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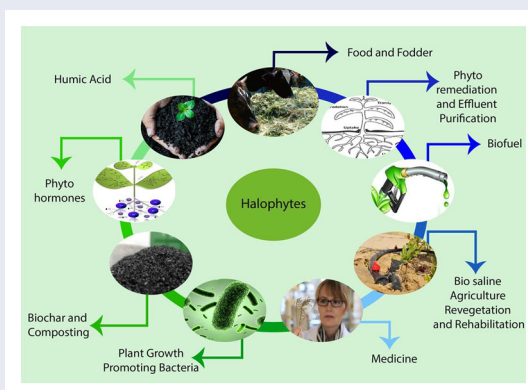
## Strategies in improving plant salinity resistance and use of salinity resistant plants for economic sustainability

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### ABSTRACT

Production of food, fodder and plant vegetation declined rapidly around the world due to climate change, increase in saline areas and loss of productive lands. A major challenge of sustainable development goals is increasing crop yield and food security by using non-conventional plants in agriculture. Hence, there is a need to develop halophyte based saline agriculture to meet growing demands to feed the world population. Halophytes are the natural inhabitants of salt contaminated degraded soils in diverse environments and offer a multitude of potential applications for sustaining crop productivity. Salt tolerance in halophytes is associated with the plant eco-physiological adaptation that play important roles in their survival and especially adaptation to adverse conditions. Priority attention is required to exploit saline lands and halophytes for economic purposes that will ultimately reduce energy, fresh water and food crises. High nutritional values, resistance to soil containments and production of industrially important products from halophytes offer solutions to apply biotechnological applications that could play an essential role in the production of food, fodder and medicinal supplements. The reclamation of degraded lands, removal of pollutants and the production of alternative energy sources are other emerging fields of applications of these groups of extremophile plants. To increase economic potential and agro-management systems, revegetation and rehabilitation of halophytes are recommended for landscaping, phytoremediation and effluent purification. This review summarizes the perspective of halophytes existence in saline, arid and semi-arid regions as promising alternative sources for industrial applications.



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**KEYWORDS** Animal fodder; biofuel; halophytes; land degradation; medicinal plants; salt tolerance

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## Introduction

Food security is threatened by an exceptional increase in the world population while climate change and rapid industrialization impact agricultural sustainability (Anderson et al., 2020). Earth temperature has increased approximately 1 °C globally in the last century and it has been predicted that it could further rise in coming decades (Rohde et al., 2013). Due to global warming, arable land loss will be increased significantly (two folds) by the end of this century (Salvia et al., 2019). An aging population is another global issue as it requires vast supply of healthy foods. In addition, populations migrating to saline arid areas that leads to problems of water shortage, local poverty, social instability and health issues (Kwak, 2019). To subsist the global crisis of food, energy supply and environmental changes, new non-conventional and economically valuable crops are required to ensure continuous industrial development. Therefore, utilizations of marginal saline lands and brackish water are important for the sustainable development of agriculture (Khan & Qaiser, 2006). The world population is estimated to be about 9.5 billion by 2050, which will double the food requirement and will increase daily calorie intake (FAO & UNICEF, 2018). Water is a renewable resource but due to its global distribution, it is limited for human and animal consumption. About 2.5% of total water is of fresh water, from which nearly two third is frozen in glaciers (Mikosch et al., 2020).

Because of various environmental factors such as exiguous rainfall, water contamination dismal irrigation and poor agricultural systems, our productive lands are becoming more and more saline. (Mishra & Tanna, 2017). About 7% of total world area is affected by salinity and 20% area is damaged by excess salt accumulation (Gangwar et al., 2020; Mora et al., 2020). Approximately 10% of the annual crop yield is reduced due to salinity (Panta et al., 2014; Yue et al., 2020). High concentration of sodium in the soils are harmful to plant growth, germination, transpiration, photosynthesis, membrane properties, hormone regulation, enzymatic activity and it leads to the production of reactive oxygen species in plant tissues which result in plant death (Oney-Birol, 2019). Salinity today is a key restraint to agricultural productivity (Shahzad et al., 2019). Salinity when combine with heat, drought, flooding and heavy metal stress can even be more harmful to plant growth and physiological performance. Temperature above the optimal range discerned as heat stress for plants which interrupts cellular homeostatic, decelerates growth and development and sometimes causes mortality (Balfagón et al., 2019). Drought severely affects approximately 20% of the world agricultural lands and leads to the reduction of water content, closure of stomata, leads to cell shrinkage and reduces gas exchange which arrests photosynthesis (Cosgrove, 1987; Kogan et al., 2019).

Changes in the soil moisture content in water deficit conditions interrupts rates of carbon storage, carbon cycling dynamics and structures of microbial community which subsequently cause land degradations (Vicente-Serrano et al., 2020).

### **Potential of halophytes to provide sustainable solutions for economic purposes**

Salinity and other stresses are consecutive global processes and cannot be solved by simple measures. Therefore, integrative approaches are required to mitigate stress responses of plants by utilizing plants that are already salt resistant for future agricultural and industrial applications, particularly in semi-arid and arid regions. These plants can resist toxic levels of NaCl which can be injurious for other plants as they possess morphological features or adaptive mechanisms to grow better under saline condition (Garza-Torres et al., 2020).

