Potential of halophytes in managing soil salinity and mitigating climate change for environmental sustainability

Kathirvel Suganya
Department of Environmental Sciences, Tamil Nadu Agricultural University, Coimbatore, India

Ramesh Poornima
Department of Environmental Sciences, Tamil Nadu Agricultural University, Coimbatore, India

Paul Sebastian Selvaraj
Anbil Dharmalingam Agricultural College and Research Institute, Tamil Nadu Agricultural University, Trichy, India

E. Parameswari
Department of Environmental Sciences, Tamil Nadu Agricultural University, Coimbatore, India

P. Kalaiselvi
Department of Environmental Sciences, Tamil Nadu Agricultural University, Coimbatore, India

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ABSTRACT
Soil salinization is one of the foremost factors affecting global agricultural productivity. More than half billion hectares of agricultural land are unutilized due to excess saline condition. Hence, there is a great urge in exploring scientific interventions in restoring the saline affected areas and promote high productive and effective land utilization in order to respond to today’s global concerns of food security. While a sound drainage system is required as a permanent solution to the soil salinity problem in order to regulate the water table, this option cannot be used in larger area with high energy and cost-intensity. Phytoremediation, a plant – based approach is one of the promising technology in enhanced dissolution of Ca levels along with sodium removal through cultivating suitable halophytes. During the process, the proliferation of roots, aggregate stability, hydraulic conductivity and nutrient availability increases. These improvement in soil quality enables the growth of less tolerant crops, enhances the overall ecosystem and climatic conditions by increasing carbon sequestration. In this perspective, the chapter focuses on halophytes, its kinds, the effects of salinity on soil physical, chemical, biological health, the influence of halophytes in stress management and on the function of halophytes in carbon sequestration.

Introduction
Salinization affecting almost one billion hectares of land globally, or nearly seven percent of the world's continental extent, is considered to be one of the most vital problems for natural resources and human health. In India, approximately seven million hectares of saline soil are present (Patel et al., 2011). Much of this is in Punjab, Uttar Pradesh, Haryana, Bihar and portions of Rajasthan, which stretches over the Indo-Gangetic plains. Salinity is also found to affect semi-arid parts of Gujarat, Madhya Pradesh, Maharashtra, Karnataka, Andhra Pradesh and arid tracts of Rajasthan and Gujarat. Salinity is persistent and cost-consuming mechanism for remediation. It is a dynamic global challenge which cannot be easily solved, but instead requires a multidisciplinary solution. Several approaches have been suggested to properly rehabilitate and use the saline soils, which include agronomic practices, salt-tolerant varieties and phytoremediation. Halophytes are the plants which can flourish and survive on the "normal" soil in saline environment. Halophytes were also used to manage stressful environment and were shown to be active in boosting developed countries' economies in many parts of the world (Mishra and Tanna, 2017). Along with their potential to
sequester more carbon dioxide, halophytes would be a stronger way to meet climate change and desertification during 2050 as well as restore salt-affected soil, since this halophyte will grow more biomass.

**Soil Salinity and its impact on plants**

Soil salinity results in soil erosion and decreased agricultural productivity thereby dwindling the economic returns (Hu and Schmidhalter, 2004). This is a consequence of multiple interactions amongst the physiological, morphological and biochemical processes which includes germination, development, nutrient and water uptake (Akbarimoghaddam et al., 2011). Salinity affects the crop during all growth stages like germination, vegetative and reproductive stage. They exert an osmotic stress, ion toxicity and reduces the nutrient availability (N, K, Fe, Ca, P, Zn) thereby resulting in oxidative stress and reduces the efficiency of water – use. Due to the precipitation of Ca ions along with phosphate ions, the P uptake by plants gets reduced (Bano and Fatima, 2009). Furthermore, certain elements like sodium, boron and chlorine exerts specific toxicity to plants. Exorbitant accumulation of sodium ions in the cell wall results in osmotic stress (Ghanem et al., 2021). Excess salinity also influences the photosynthesis, transpiration, respiration, nutrient balance, membrane properties, metabolic and enzymatic activities. This further imbalance the cellular homeostasis resulting in reactive oxygen species (ROS) production which in turns leads to cellular apoptosis (Mahajan and Tuteja, 2005; Munns, 2005).

