plants apart from gene resources for the development of the transgenic plants. Therefore, halophytes have a special place in assisting our understanding of salinity tolerance and important for climate change challenges.

Keywords Halophytes · Salinity tolerance · Coastal ecosystem · Inter-tidal zone

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Introduction

To achieve the World's food production for the need of an increasing population is very challenging because of decreasing availability of arable land resulting from urbanization and land degradation by soil salinization/other degrading processes. Soil salinization is expected to rise in the present scenario of global climate change (Shabala et al. 2014; Flowers and Muscola 2015). Soil salinization has become a serious global issue due to the changing climate and anthropogenic activities which not only reduces soil quality and agriculture productivity but also continuously decreasing the agricultural land area (Bhaduri et al. 2016; Shao et al. 2019). Soil salinization and increasing drought will be the main contributing factors to increase the soil salinity in the arid and semi-arid regions of the World. Additionally, the area of salt-affected land is increasing year by year because of high evapotranspiration, less rainfall, use of poor-quality water, poor irrigation practices and human-made activities (Shao et al. 2019). Seven percent of the total land and one-third of irrigated land of the World are affected by the salinity (Flowers and Colmer 2008). According to NHO (National Hydrographic Office, Dehradun, India), the revised coastline length of India is 11,084.50 km which is shared by 13 different states and union territories (Gujarat, Maharashtra, Karnataka, Kerala, Tamil Nadu, Andhra Pradesh, Odisha, West Bengal, Goa, Daman & Diu, Puducherry, Andaman and Nicobar Islands, and Lakshadweep & Minicoy Islands) (CWC 2016). Gujarat has the longest coastal line among the different states of India. With the considerable coastline, India has 6.72 m ha salt-affected soil and Gujarat alone has the largest salt-affected area of 2.22 mha (Mandal et al. 2009). Despite the advancement of technologies and techniques, genetic-engineering and breeding of salt-tolerant plants require many years to achieve (Flowers and Muscola 2015). Another approach may be the domestication of halophytes which have inherent genetic makeup to tolerate high salinity with economic values (Glenn et al. 1999) and can be alternative crop plants for cultivation in salt-affected lands.

Halophytes are defined in numerous ways with time and the advancement of research in the field of halophytes. Halophytes are the plants which are capable of growing at 0.5% sodium chloride content (Chapman 1942). Later, the plants grow and complete their life cycle in high salt content (Waisel 1972). Similarly, Breckle (1995) also suggested that plants that grow and complete their entire life-cycle in saline habitats are halophytes. Halophytes are the plants which survive to reproduce in environments where the salt concentration is around 200 mM NaCl or more (Flowers et al. 1986; Flowers and Colmer 2008). Recently, salt-tolerant plants (halophytes, including salt marsh and mangrove plants) are highly evolved and specialized organisms with well-adapted morphological and physiological characteristics allowing them to survive in the soils possessing high salt concentrations as defined by Khan and Duke (2001).

Effect of Soil Salinity on Plants

Among all salts, sodium chloride is highly soluble and found in higher concentrations in saline soils. Thus, sodium (Na^+) ion plays the primary role in the ionic toxicity in the plants growing on saline soils (Munns and Tester 2008). The movement of different salts into the plant is caused by the transpirational flux that is required for maintaining the water potential in the plant (Mahajan and Tuteja 2005). The Na^+ is highly toxic in a cytosolic concentration of about 100 mM. Na^+ shows cytotoxic effects in dual ways: firstly, it has a high charge to mass ratio (in comparison to K^+) which disrupts water structure and lower down hydrophobic interactions within proteins (Pollard and Jones 1979; Jones and Pollard 1983) and secondly, Na^+ inhibits enzyme activity, either directly through binding with inhibitory sites or indirectly through displacing $K^+$from its activation sites (Serrano 1996). In both cases, competition between Na^+ and K^+ ions is critical, and Na^+ to K^+ ratio in the cytosol is the main determining factor for Na^+ toxicity (Amtmann and Sanders 1998). There are protein transporters at the root epidermis which transport Na^+ and K^+ but when Na^+ present excessively in the soil which competes with K^+ ions for intracellular influx (Amtmann and Sanders 1998; Blumwald et al. 2000). The K^+ ion transporter has an affinity for Na^+ ions called Na^+/K^+ symporters (Blumwald et al. 2000). So, high soil Na^+ content negatively affects intracellular K^+ influx because most of the cells retain high K^+ and low Na^+ concentration in the cytosol accomplished by the coordinated regulation of different transporters for proton, potassium, calcium and sodium (Mahajan and Tuteja 2005). The influx of Na^+ causes many harmful effects on plants by dissipating the membrane potential, affecting the functions of some enzymes, generating the reactive oxygen species and reducing the photosynthesis process (Hasanuzzaman et al. 2014; Himabindu et al. 2016; Mishra and Tanna 2017). Additionally, higher sodium influx cause osmotic imbalance, disorganization of the membrane, inhibition of cell expansion and division, and in severe stress condition, it causes plant death (Niu et al. 1995; Yeo 1998).