### **Introduction to halophytes**

Plants that can grow and complete their life cycle in high salt concentrations (up to 200 mM NaCl and more) are termed as halophytes. The plant kingdom contains a small group of species belonging to halophytes (1%) which evolved highly unique abilities for salt resistance through adaptive features in harsh environmental conditions (Yuan et al., 2019). Halophytes have polyphyletic origins where less than 5% species of Poaceae, Fabaceae and Asteraceae families are halophytes. Individuals of halophytes show diversity in habitats and their eco-physiological responses toward different stress conditions. Halophytes have received increased attention in the last few years as they became model species in salt tolerance research. In addition, they are also a potential source of biomass, fuel wood, medicinal products, forage, edible oil, bioenergy, and for landscaping and ornamental applications (Table 1). In addition, halophyte are also used for phytoremediation of polycyclic aromatic hydrocarbons from contaminated saline areas (Shang et al., 2020). Among all abiotic stresses, salinity is the most prominent stress factor that limits plant growth in degraded landscape areas in

**Table 1.** Multifunctional uses of halophytes for industrial applications.

Species	Applications	References
<i>Crithmum maritimum</i>	Ornamental, vegetable, medicine	Houta et al., 2011
<i>Atriplex hortensis</i>	Food, fodder, fuel, fiber, medicine	Stihi et al., 2008
<i>Aster tripolium</i>	Pharmaceutical, cosmetics, vegetable	Lopes et al., 2016
<i>Mesembryanthemum Crystallinum</i>	Ornamental ground cover, medicine, vegetable	Seo & Ju, 2019
<i>Sporobolus virginicus</i>	Ground cover, food, domestic forage	Rao et al., 2017
<i>Pennisetum Clandestinum</i>	Ground cover, food, biofuels	Seeman et al., 2016

Pakistan and worldwide (Ijaz et al., 2020). Salinity impacts the growth of salt sensitive plants known as glycophytes compared to halophytes like mangroves e.g. *Avicinia marina*. Plant species which can grow in saline flooding conditions and are termed as hydro-halophytes while those halophytes which grow in saline arid soil are known as xerophytes (Grigore & Toma, 2017).

### **Mechanisms of salt tolerance in halophytes**

Halophytes have evolved different salt tolerance mechanisms to survive and grow optimally through an adapted metabolic steady state in a saline environment as compare to glycophytes (Figure 1) (Niu et al., 1993). Halophytes follow mainly two strategies for salt resistance, salt tolerance and salt



**Figure 1.** Adaptations in halophytes to survive in saline lands with brackish water irrigation.

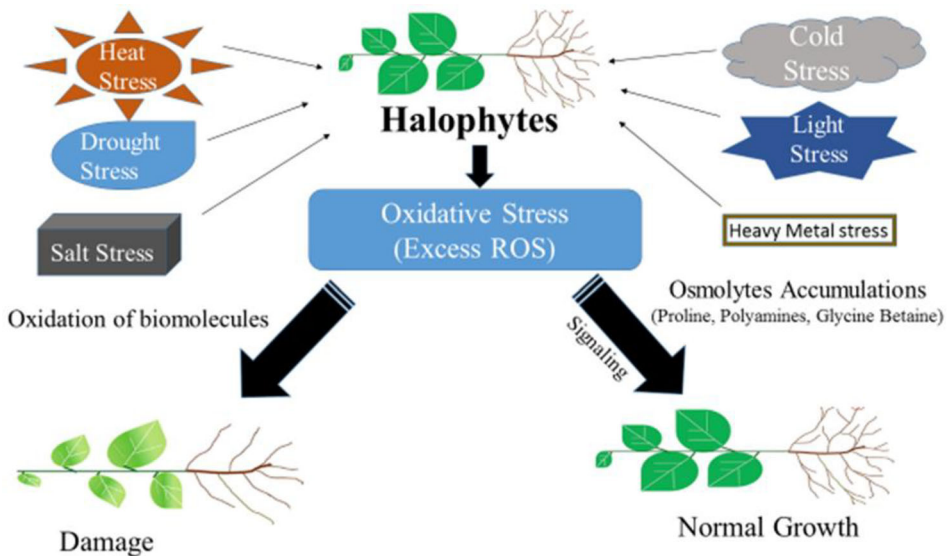
avoidance, in order to grow, germinate, reproduce and complete their life cycles (Sabovljevic & Sabovljevic, 2007).

### Salt tolerance

Halophytes can resist salt stress via cellular, tissue specific and whole plant mechanisms by adapting their morphological, anatomical and physiological status (Niu et al., 1993; Shoukat et al., 2020). Succulence causes an increase in cell size, decrease in growth or surface area of tissues leading to higher water content which helps the plant to cope with salinity stress. Proline, glycine betaine, sugars and polyols are compatible solutes to provide an osmotic balance to the ionic load in vacuoles while not interfering with other biochemical reactions (Figure 2). Some halophytes produce proline analogues under salt stress to survive due to their ability to protect the protein turnover machinery, stabilize proteins and prevent enzymes from denaturation (Shoukat et al., 2020; Thakur & Sharma, 2005). For example 4-hydroxy-N-methyl proline is a proline analogue found in *Melanleuca bracteata* (Nelson et al., 1998).