**Halophytes and its types**

Indeed, halophytes are known since 18th century, but information regarding the plants tolerant to salinity are available since 1500s. Flowers and Colmer (2008) has stated that halophytes are plants that normally develop and multiply in saline concentration exceeding 200 mM of sodium chloride (nearly 20 dS m⁻¹). Nearly, 1% of the flora worldwide are halophytes. Even under excess saline condition, halophytes can easily complete their lifecycle (Stuart et al., 2012). Halophytes are often referred to as euhalophytes because they have greater production with increased amounts of salt and exhibits better growth under saline environment compared to fresh water environments (Yensen, 2008). In a range of ecosystems, from pristine semi-desert alkaline, mangroves, steppe to semi-natural pastures and meadows, halophytes can be found all over the world. *Spartina anglica* is an excellent example of an ecologically wide niche halophyte. It is found in marshes and cultivated in irrigated, low-drainage arable fields in the tropics, and is polluted by salt in urban boreal areas during ice and snow recovery periods. The categorization of halophytes as given by Walter (1961) is given in Table 1. According to the ecological characteristics, halophytes are grouped as (a) obligate halophytes, (b) facultative halophytes, and (c) habitat-indifferent halophytes. Obligate halophytes occur exclusively under salty conditions. They exhibit satisfactory growth and development under high salt conditions. A considerable number of Chenopodiceae are included in this group. Facultative halophytes can thrive in salty soils, but also grow under normal conditions. In this group are Poaceae, Glaux maritima, Glaux maritime, Plantago, Cypraceae, Brassicaceae, and several dicotyledons.

**Table 1. Classification of halophytes (Walter, 1961)**

| Types of halophytes  | Characteristics and examples |
|----------------------|-----------------------------|
| Salt excluding       | In these plants, the root system possesses an ultrafiltration mechanism and this characteristic leads to establishment of such species as the dominant component of the mangrove vegetation. Example: *Rhizophoramucronata*, *Ceriopsandoleana*, *Bruguieragymnorrhiza* and *Kandelia* |
| Salt excreting       | These plants regulate internal salt levels through foliar glands. Example: *Avicenniaofficinalis*, *Avicennia alba*, *Avicennia marina*, *Aegiceroscorniculatum*, and *Acanthus ilicifolius* |
| Salt accumulation    | They accumulate high concentrations of salt in their cells and tissues and overcome salt toxicity by developing succulence. Example: *Sonneratiaapetala*, *Sonneratiaacida*, *Sonneratia alba*, *Limnitzeraracemosa*, *Excoecariaagallocha*, *Salvadorapersica*, *Sesuviumportulacastrum*, *Suaedanudiflora*, and *Pentatropissianshoides* |
Habitat-indifferent halophytes are those that don't care about their environment can flourish in the wild in saline soils. Nevertheless, they prefer low saline or saline-free soils. They will compete with species that are vulnerable to salt but still prosper in saline surroundings (Cushman, 2001).

**Mechanism of adaptation to saline stress**

The abundance, distribution and physiology of halophytes are intensively studied (Yensen, 2008; da Silva *et al.*, 2008; Lokhande and Suprasanna, 2012). Halophytes do not take up salts by influencing the growth activity, photosynthetic activity and turgor. The salt accumulation by older leaves accelerates the death. This injury influences the assimilation and hormone regulation ultimately affecting the development of plants (Van Zelm *et al.*, 2020). Regardless of the polyphyletic origin, halophytes possess similar mechanisms of osmotic adjustment: inorganic salt accumulation, NaCl particularly, in the vacuole and the accumulation of organic cytoplasm in the solutes. There is a growing difference between ion transportation systems of halophyte and glycophyte. Tonoplast antiporters are substantial in halophytes, but in glycophytes with salt tolerance, it would have been stimulated with NaCl and might not be found in glycophytes with salt sensitivity. The vacuoles present in the halophytes may have an altered lipid structure to avoid the leakage of Na$^+$ ions to cytoplasm (Glenn *et al.*, 1999; Van Zelm *et al.*, 2020). Furthermore, halophytes possess vacuoles of larger size. While all halophytes accumulate excess salt, the overall salt build-up in the shoot portion is mainly species-specific, according to various accommodative strategies. The numerous adaptive mechanisms include ion partitioning, synthesis of osmolytes, germination responses, osmotic adaptation, succulence, selective ion transportation and absorption, enzymatic responses, excess salt and genetic modulation (Koyro *et al.*, 2011; Ghanem *et al.*, 2021). The general mechanism of saline tolerance is presented in Figure 1. Various salt tolerance mechanism of plants includes (i) Ion concentration and accumulation, (ii) ROS signaling, (iii) Antioxidant defense mechanism/Antioxidant enzymes, (iv) Biochemical and physiological changes, (v) Osmotic regulation and (vi) Sulphur metabolism.