Mechanisms of Salt Tolerance in Halophytes

Halophytes have evolved salt tolerance mechanisms operating at various levels, anatomical, morphological, physiological, molecular and ecological levels that help plants to cope with salty conditions (Hasanuzzaman et al. 2014; Flowers and Muscola 2015). These plants have adjusted well to complete the life cycle under the saline environment with different types of adaptation mechanisms such as ion compartmentalization, succulence, osmotic adjustment, regulative ion transport and uptake, production of osmolytes, maintenance of energetic and redox status, and salt excretion or inclusion (Lokhande and Suprasanna 2012) (Fig. 1). For salinity tolerance,

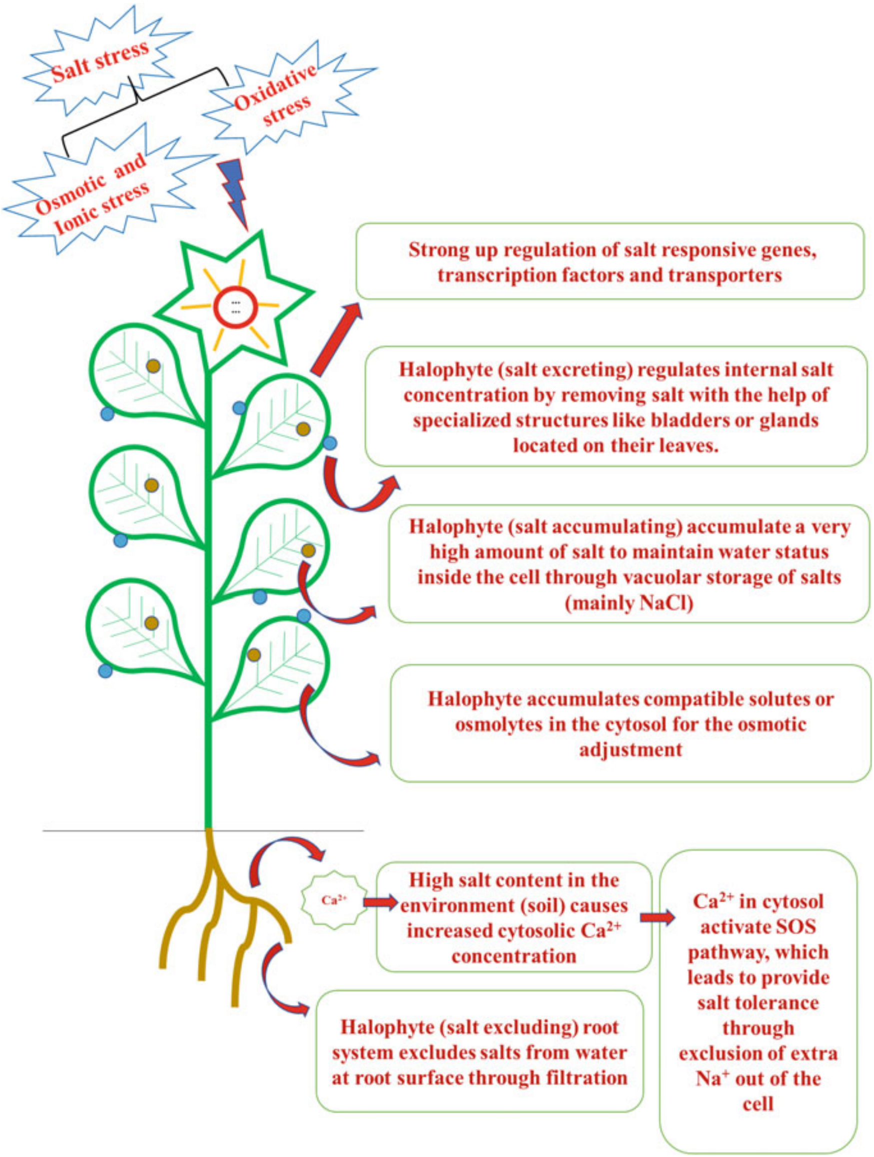

Fig. 1 Adaptive mechanisms employed by halophyte for salt tolerance

halophyte species also synthesize compatible solutes for protecting cellular structures and maintaining water potential inside the cell (Schat et al. 1997; Sharma and Dietz 2006).

Halophytes are extremophiles; these are found in salt marshes and other salty environments like saline depressions, inland deserts and rocky coasts or sand dunes.