### Salt avoidance

Avoidance of NaCl is very useful mechanisms in halophytes for salinity resistant and longtime survival under adverse environmental conditions. The lower stomatal conductance reduce transpiration stream and the xylem



**Figure 2.** Mechanism of abiotic stress tolerance in halophytes by osmolytes accumulations generated by stress conditions.

loading of NaCl to maintain salt up to sub-toxic levels. Salt tolerant plant avoid the salt uptake by lower root development and physiological exclusion of toxic ions by root membranes.

### **Salt exclusion**

Salt exclusion is defined as the plant's ability to exclude NaCl through filtration at the surface of the root. Membranes of roots protect salt accumulation in the cytoplasm by excluding most of the sodium and chloride in the soil solution or by salt accumulation at root and root/stem junctions (Godfrey et al., 2019). This in turn reduce the shoot  $\text{Na}^+$  and  $\text{Cl}^-$  loading and protect plants from salt toxicity. The pericyclic and xylem parenchyma cells, root cortex and phloem cells are the key locations for salt exclusion in plants. Blocking  $\text{Na}^+$  influx into the root by salt exclusion is performed by several transporters activated by the SOS (salt overly sensitive) signaling pathway and nonselective cation channels (Tester, 2003). Two important members of the nonselective cation channels may be the cyclic nucleotide-gate channels (the CNGCs) and the glutamate-activated channels (the GLRs). In the  $\text{Ca}^{2+}$ -insensitive pathway, nonselective cation channels (NSCCs) pathways like HKT1 (high-affinity potassium transporter), KUP ( $\text{K}^+$  uptake permeases), and HAK (high affinity  $\text{K}^+$  transporter) may be involved (Munns, 2005; Tester, 2003).

The regulation of the sodium exclusion is highly associated with the salt tolerance ability of the plant. For example, *Phragmites communis* accumulate much more salts in the roots that prevent salt from entering the shoot while allowing water to pass through. Grasses from *Agropyron*, *Aeluropus*, *Puccinellia* and *Distichlis* genera exclude sodium ions significantly *Thinopyrum* has aptness to sustain negative membrane potential in roots which leads to a greater retention of potassium ions in shoots (Flowers & Colmer, 2008; Roy & Chakraborty, 2014). For instance, *Phragmites karka*, excludes additional salts from the plant body to protect themselves from the toxic effects of salinity through leaf senescence and leaf shedding (Acosta-Motos et al., 2017; Franco et al., 1997; Hameed et al., 2012). Plant roots undergo some physiological and structural changes to avoid high salt concentration through salt exclusion. Salinity leads to a shorter growth and to salt-induced alterations in the chemical and physical properties of the cell walls of the root tips. NaCl stress increases the membrane surface in root cells which show an increase in the quantity of vesicles in the epidermis and middle cortex cells (Koyro, 1997). The number of mitochondria increase in the epidermal and in the cortex cells after salt stress thus indicating an additional supply of energy for osmotic adaptation and for selective uptake and transport processes (Aslamsup et al., 2011; Koyro, 1997:

Mckay et al., 1994). Most of the salts excluded from mangroves, including *Kandelia*, *Bruguiera*, *Ceriops*, *Rhizophora*, *Avicennia*, *Sonneratia*, *Lumnitzera*, *Laguncularia* and *Aegiceras* genera, is through roots (Krauss & Ball, 2013; Slama et al., 2015; Wang et al., 2011).

### **Salt secretion**

The word salt glands refers to plant structures and functional mechanisms that directly involved in removal of excessive salt through secretion to avoid cell damage. Specialized salts glands are present in some halophytes for the excretion of additional salts onto the plant's leaf surfaces which is a well-known mechanism for regulating mineral content. Salt secretion with salt glands are recorded in 50 species in 14 angiosperm dicotyledonous families and divided in four major flowering plants groups: *Caryophyllales*, *asterids*, *rosids* and *Poaceae* (Marcum & Murdoch, 1990; Santos et al., 2016). Plant are divided in two sub groups 1) recretahalophytes and 2) secreters on the basis of the salt glands (Breckle, 1990; Liphshitz et al., 1974). Functionally there are two division in halophytes for salt secretions 1) directly secrete salts to the surface of the leaf (exo-recretahalophytes), and 2) and plants that collect salt in the vacuole of a specialized bladder cell (endo-recretahalophytes) (Breckle, 1990; Ding et al., 2010). From structural perspective most of the salt glands appear largely epidermal in origin and thus found principally on the trichomes (Esau, 1965).