**Figure 1: General mechanism of saline tolerance by halophytes (adapted from Ahmad and Prasad, 2011)**

**Ion concentration and accumulation**

A few halophytes developed specialized structures for salt excretion, the salt glands, capable of removing surplus salt from the plant tissues to improve tolerance to salinity (Yuan *et al.*, 2016). Salt-gland halophytes are often referred to as recretohalophytes. The arrangement of epidermis and its functionality in salt exclusion differs among recretohalophytic species. Salt glands can also be divided into four different classes according to their structural similarities: multicellular salt glands, single cell vacuolated secretory hairs, salt bladder and bicellular salt glands (Dassanayake *et al.*, 2017). The most commonly used salt glands are multi-cells (4-40 cells) that can be differentiated...
intodistal secretory cells and basal cells. The secretory cells are linked in various plasmodesmata to the mesophyllic cells around them. Thus, salt is deliberately carried into the secretory cells via the collecting cells (Dassanayake et al., 2017). The outside surface is coated with cuticle in the secretory cells. The permanent cuticle thickens over the capsule in certain species, forming a cuticular chamber to store salts. The Na\(^+\) ion is carried to the vacuole by means of the Na\(^+\)/H\(^+\) antiporter following cytoplasm. The vacuolar membrane contains two forms of H\(^+\) pumps: pyrophosphatase (V-PPase) and H\(^+\)-ATPase (V-ATPase) (Dietz et al., 2001; Ghanem et al., 2021). Comparatively, V-ATPases are the most powerful H\(^+\) pump in the plants. It plays a crucial role in balancing the solute homeostasis, the energy consumption of secondary transport thereby promoting vesicle fusion. The plant’s viability relies on the activity of V-ATPase under stressed conditions (Dietz et al., 2001). Several studies validate the role of the stress-reporter route in ion homeostasis and salt tolerance (Hasegawa et al., 2000; Van Zelm et al., 2020). The chief proteins, namely, SOS1, SOS2 and SOS3, are part of the Salt Overly Sensitive (SOS) signaling pathways. For the regulation of Na\(^+\) cellular efflux, SOS1, which encodes the Na\(^+\)/H\(^+\) antiporter plasma membrane, is important. It also makes Na\(^+\) transport from root to shoot easier over long distances. This protein's over-expression confers plant salt immunity (Shi et al., 2000, 2002). Ca\(^+\) signals are activated by SOS2 gene, which codes for the serine/threonine kinase. This protein has a well-developed catalytical N-terminal domain and a regulatory C-terminal domain (Liu et al., 2000; Ghanem et al., 2021). SOS3 protein which is a Ca\(^+\) myristoylated, binding protein and contains an N-terminal myristoylation site is one of the third kind in the SOS stress-signaling process. This platform has a prime role in providing salt tolerance. C-terminal regulatory region of SOS2 protein comprises of a FISL motif (also referred to as NAF domain), which has about twenty-one amino acid long chain, and is the interaction site for Ca\(^{2+}\) SOS3 protein binding. This association of SOS3 and SOS2 leads to kinase activation (Guo et al., 2004; Meng et al., 2018). The SOS1 proteins then phosphorylated by active kinase, thus improving its activity in transport. It also controls the pH homeostasis, vacuole functions and membrane vesicles in addition to providing salt tolerance (Quintero et al., 2011).

**Figure 2: Response to salinity stress through SOS pathway (Gupta and Huang, 2014)**

**ROS Signaling**
The detoxification pathways for Reactive Oxygen Species (ROS) plays a vital role in responding to salt stress through the development of toxic radicals from the mitochondrial and chloroplast electron transportation chains (Meng et al., 2018). Both non-enzymatic and enzymatic elements are present in the antioxidant defense mechanism. One such mechanism that takes occurs in the chloroplast is the ascorbate-glutathione pathway. This system includes several enzymes like monodehydroascorbate reductase (Am-MDAR) (Kavitha et al., 2010), ascorbate peroxidases (Li et al., 2012; Cao et al., 2017), glutathione transferases (SbGST, SsGST) (Jha et al., 2014) and superoxide dismutases (TaSOD) which can be found in various halophytes and plays a prime role against the oxidative stress induced by salt.