Based on the different salt adaptation mechanisms (Fig. 1), halophytes have been classified into three categories: (a) salt excluding, (b) salt excreting and (c) salt accumulating. Salt excluding plants have evolved with a particular type of root system that works based on the ultrafiltration mechanism. Their root system excludes salts from water at the root surface through filtration (Kim et al. 2016). The *SOS1* gene (salt overly sensitive) is mainly expressed in the root cell membrane and plays an important function in Na^+ extrusion (Sreeshan et al. 2014). The *SOS* pathway is activated by Ca^{2+} ions and Ca^{2+} ion significantly provides salt tolerance to plant (Knight et al. 1997; Mahajan and Tuteja 2005). The high salt content in the environment causes increased cytosolic Ca^{2+} concentration which is released from the apoplast and intracellular compartments (Knight et al. 1997). The *SOS* pathway causes the exclusion of extra Na^+ out of the cell with the help of plasma membrane Na^+/H^+(*SOS1*) antiport and supports to maintain homeostasis of cellular ions. There are three proteins such as *SOS1*, *SOS2* and *SOS3*, work in a coordinated manner in the *SOS* pathway for reducing the salinity effects (Mahajan and Tuteja 2005). Salt excluder halophytes include *Kandelia candel, Avicennia marina, Bruguiera gymnorrhiza*, *Ceriops candolleana* and *Rhizophora mucronate* (Drennan and Pammenter 1982; Waisel et al. 1986; Hasanuzzaman et al. 2014). Salt excreting plants regulate internal salt concentration by removing salt with the help of specialized structures like bladders or salt glands located on their leaves, such as: *Acanthus ilicifolius, Aeluropus lagopoides, Aegiceros corniculatum, Acanthus ilicifolius* and *Aeluropus littoralis* (Barhoumi et al. 2007; Hasanuzzaman et al. 2014; Sanadhya et al. 2015). Salt accumulator plants accumulate a very high amount of salt to maintain water status inside the cell. Halophytes have evolved with the mechanism of osmotic adjustment through vacuolar storage of salts (mainly NaCl) and organic molecules accumulation in the cytosol. The mechanism of Na^+ and Cl^- entry in halophyte cells is not fully known but might involve different types of ion channels, transporters and pinocytosis (Hasanuzzaman et al. 2014). The Na^+/H^+ antiporters are required for the uptake of Na^+ ions into the vacuoles and this transporter gets energy with proton motive force producing H^+-ATPases (proton-adenosine triphosphatase) and H^+-PPases (proton-pyrophosphatase) (Bassil et al. 2011; Munns and Tester 2008). It is also reported that halophytes often possess large vacuoles such as in the case of *Suaeda maritima*, 77% volume of mesophyll cells are occupied by vacuoles (Hajibagheri et al. 1984) which makes them efficient for accumulating about 500 mM salt in the cells (Dracup and Greenway 1985). Although the amount of salt accumulated in shoots is not the same for all halophytes, this depends on the adaptive strategies occupied by different species of halophytes for salt tolerance (Fig. 2). This accumulated salt causes the development of succulence in the halophytes, such as *Sonneratia acida*, *Sonneratia apetala, Sonneratia alba*, *Excoecaria agallocha*, *Limnitzera racemose, Salvadora persica*, *Suaeda nudiflora, Sesuvium portulacastrum*, *Pentatropis siansh, Suaeda maritima*, *Clerodendron inerme, Ipomoea pes-caprae, Heliotropium curassavicum, Salicornia brachiata, Salicornia persica, Halimocnemis pilifera* and *Sporobolus arabicus* (Ravindran et al. 2007; Hasanuzzaman et al. 2014; Rathore et al. 2016; Mangalassery et al. 2017).

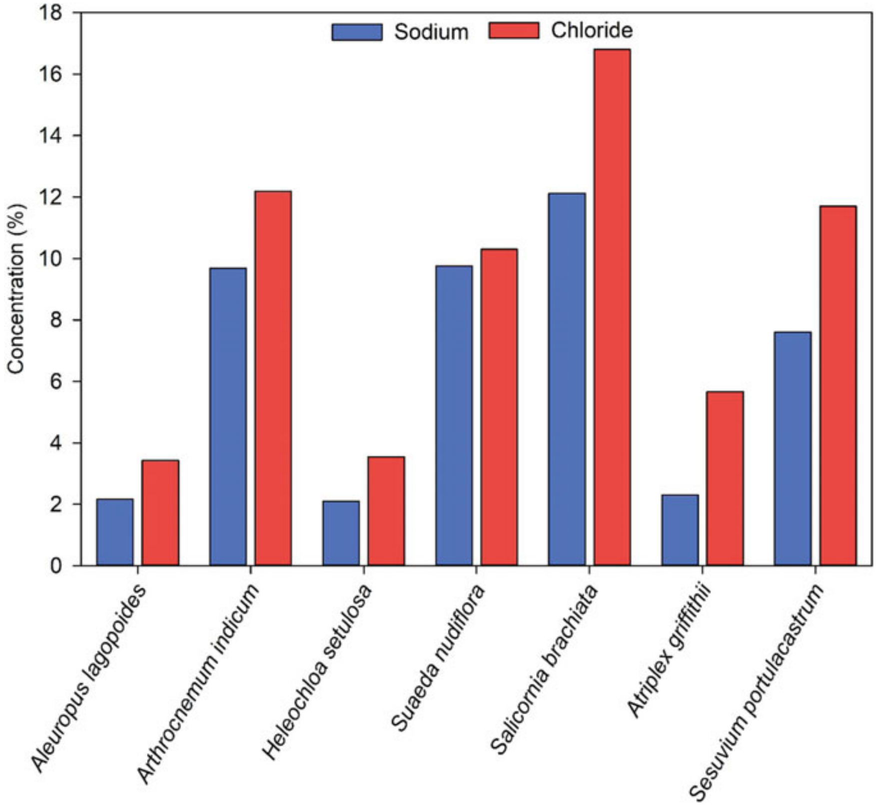

Fig. 2 Sodium and chloride content in the shoots of halophytes growing in coastal saline soils of Gujarat, India