Salt glands evaporate the water and the salts still remain on the leaf, this is the most common mechanisms, while some plants shed their older leaves in order to avoid excess salts accumulation in younger and growing tissues (Rozentsvet et al., 2017). Halophytes have some specialized glands to exclude salts, these glands are present on every aerial part of the plant and are rich in mitochondria. These are transit cells, not storage cells, due to lack of central vacuoles; water evaporates from these glands and salts remain on the leaf surface in the form of crystals which are blown away by wind or air (Flowers et al., 2010; Maathuis et al., 1992). Salt glands are categorized into four groups, salt bladders, multicellular salt glands, bicellular salt glands and unicellular vacuolated secretory hairs. 50% of halophytes contain salt bladders which store up to 1 M NaCl and other salts which have to be transported from roots to leaves. In the growing plant body, salt bladders sequester excessive sodium from metabolically active cells. Bladders have 10 times bigger diameter than epidermal cells and have a 1000 times higher volume hence sequester higher amounts of sodium than traditional leaf vacuoles. Ions need to cross the plasma membrane, pass the cytoplasm and get loaded into vacuoles of the salt damper (Shabala et al., 2014; Yuan et al., 2019). Salt bladders acts as a secondary epidermis as they



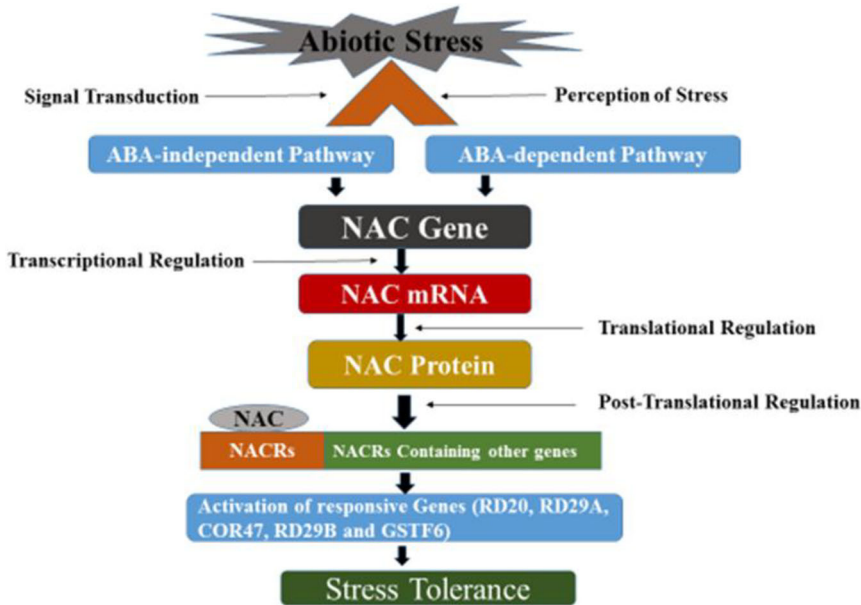
help reducing water loss and UV-induced damage to the photosynthetic apparatus. In *Chenopodium quinoa*, salt bladders are present on the stem, upper or lower leaf surface and panicles. In quinoa epidermal bladder, cells protect the photosystem from UV damage (Ruiz et al., 2016). In *Mesembryanthemum crystallinum* epidermal bladders, cells accumulate water and metabolites like beta-alanine, malate, flavonoids, cysteine, pinitol, inositol, and calcium oxalate crystals, hence provide protection through reactive oxygen species (ROS) scavenging (Morokuma et al., 2020). Salt glands secrete cations especially sodium ions, for instance in *Tamarix aphylla* cation excretion is as follows: divalent cation > monovalent cation (Berry, 1970), in *Glaux maritima*  $\text{Na}^+ > \text{K}^+ > \text{Ca}^{2+}$  (Rozema, 1977) and in *Limonium vulgare*  $\text{Na}^+ > \text{K}^+ > \text{Ca}^{2+}$  (Waisel, 1972). Long-term adaptation to the saline environment is selective secretion of salts. Still, the mechanism for the preferential secretion of certain ions has not been explained in detail yet (Kobayashi, 2007). The excretion pathway of salts via the bicellular salt glands is not well understood (Oi et al., 2014).

### **Purpose of halophyte cultivation**

Halophytes are very useful for agricultural, ecological and industrial purposes due to the production of valuable products in their tissues (Jayatissa et al., 2008). Salt resistant plants are important for the maintenance of the ecological balance toward agricultural and nonagricultural economic outcomes (Nikalje et al., 2019). Halophytes can be exploited for important bioactive metabolites for commercial value and could be cultivated for food, fodder/forage, fuel and medicinal crops on saline lands with the help of salty water irrigation. Many salt resistant plants are hyper-accumulators of different heavy metals and salts and are being utilized for environmental remediation. *Halopyrum mucronatum* shoots accumulate 644 mg/kg iron, 63 mg/kg zinc and 9.2 mg/kg chromium (Liang et al., 2017). *Ipomoea pes-caprae* accumulates 3.3 mg/kg lead in their shoots while *Heliotropium bacciferum* shoots contain 20.5 mg/kg lead or >20 mg/kg ions (Mujeeb et al., 2020). For instance, *Salsola imbricate* plants grown on industrial area store/sequester 10 mg/kg lead and 98 mg/kg sodium ions in their shoots (Nikalje et al., 2019).