**Antioxidant defense mechanism/ Antioxidant enzymes**

Besides enzymes that specifically scavenge ROS, several other proteins/enzyme groups exhibited a promising result in enhancing the antioxidant capability of crops (Meng et al., 2018). Metallothioneins, for instance, can attach themselves to heavy metals thereby facilitating cellular detoxification of the nonessential metals and maintaining a homeostasis in essential metals. Other metallothioneins include S – adenosylmethionine synthetase (Qi et al., 2010), The CCCH – type zinc finger proteins and glycosyltransferase (Zheng et al., 2017) was also found to involve in salt tolerance by reducing the
oxidative stress. Anthocyanin and Ascorbate is another important antioxidant in the cell. Salt plants (150 mM NaCl) have shown an improvement in both Ascorbate Peroxidase (APX) and S nitrosylated APX along with an increase in H2O2, S-nitrosothiol (SNO) and NO contents that can prompt APX induction. Exogenous ascorbate application reduces the detrimental impact of saline stress in different plant species and facilitates the regeneration of plants from stress (Agarwal and Shaheen, 2007; Meng et al., 2018). Glutathione, that reacts with superoxide, hydroxy radicals and hydrogen peroxide, is another antioxidant in stress reduction, which functions as a scavenger of free radical. It can also contribute through ascorbate glutathione cycle to regeneration of ascorbate. Under salinity stress, exogenous addition of glutathione facilitated in stabilizing the permeability of plasma membranes and cell viability of Allium cepa (Aly- Salama and Al-Mutawa, 2009). There have been several experiments validating the variations in antioxidant enzyme expression or activity; which often relate to the highly tolerant and sensitive genotype.

**Osmotic regulation**

Osmotic adjustment to sustain the water balance is one of the major adaptive mechanism found in halophytes under saline stress (Flowers and Colmer, 2008). Apart from accumulating and sequestering the inorganic ions in the vacuoles, they also promote the secretion of organic solutes to maintain the stability of protein in cells in response to the changes in water potential (Glenn et al., 1999; Van Zelm et al., 2020). Plants produce various organic solutes like sucrose, trehalose, proline, polyols and quaternary ammonium compounds like alaninebetaine, choline- O-sulfate, glycine betaine, prolinebetaine, and pipocletabetaine. These highly soluble organic solutes are low molecular weight compounds which are nontoxic even at higher concentration (Ashraf and Foolad, 2007) without upsetting the cellular functions and intracellular mechanisms. In addition, these solutes protect the subcellular structures and eradicates the oxidative damage caused by ROS; balances the enzymatic activities under abiotic stress and prevents the dehydration of cellular components (Ashraf and Foolad, 2007; Meng et al., 2018). This mechanism is often found in halophytes and glycophytes under abiotic stresses, nevertheless, the production process is energy – dependent thereby utilizing numerous ATP molecules.

**Sulphur metabolism**

ATP – S is regarded as a rate limiting compound in S – assimilation pathway and overexpressed under saline stress (Ruiz and Blumwald, 2002). Salinity governs production of the main enzymes like APX activity and sulfate assimilation. Furthermore, in order to stabilize the GSH demand, the rate of Cys synthesis is linearly related to Ascorbate Peroxidase (APX) activity (Koprivova et al., 2008). Salinity is also responsible for the action of other sulphate assimilation enzymes, SAT and the OAS-TL cytosolic isoform (Figure 3). Salinity was reported to induce OAS-TL gene transcription and translation possibly as an adaptation/protection against higher salinity levels, because of greater demand for Cys and/or other S – containing compounds which is required for the plant (Romero et al., 2001; Meng et al., 2018).