Halophytes of Gujarat Coastal Area

Due to favourable climatic and soil conditions of the coastal area of Gujarat which is habitat for different vegetation, comprises of mangrove and halophytes (Fig. 3). Joshi (2011) divided halophytes occurring in Gujarat into three main categories: (1) succulent halophytes, *Salicornia brachiata* Roxb., *Arthrocnemum indicum* (Willd.) Moq., *Haloxylon salicornicum* Bungeex. Boiss., *Salsola kali* Linn, *Sesuvium sesuvioides* Fenzl., *Sesuvium portulacastrum* (L.) Linn., *Suaeda fruticosa* (L.) Forssk., *Suaeda maritima* (L.) Dumort., *Suaeda monoica* Forssk., *Suaeda nudiflora* (Willd.) Moq. (2) Non-succulent halophytes *Aeluropus lagopoides* (L.) Trin. ex Thw., *Heleochloa setulosa* Trin., *Juncus maritimus* Lam., *Sporobolus virginicus* (L.) Kunt. (3) shrubby halophytes *Atriplex griffithii* Moq., *Limonium stocksii* Boiss., *Salvadora persica* Linn., *Tamarix aphylla* (L.) Karsten. In coastal saline areas, halophytic plants are one of the most important contributors to the proper functioning of the coastal ecosystem (Joshi 2011; Rathore et al. 2017).

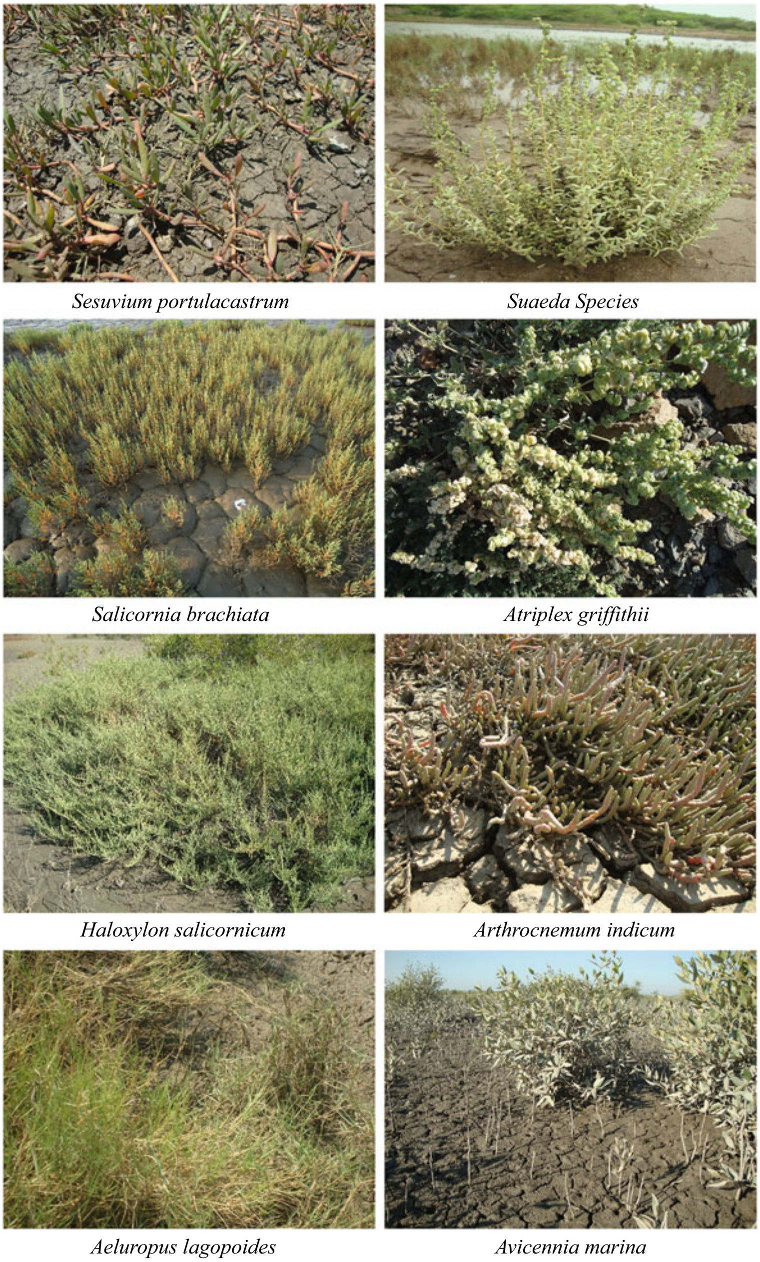

Fig. 3 Halophytes growing at the coastal region of Gujarat (India)