### **Identification of genes that improve salt tolerance**

Genes which are regulated under salt stress can be recognized either at RNA or protein levels but finding the key genes is still improbable, because a multitude of mechanism are operating concurrently to mitigate salt stress. Hence, it is very important to highlight those mechanisms in detail to



**Figure 3.** Role of NAC transcription factors in plant stress tolerance.

develop a better understanding of stress tolerance and utilize the knowledge in crop improvement using biotechnological aspects (Flowers & Muscolo, 2015; Kosová et al., 2013). Halophytic genomes are more complex due to the presence of additional transposons in gene sequences. Overexpression of aquaporins can improve a plant's tolerance to abiotic stress. SpAQPI is an aquaporin gene in *Sesuvium portulacastrum* that has been used to enhance salt tolerance in transgenic tobacco plants (Chang et al., 2016). Liu et al. (2017) observed improved salt tolerance of *Arabidopsis* by inserting PutNHX1 and SeNHX1 genes from *Puccinellia tenuiflora* and *Salicornia europaea*. NAC is one of the largest family of stress responsive transcription factors in plants where NAC (NAM, AATAF and CUC) is the combination of three transcription factor (Hu et al., 2006). NAC transcription factors shows organ specific expression and the level of expression is affected by stress stimuli. NAC transcription factors have very complex networks of signal transduction (Samo et al., 2019). Under abiotic stresses, NAC transcription factors play a vital role in ABA-dependent and ABA-independent pathways, NAC proteins and their corresponding cis-acting elements (NACRS) are responsible for constituting NAC regulons (Figure 3). Overexpression of these factors in transgenic plants also stimulate other stress responsive genes like RD20, RD29A, COR47, RD29B and GSTF6 (Flowers et al., 1977; Wu et al., 2018). Overexpression of RD26 for instance leads to stress-induced morphological changes in plants such as larger leaf blades and shorter petioles in RD26-overexpressing plants while

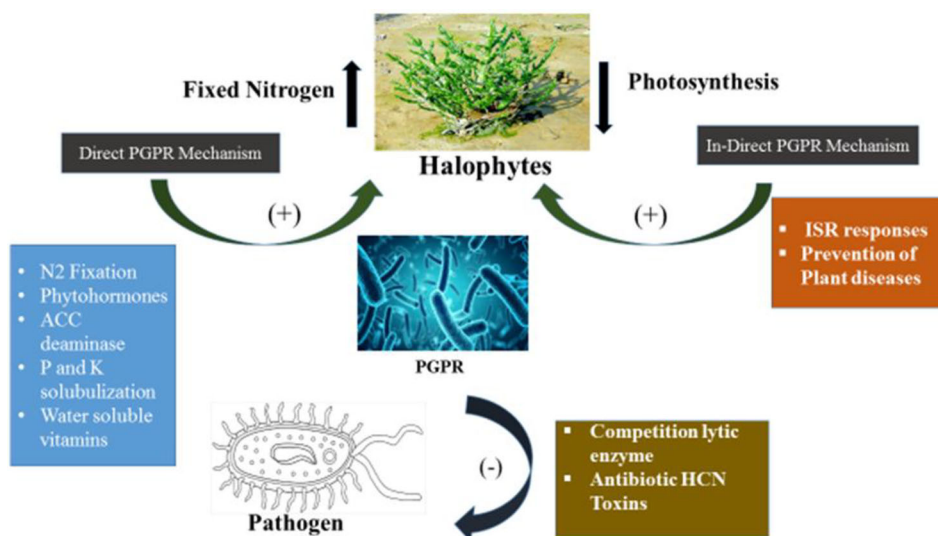
smaller leaf blades and longer petioles were found in RD26-repressed plants (Nakashima et al., 2012).

Under stress, most plants slow down cell growth to secure resources to overcome stress conditions. CBF/DREB transcription factors binds to the DRE/CRT element. DRE/CRT element present in the promoter of stress responsive genes which leads to the ectopic expression of CBF/DREB proteins. CBF/DREB proteins influence the cell division and expansion machinery under stress. However, CBF1 and DREB1A both improve cold stress tolerance at 1 °C and even more at 10 °C in *Arabidopsis* (Chinnusamy & Zhu, 2003; Li et al., 2012; Sahu & Shaw, 2009; Zhu, 2001).