**Figure 3: Salinity tolerance through sulphur metabolism (Khan et al., 2014)**

**Improving soil physical properties**

The physical characteristics of soils are usually influenced by plants, such as porosity of soil, soil hydraulic permeability (Ks) and bulk density. By growing salt-tolerant plants by their various practices, these properties can be increased. Plant
roots are required to preserve the soil structure and plant cultivation with less depth must produce macropores in the soil profile to increase the porosity of the soil (Yunusa and Newton, 2003). The root further removes the air trapped from the pores. It also facilitates leaching of Na and replaces it with other soil cations that can tolerate a range of salinity levels during phytoremediation, induced by deep-rooted vegetation. The rooting mechanism of these plants greatly improves soil porosity. Deep tillage has been proven useful for the improvement of low-porosity subsoils, but without vegetation cover, these advantages are not lasting (Cresswell and Kirkegaard, 1995; Van Zelm et al., 2020). Roots of certain plant organisms may be considered as a biological tiller. It proves to be a promising alternative to the deep laying needed for the enhancement of dense subsoils. Some plants like Paspalum notatum, Atriplex, Suaeda fruiticosa, and Festuca arundinacea consist of strong root systems, which can expand in compact soil layers, thereby improving soil porosity. The plant should also be used for salt-affected soils with an active and powerful rooting mechanism. Many studies stress that the plantation on salt-affected soils with salt-tolerant plant species helps to improve the soil's hydraulic permeability, as interactive processes such as structural stability, soil porosity, leaching of salts and organic matter.

**Improving soil chemical properties**

Several chemical properties of the soil like EC, pH, organic matter, sodium adsorption ratio (SAR) are governed and improved by growing salt tolerant crops. In soil under cultivation of halophytes, an increase in soil permeability was observed due to reduction in EC in the top layer. The growth of Leptochloa fusca, Spartina Haloxylon recurvum, Distichlis, Suaedanudiflora, and Aeluropus can be recommended to minimize soil salinity. The pH of the soil is reduced by halophytes. The pH reduction in soil may be attributed to root OH⁻, H⁺, HCO₃⁻ and other organic anions, which react with the soil complexes eventually disrupting the balance of cations and anions in the soil (Helyar and Poster, 1989). In addition, microbial activity has been observed in root exudates and root respiration, as an outcome of which vegetation is added to organic matter which causes changes in soil solution quality. Root Efflux of H⁺ is usually seen in the plant's roots, which induces a decreased soil pH under saline conditions. This reduction makes it possible to take up macro and micronutrients, as growth and yield of the crop are predicted to improve after phytoremediation on these soils.

**Role of halophytes in Carbon sequestration**

Wild salt resistant plants, halophytes, in the global coastal deserts and inland salt deserts and secondary salinization zones in irrigation districts, could expand on 130 x 10⁶ hectares of potentially arable soil. As biomass crops, halophytes can sequestrate up to 0.7 Gt Carbon, close to tree plantations, or indirectly consume C from the environment by supplying fresh fruit, fodder and energy crops. New cropland from unused saline land can be created. The best-performing halophytes have annual biomass yields ranging from 9 to 20 tonnes, across a variety of soil, water and climate requirements. If the arable lands are planted with halophytes with 5 tonnes of carbon net productive energy annually, which is around 10% of all emissions of fossil fuel, nearly 20% of the carbon burden remains in the atmosphere (Glenn et al., 1992). Halophytes thus play an important part in a global climate change mitigation biomass plan. Salt marshes are dynamic, highly active, biotic and abiotic forces in the management of habitats. Several abiotic factors like the waterlogging and soil salinity plays a vital role in governing the occurrence, distribution and abundance of plants. This salt marches can survive in a diverse climate, hydrology, topography and geology with any degree of anthropogenic interferences along with a diverse biotic control (i.e. competition, physiological tolerance). These factors decide the establishment of a marshes in a specific climatic condition. If the entire halophyte land were planted, they would sequester nearly 715 x 10⁶ mt of C accounting for nearly 12% of annual C released through fossil fuel and 24% of the fraction that is left over in the atmosphere (Glenn et al., 1992).

**Conclusion**

Salinized wastelands need to be used for plant production in order to meet the demand for foodstuffs, feed, and raw materials that are decreasing day by day because of the growth in the world population. The use of plants (halophytes) for soil remediation, for the purpose of phytoremediation is one of the eco-friendly approaches to soil salinity management. Halophytic
reactions to increasing salinity are diverse in development. Not only can these plants rehabilitate salt-contaminated land, they also provide fruit, forage, fuelwood and industrial raw material, thereby eventually increase the farmer’s income in salt-affected areas. Different resistance mechanisms like halosucculence, ion division (inclusion/exclusion), osmoregulation, enzyme and non-enzymatic antioxidants, and the preservation of redox and energy state have been developed to create evolving environmental conditions. These plants are able to secure carbon and contribute to climate change reduction strategies.

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