Halophyte for Amelioration of Saline Soil

The acreage of saline soils in the world is expanding day by day due to climate change and there is an urgent need to develop salt-tolerant crops to survive with the adverse condition of soil salinity. The amelioration of salinity has been predominantly achieved through washing and leaching of salt with excessive amounts of good quality water. However, mostly saline soils occur in arid and semi-arid regions, where rainfall is scanty and the availability of good quality waters is limited. Therefore, other biological remedial measures can be used, such as plantation/cultivation of salt-tolerant plants that can take up salt from the soil and reduce the soil salinity. For this purpose, halophytes are the candidate plants that have the capacity to accumulate and remove the salts from the soil and can effectively remediate the salt-laden soils (Hasanuzzaman et al. 2014). The halophytic plant can grow satisfactorily under higher soil salinity and they have many applications as food, fodder, oil, cosmetics, pharmaceutical, nutraceutical, industrial, ecological and agricultural. Sometimes, the productivity of halophytes is equivalent to conventional agricultural crops. *Kosteletzkya virginica*, a grain-crop for seawater-based agriculture, yielded 957 kg ha^{-1} seed containing 20.64% oil (Ruan et al. 2008). *Salicornia bigelovii* (a highly salt-tolerant stem succulent annual halophyte) is suggested as oilseed crop, since it produces a high yield of seeds (2t ha^{-1}) with a high protein (31%) and oil (28%) content which is similar to soybean yield potential and quality of seed (Glenn et al. 1999). *Salicornia brachiata*, an oilseed halophyte, yielded 4.5–7.1 t ha^{-1} dry biomass and 0.49–0.91 t ha^{-1} seeds (Pandya et al. 2010). It can accumulate 30–40% salt of its dry weight (Jha et al. 2009). The biomass of *S. brachiata* is used for the production of high-valued vegetable salt (Ghosh et al. 2005) and seeds are used for oil production (Fig. 4). The seeds of *S. brachiata* produce a special type of oil which is high polyunsaturation

Fig. 4 Edible oil (rich in PUFA) from seeds of *Salicornia brachiata* and vegetable salt from biomass of *S. brachiata*

and rich in linoleic acid (essential amino acid) that shows similarity with safflower oil (Eganathan et al. 2006; Pandya et al. 2006). *Chenopodium quinoa* is a facultative halophyte, an important grain cash crop that can yield 441 kg ha^{-1} under saline soil conditions with 13.45% protein content (Eisa et al. 2017). Oil content in the seeds of *Arthrocnemum indicum*, *Alhaji maurorum*, *Cressa cretica*, *Halopyrum mucronatum*, *Haloxylon stocksii* and *Suaeda fruticosa* varied from 22 to 25% with unsaturation of 65–74% (except in *A. maurorum*) and suggested that *S. fruticosa* can be used as a source of oil for human consumption (Weber et al. 2007). Few halophytic plants are good source of fodder for animal feeding in the coastal area but those may cause nutritional barriers owing to high salt concentration and antinutritional compounds. Common grasses found in the area of salt-affected soil are *Leptochloa fusca*, *Lasiurus scindicus*, *Panicum turgidum*, *Dactyloctenium sindicum*, *Cynodon dactylon*, *Paspalum vaginatum*, *Sporobolus marginatus*, *S. ioclados*, *Chlorisgayana*, *Chloris virgata*, *Echinochloa turnerana*, *Echinochloa colonum* and *Puccinellia distans* which can be used to feed the animals (Khan and Qaiser 2006). *Aeluropus lagopoides* had better ion uptake, ion partitioning and forage quality traits (protein, proline, fiber, ash and sugar content) which is found to be an ideal forage grass for saline agriculture on saline black soils (Rao et al. 2005).

Hamidov et al. (2007) investigated the ability of *Portulaca oleracea* to remove salt from the soil and reported that it could remove 570 kg ha^{-1} salt with biomass production of 3.25 t ha^{-1}. It was observed that *Suaeda maritima*, *Sesuvium portulacastrum*, *Excoecaria agallocha*, *Clerodendron inerme*, *Ipomoea pes-caprae* and *Heliotropium curassavicum* can remove 504, 474, 396, 360, 325 and 301 kg ha^{-1}salt, respectively from saline soil in 4-month growth time (Ravindran et al. 2007). Above ground biomass of *Salicornia brachiata* can remove 334 kg ha^{-1} sodium and 493 kg ha^{-1} chloride from inter-tidal soils of coastal Gujarat, India (Chaudhary et al. 2018). Bioaccumulation factor (BF, ratio of the content of Na^+ in aboveground parts to that in soil) and translocation factor (TF, ratio Na^+ content in aboveground parts that in the belowground parts) varied from 2.23 to 16.15 and 1.03 to 5.34, respectively in the *Salicornia brachiata* (Chaudhary et al. 2018). Plants with higher BF (> 1) and TF (>1) for Na^+ are reliable candidates for remediation of saline soils (Table 1). *Salicornia brachiata* maintain a higher Na^+/K^+ ratio in shoots compared to roots due to shoot succulence (Table 2) and reduce the soil salinity (Table 3) along with improvement in microbial activity (Table 4). Ouni et al. (2013) found that *Tecticornia indica* and *Suaeda fruticosa* produced 7.4 t ha^{-1} and 2.2 t ha^{-1} dry biomass, respectively with 0.75 t ha^{-1} and 0.22 t ha^{-1} sodium accumulation, respectively at Soliman