In *Paspalum vaginatum*, the metallothioneine gene plays a vital role in salt tolerance. Under salt stress, *Spartina alterniflora* upregulates the expression of genes like cation transport protein, plasma membrane protein 3 and vacuolar ATPase (Roy & Chakraborty, 2014). The expression of the AcBADH gene from *Atriplex centralasiatic* and SIBADH gene from *Suaeda liaotungensis* enhances glycine betaine accumulation in roots and leaves which is known to protect organisms against salinity stress. The vacuolar H<sup>+</sup>-pyrophosphatase promoter from *Thellungiella halophila* (TsVP1) was cloned and compared with the AVP1 promoter from *Arabidopsis thaliana*. Sequence analysis indicated that both promoters have seven same motifs at similar positions. Transgenic *Arabidopsis* were produced with expression of the GUS reporter gene to determine in which tissues these promoters are active. The GUS reporter gene with TsVP1 promoter had strong expression (5fold) in roots under salt stress (Sun et al., 2010). In spinach, 300 mM NaCl induced BADH expression by 3 fold while in barley by 8 folds, which indicates that the BADH gene expression is induced by salinity (Karthik et al., 2014; Yin et al., 2002; Yu et al., 2014; Yuan et al., 2016). Glycine betaine and choline both play important roles is osmotic adjustment of plants under stress conditions. They act as osmo-protectant protecting the sub-cellular structures, transcriptional and translational machineries and intervene as molecular chaperones in refolding of enzymes and help in stabilizing photosystem II to avoid oxidative stress (Wani, 2013).

### ***Improvement of halophytic biomass by growth promoting bacteria***

Plant growth promoting (PGP) bacteria are involved in various metabolic interactions that influence plant fitness and soil quality, thereby increasing agricultural productivity and stability of soil (Rajput et al., 2019). Microorganisms that have plant growth promoting traits are an effective strategy to alleviate biotic or abiotic stress effects on plants through several stress resistant mechanisms (Busby et al., 2017). These microbes improve soil-water-plant relationships, exploit phyto-hormonal signaling and trigger



**Figure 4.** Mechanism of plant growth promoting rhizobacteria for enhancement of halophytes growth.

various mechanisms to enhance stress tolerance. PGP bacteria improve plant growth by direct or indirect mechanisms. In direct mechanisms, PGP rhizo-bacteria enhance plant growth by nitrogen fixation for plant use, ammonia production, solubilization of mineral phosphate, sequestration of iron for plants, production of phytohormones and improve biological plant pathogen control. In indirect mechanisms, PGP rhizo-bacteria prevent infectious diseases of plant roots, induce systematic resistance responses to enhance defense against pathogens and induced the production of hydrogen cyanide which chelate iron and make it available to plant roots (Figure 4) (Paul & Lade, 2014; Qin et al., 2017).

Microbes associated with the rhizosphere of halophytes can tolerate up to 30% of NaCl concentration and improve soil fertility and quality to enhanced plant growth under stress environments (Ruppel et al., 2013). *Azospirillum halopraeferens* and *Bacillus licheniformis* increase *Salicornia bigelovii* growth when irrigated with seawater. *Salicornia brachiata* tolerates saline stress by reducing ethylene production by 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity (Handa & Mattoo, 2010; Kirby, 2016; Rahman et al., 2017). *Rhizobium* promotes plant growth as it is nitrogen fixing bacteria and nitrogen is required for the synthesis of nucleic acids, enzymes, proteins and chlorophyll hence it is very important for plant growth and development (Ju et al., 2020). *Basidiomycota* and *Ascomycota* are very effective metal detoxifying fungal agents which can boost salt resistance of plants by improving the mineral and potassium ion uptake, maintaining the sodium potassium ratio and osmotic balance by

increasing osmolytes concentrations inside plant cells (Bukhori et al., 2020). *Trichoderma harzianum* induces the growth of *Suaeda salsa* by increasing water uptake, the concentration of proline, organic acids, soluble sugars, amino acids, superoxide dismutase activity and decreasing malondialdehyde concentration (Ma et al., 2018). Accumulation of compatible solutes accommodates the ionic balance of vacuoles without disrupting intracellular biochemical reactions, have minimal effect on pH and the capacity to preserve enzymes activities. *Cryptococcus neoformans*, *Stagonospora nodorum*, *Aspergillus niger* and *Fusarium graminearum* synthesize trehalose which protects plants cells by preventing protein denaturation under osmotic stress conditions (Cervantes-Chávez et al., 2016; Zhang et al., 2019). Sulfate reducing bacteria develop metal tolerance in *Spartina maritime* by sulfate reduction which produces hydrogen sulfide that can react with heavy metal ions to form insoluble metal sulfides or reduce metal directly into less toxic or less soluble forms by enzymatic reactions (Quillet et al., 2012; Nikalje et al., 2017).

### **Application of biochar and compost and their mixture**

Soil health is very important for plant growth and food production, thus degraded soils require new sustainable technologies to recoup. Biochar is a solid material formed from thermal decomposition of plants while the transforming biomass forms into bio-oil and syngas as byproduct (Cha et al., 2016). For the improvement of soil health and crop yield, biochar is applied due to its multiple benefits; it energizes soil fertility, as it adds nutrients to the soil like potassium, phosphorus and micronutrients or holds nutrients from the soil itself, and positively affects useful microorganisms (Debode et al., 2020). Biochar application rates less than 5% biochar could be sufficient to recover degraded soils (Zheng et al., 2018). Biochar increases the pH of the soil which reduces the acidity of contaminated soil, minimizes methane or nitrous oxide emissions. Biochar is also capable of conservation of soil water retentions thus reducing drought effects on crop yields (Rawat et al., 2019).