Table 1 Bioaccumulation factor (Na^+) and translocation factor (Na^+) of *Salicornia brachiata* (Mean ± standard error, n = 108)

Factor	Value
Bioaccumulation factor	8.90 ± 2.22
Translocation factor	3.66 ± 0.69

Table 2 Na^+/K^+ ratio in *Salicornia brachiata* (Mean ± standard error, n = 108)

Plant part	Na^+/K^+ratio
Aboveground	14.05 ± 2.97
Belowground	5.02 ± 1.51

Table 3 Effect of *Salicornia brachiata* on soil characteristics and nutrient contents (Mean ± standard error, n = 108)

Soil characteristics	*Salicornia* root zone soil	Control soil (without vegetation)
pH	8.28 ± 0.01	8.17 ± 0.03
EC (dS m^{-1})	20.49 ± 0.47	29.28 ± 0.84
Organic carbon (%)	0.70 ± 0.02	0.71 ± 0.01
NO_3^--N (mg kg^{-1})	1.38 ± 0.08	2.88 ± 0.18
NH_4^+-N (mg kg^{-1})	5.65 ± 0.32	6.67 ± 0.41
P (mg kg^{-1})	14.97 ± 0.47	13.98 ± 0.64
Na^+ (g kg^{-1})	17.01 ± 0.41	23.93 ± 0.75
K^+ (g kg^{-1})	1.69 ± 0.02	1.56 ± 0.03

Table 4 The concentrations of fatty acid methyl ester (FAME) microbial biomarkers in the soil influenced by the *Salicornia brachiata.* (Mean ± standard error, n = 108)

FAME (nmol g^{-1})	*Salicornia* root zone soil	Control soil (without vegetation)
Total FAMEs	37.98 ± 1.83	22.22 ± 1.29
Total Bacterial	16.35 ± 0.88	9.30 ± 0.64
Gram-positive	6.44 ± 0.34	3.81 ± 0.21
Gram-negative	10.38 ± 0.58	5.47 ± 0.42
Fungal	1.73 ± 0.15	0.77 ± 0.05
Actinomycetes	2.12 ± 0.11	1.23 ± 0.07

sabkha (North-East Tunisia). In another study, *Arthrocnemum indicum*, *Suaeda fruticosa* and *Sesuvium portulacastrum* could remove sodium 2504, 711, 802 kg ha^{-1}, respectively and significantly reduced the soil salinity (Rabhi et al. 2008). Among *Tecticornia pergranulata*, *Sclerolaena longicuspis* and *Frankenia serpyllifolia* cultivated on brine-affected soil, *T. pergranulata* showed the highest shoot Na^+content (98 g kg^{-1}), bioaccumulation (14.21) and translocation (23.09) factors for Na^+ with higher remediation potential of brine affected soil (Shaygan et al. 2018). Plantation of *Atriplex halimus* decreased electrical conductivity for saline-sodic soil from 39.2 to 26.5 dS m^{-1} and from 6.2 to 4.9 dS m^{-1} for saline soil; furthermore, sodium adsorption ratio was also significantly reduced (Abdul-Kareem and Nazzal 2013). *Suaeda monoica* was evaluated for the amelioration of paper mill effluent treated soil and it was observed that electric conductivity of soil was reduced from 4.75 to 2.10 dS m^{-1} with an accumulation of 172.20 mg NaCl g^{-1} (Malik and Ravindran 2020). *Sesuvium portulacastrum* had reduced the soil salinity (from 7.1 dS m^{-1}

to 4.9 dS m^{-1}) and sodium adsorption ratio (20.9–13.5) in 90 days growth which produced biomass of 8.1 t ha^{-1} and removed 595 kg Na^+ ha^{-1} (Lokhande et al. 2009). Halophytes improve fertility as well as the microbial quality of soil under saline conditions (Tables 3 and 4). Remediation of saline soils by the halophytes is an economical method since chemical and water availability for leaching in arid and semi-arid regions are expensive. It has been proven that many halophytic plants have the potential to accumulate a substantial quantity of salt (hyper accumulator) and have great potential to ameliorate the saline soils of arid and semi-arid regions (Chaudhary et al. 2018; Rathore et al. 2016).

Plant Growth-Promoting Rhizobacteria from Halophytes

Salt tolerant plant growth-promoting rhizobacteria (PGPR) isolated from the rhizosphere of halophytes have the potential to ameliorate salinity stress in crop production through physiological and molecular mechanisms (Arora et al. 2020) which is an alternative to the plant breeding and genetic engineering approaches. Halophytes are valuable bio-resource for halotolerant bacteria with plant growth-promoting traits (Fig. 5) which accelerate the growth of plants and increase the tolerance in agricultural crop plants for enhancing productivity and soil fertility (Etesami and Beattie 2018; Egamberdieva et al. 2019) which is an eco-friendly and sustainable approach. Salt tolerant PGPR efficiently improves the growth of plants under salt stress conditions by various mechanisms include improvement in nutrient availability (biological N_2, solubilization of phosphorus, potassium, chelation of iron and zinc by siderophores), production of phytohormones (indole acetic acid, gibberellins and cytokinins), protection from salt toxicity through activation of antioxidant enzymes (superoxide dismutase, peroxidase, catalase, ascorbate peroxidase, guaiacol peroxidase and ACC deaminase), production of osmolytes (soluble sugars, amino acids, polyols and glycine betaines), increased expression of salt overly sensitive genes and transporters, control of phytopathogen and production of secondary compounds (exopolysaccharides which reduce Na^+ accumulation and uptake by the roots, increase soil aggregate formation and water retention) (Shahzad et al. 2017; Etesami and Beattie 2018; Arora et al. 2018; El-Esawi et al. 2018; Egamberdieva et al. 2019; Arora et al. 2020).

Jha et al. (2012) isolated the PGPR (*Brachybacterium saurashtrense* sp. nov. and *Pseudomonas sp.*) from roots of *Salicornia brachiata* that were halotolerant and improved the growth of *Salicornia* under salt stress conditions. *Klebsiella*, *Pseudomonas*, *Agrobacterium* and *Ochrobactrum* were isolated from the roots of *Arthrocnemum indicum* with growth promoting traits (*nifH* gene positive, indole-3-acetic acid production, phosphate solubilisation activity, 1-aminocyclopropane-1-carboxylate deaminase activity and capable of reducing acetylene) (Sharma et al. 2016). The ACC deaminase producing PGPR, *Arthrobacter soli*, *Bacillus flexus*, *Isoptericola dokdonensis* and *Streptomyces pactum*were isolated from *Limonium sinense* which stimulated the growth of the host plant and also influenced the

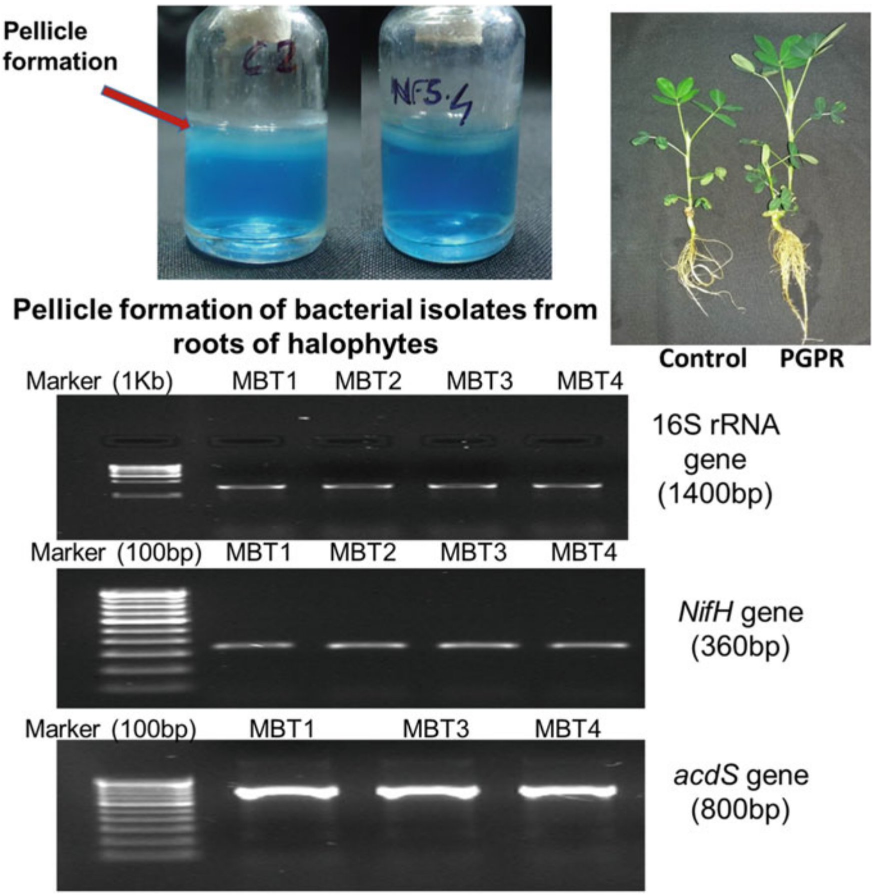

Fig. 5 Halotolerant plant growth promoting rhizobacteria isolated from halophytes