Biochar and compost seem useful for biomass production as found in *Phragmites karka* due to efficient water retention and improved photosynthesis (Abideen et al., 2020). For instance, application of sole biochar improved the water supply of *Chenopodium quinoa* in sandy soil (Buss et al., 2012). Growth of *Sesbania canabina* and *Kosteletzkya virginica* increased by 1.5% by the application of biochar and compost while the total biomass increased by 309% and 70%, respectively (Luo et al., 2017; Qin et al., 2017). However, biochar has several limitations, including adverse physical changes to the soil as well as to soil biota, leading to leaching of nutrients, and contaminant mobility (Nair et al., 2017). In order

to abolish the harmful effects of biochar it is recommended to combine biochar with other soil amendments like compost (Abideen et al., 2020). Combination of biochar and compost exerts synergic effects on soil fertility, crop yield and reduces soil contaminant mobility. Combination of biochar and compost at the rate of 1.5% significantly increased the growth of *Sesbania canabina*, *Phragmites karka* and *Kosteletzkya virginica* while combination at the rate of 10% leads to the harmful impacts on growth (Adli, 2019; Wu et al., 2017).

### **Role of humic acid in plant salt tolerance mechanisms**

Humic acid is not a fertilizer but a soil component that can enhance photosynthesis, respiration, cell membrane permeability, water holding capacity, phosphate uptake and it reduces the uptake of sodium ions or toxic elements (Guo et al., 2019). Humic acid provide energy to soil microbes thus making soil more fertile improving root growth by stimulating auxin signaling (Gayathri et al., 2020). Humic acid stimulates H<sup>+</sup>-ATPase activity in cell membranes which has very important roles in many biochemical pathways and it also influences many metabolic processes like photosynthesis, respiration and nucleic acid synthesis (Matuszak-Slamani et al., 2017). Humic acid increases the concentration and activity of reactive oxygen species scavenging enzymes and anti-oxidative enzymes to disable oxygen free radicles produced in plants under salt stress (Ullah et al., 2018). In *Terminalia arjuna*, plant height, number of leaves, leaf area, concentration of chlorophyll, total carotenoids, nitrogen, calcium, phosphorus and proline are significantly increased under humic acid treatments (El-Kady & Borham, 2020). Root traits and aboveground biomass of *Lycium ruthenicum* increased by 60.57% when treated with humic acid (Feng et al., 2020).

### **Role of gibberellin, auxin and ascorbic acid in salt tolerance**

Phytohormones are synthesized and translocated in different tissues and consequently, hormone transporters are essential for precise regulation of plant growth and development. Phytohormones are also called plant growth regulators and act as chemical messengers involved in the regulation of plant responses against stresses (El-Maboud, 2019). Salt stress rapidly induces the abscisic acid level by activation of abscisic acid biosynthesis genes like zeaxanthin oxidase and ABA-aldehyde oxidase as it helps in osmotic adjustment by closing stomata and through accumulation of osmo-protectants (Rasheed et al., 2019). When abscisic acid was sprayed on *Prosopis strombulifera* under salinity, it had higher levels of soluble carbohydrates and improved root development (Llanes et al., 2019). *Suaeda maritima*

exhibited a higher growth rate with abscisic acid treatment under saline conditions (Somasundaram, 2019). Auxin plays an important role in organogenesis, cell elongation, tissue development and apical dominance in plants. Under high salt stress, plants produce auxins by overexpression of auxin biosynthesis gene like YUCCA3 (Bouzroud et al., 2019). Halotropism is a response of plant roots to avoid a saline environment. *Limonium bicolor* contain multicellular glands which show positive halotropism by regulating auxin under salt stress (Leng et al., 2019). *Tamarix aphylla* showed 79% maximum rooting response under 2 mg/l auxin treatment (Sharma et al., 2018). Gibberellins produced by environmental and developmental stimuli, interact with other hormones to regulate metabolic pathways hence they are involved in seed germination, endosperm mobility, flowering, leaf expansion and stem elongation. Under salt stress, gibberellins interact with polyamines to regulate ion accumulation in plant tissues (Gonzalez & Palomares, 2019; Zulfiqar et al., 2019). Ahmed et al. (2014) studied the seed germination rate of *Halogeton glomeratus*, *Lepidium latifolium*, and *Peganum harmala* under different salt treatments (0-400mM NaCl) and with kinetin, thiourea and gibberellin application. Dormancy increased progressively with increased salt treatments, while gibberellins induced seed germination observed only in *Lepidium latifolium*. Kinetin enhanced seed germination of *Halogeton glomeratus* and *Peganum harmala* but not in *Lepidium latifolium* while thiourea improved seed germination in all tested species under all saline treatments.