flavonoids accumulation (Qin et al. 2014). The five PGPR isolates (*Bacillus endophyticus*, *Bacillus tequilensis*, *Planococcus rifietoensis*, *Variovorax paradoxus* and *Arthrobacter agilis*) were isolated from *Salicornia europaea* which had PGPR properties (1-aminocyclopropane-1-carboxylate deaminase activity, indole-3-acetic acid and phosphate-solubilizing activities) and significantly stimulated the growth of the host plant (Zhao et al. 2016). Zhou et al. (2017) identified three PGPR (*Micrococcus yunnanensis*, *Planococcus rifietoensis* and *Variovorax paradoxus*) from halophytes with the ability to secrete 1-aminocyclopropane-1-carboxylate deaminase as well as other plant-growth-promoting traits which enhanced salt stress (NaCl concentrations 50–125 mM) tolerance of sugar beet as well as enhanced the seed germination and plant biomass, higher photosynthetic capacity and lower stress-induced ethylene production. The PGPR (*Bacillus sp.* and *Arthrobacter pascens*) were isolated rhizospheric soils of *Atriplex leucoclada* and *Arthrobacter pascens* plant growth-promoting traits (phosphate solubilization, bacteriocin and siderophore production) and inoculated to maize under induced salinity stress which increased fresh and dry weight of shoot and root with increased accumulation of osmolytes (sugar and proline) and antioxidant enzymes (superoxide dismutase, peroxidase, catalase and ascorbate peroxidase) activities (Ullah and Bano 2015). Mukhtar et al. (2020) isolated the five PGPR (*Bacillus safensis*, *Bacillus pumilus*, *Kocuria rosea*, *Enterobacter aerogenes* and *Aeromonas veronii*) from rhizospheric and nonrhizospheric soils of halophytes (*Salsola stocksii* and *Atriplex amnicola*) and inoculated to maize, all bacterial isolates positively affected the maize growth under salinity stress resulted in high concentrations of proline, glycine betaine and malondialdehyde.

Stress Tolerant Genes from Halophytes

Halophytes complete their life cycle under extremely saline soil conditions and are bioresources of salt-tolerant genes and give tools for developing transgenic crops with improved stress tolerance for saline agriculture. A large number of transporters, including antiporters (*NHX*, *SOS*, *HKT*, *VTPase*), ion channels (Cl^{-1} channels, water channels, Ca^{+2} channels); assisted genes (*APX*, *CAT*, *GST*, *BADH*, *SOD*) and stress-inducible promoters have been identified from the different halophytes (*Salicornia brachiata*, *Aeluropus lagopoides*, *Populus euphratica*, *Thellungiella halophile*, *Chenopodium quinoa*, *Puccinellia tenuiflora*, *Atriplex gmelini*, *Suaeda salsa*, *Salicornia europaea*, *Aeluropus littoralis*, *Spartina anglica*, *Salsola soda*, *Suaeda corniculata*, *Phragmites australis*). These genes were over-expressed in model plants and many agricultural crops (tobacco, rice, alfalfa, soybean, jatropha and cotton) (Himabindu et al. 2016; Mishra and Tanna 2017; Khedia et al. 2018; Jha et al. 2019) for improved stress tolerances. Salt responsive genes family adopt a different strategy for stress tolerance. Among different strategies; Na^+ efflux, sequestration of Na^+ in cell-organelles such as vacuoles, loading of Na^+ on xylem and inhibition of Na^+ influx are the most common strategy which is commonly regulated by a single gene or by a multigene family. Promoters and transcription factors also play a vital role in stress tolerance by activating series of adaptation/ tolerance pathways, following two major routes, either ABA-dependent or ABA-independent pathways. Signal transduction plays a vital role in the activation of gene cascade following the phosphorylation of genes using protein kinases. Antioxidant encoding genes are also involved in imparting stress tolerance by quenching reactive oxygen species and protecting plants from oxidative damages.

Conclusions

Soil salinity problem is increasing throughout the world and there is an urgent need to search for improved saline soil and alternative approaches to meet the global food security challenge. Halophytes have anatomical, physiological and biochemical mechanisms to cope with severe adverse conditions of soil salinity and these have the potential applications for food, fodder and industries which could be efficiently used for amelioration of saline soils because of higher accumulation of salt. However, the selected halophyte should have the capability to produce higher biomass with higher salt content simultaneously should have economic values. Salt tolerant plant growth-promoting rhizobacteria is an emerging biological tool for mitigation of salt stress in the crop plants and halophytes are resources for the developmentof novel bioinoculant/bioformulation for saline agriculture.

Halophytes are sources for identification and isolation of novel salt responsive genes and promoters which can be explored for the development of transgenic crops and plant genetic engineering for stress tolerance.

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