In many halophytes, such as *Limonium stocksii*, ascorbic acid, a non-enzymatic antioxidant, plays a key role in salt tolerance which improves plant growth by quenching reactive oxygen species. Synthesis of ascorbic acid under stress conditions improves cell wall expansion, cell cycle progression, recycling of  $\alpha$ -tocopherol (lipid soluble antioxidant) and enhances synthesis of flavonoids and anthocyanin to protect plants from photo-damage under saline conditions (Hameed et al., 2015). Ascorbic acid (40–60 mM) and 96% ethanol improve the seed germination rate by 10–30% in *Crithmum maritimum* under salt stress (Meot-Duros & Magné, 2008). Pretreatment of seeds with ascorbic acid reduces the injurious salinity effects in *Atriplex stocksii* and *Suaeda fruticosa* while in *Arthrocnemum macrostachyum*, *Haloxydon stocksii*, *Desmostachya bipinnata* and *Aeluropus lagopoides* seed germination remained unchanged (Khan et al., 2006).

### **Current status (from past to present)**

Halophytes can be an important source of plant-derived products for industrial applications by utilizing biotechnological methods which will be described in the following. For the increasing human population,

agricultural prime lands and freshwater resources should be allocated for growing food crops. In contrast, millions of hectares of saline lands can be used for the cultivation of halophytes having conventional benefits with the help of biotechnological tools.

## Applications of halophytes in industrial purposes

### *Use of halophytes as food and fodders*

Halophytic biomass contains numerous edible components which can be a useful resource for dietary fibers, essential minerals, fatty acids, bioactive compounds and essential amino acids (Feng et al., 2018). *Arthrocnemum indicum* and *Halocnemum strobilaceum* are good sources of nutrients containing high levels of protein, fatty acids, fibers, minerals and vitamin C (Khan et al., 2020). The fatty acid profiles of some halophytes grips attraction for the production of cooking oil with high poly-unsaturation ranging between 70% and 80% equivalent to conventional seed oils (Khan & Qaiser, 2006). Shoots of various halophytes are used as vegetables, salads and pickles like *Salicornia bigelovi*, *Suaeda maritima* and *Portulaca oleracea*. *Salicornia europaea* has dietary fibers and flavonoids, used for treatment of obesity (Duarte et al., 2018; Kim et al., 2019). *Salicornia europaea* can be used to produce an edible oil while *Salicornia bigelovii* is a good source of omega-3 polyunsaturated fatty acids. Seeds of *Salvadora oleoides*, *Suaeda fruticose*, *Halogeton glomeratus*, *Haloxyton stocksii* and *Salvadora persica* contain optimal edible oil quality (Boestfleisch et al., 2014; Karthivashan et al., 2018; Weber et al., 2007). *Crithmum maritimum*, *Triglochin maritima* and *Halimione portulacoides* have been used as food for a long time. *Triglochin maritima* has ten times more proline while *Halimione portulacoides* has higher concentrations of glycine betaine than most other plants (Boestfleisch & Papenbrock, 2017). A polar lipidome profiling approach characterized more than 200 lipids species in fresh branch tips of *Salicornia ramosissima* and leaves of *Halimione portulacoides* which demonstrated that halophytes are a nutritional source of food (Maciel et al., 2020). Mzoughi et al. (2019) explored the nutritional and antioxidant properties of halophytes from the Salicorniaceae and Amaranthaceae families. All species had high levels of proteins, fatty acids, minerals and also exhibited low toxicity making them suitable for human consumption. *Chenopodium quinoa* is considered a pseudo-cereal with very well-documented benefits for human health. These benefits include high protein contents of the grains, being one of the few super food products from vegetal origin containing all nine essential amino acids (Mota et al., 2016). *Chenopodium quinoa* is also rich in fiber and vitamins from the B group (especially folic acid), vitamins C and E (Pereira et al., 2019). In



addition, the grains contain calcium, phosphorus, iron, magnesium, potassium, manganese and zinc, together with high concentrations of antioxidants (tocopherols), and unsaturated lipids, mainly represented by linoleic and linolenic acids (Abugoch et al. 2008; Pereira et al., 2019). Furthermore, as it is gluten free, thus providing a suitable product for people with celiac disease (Abugoch, 2009).

Due to the nutritional content and the high digestibility of halophytes, they can also be used for the feed of animals, however high salt concentrations may reduce the food quality of many halophytes. *Panicum turgidum* is a very useful salt tolerant plant which is used for cattle feed. It is being produced annually in tons/hectare biomass as fodder and proved better animal fodder than maize plants (Atia et al., 2019). *Atriplex* species fulfill the requirements of an effective fodder which can be grown at moderate salt levels. *Salicornia bigelovii* is a shrub having 14.5% crude protein which used as an effective diet for camels (Joshi et al., 2018). To improve the milk quality of buffaloes, *Cressa cretica* is used as fodder. Similarly, *Sporobolus* species are extensively used as forage. *Salvadora*, *Acacia*, *Zizyphus* and *Prosopis* are tree species of arid regions, which are used as fodder due to effective accessibility. The mineral contents in forage varies according to the grade of land and water salinity (Kumar et al., 2018; Nafees et al., 2019; Öztürk et al., 2019) (Table 2).

### Biofuel potential of halophytes

Biofuel production from halophytes reduces the competition for fresh water or fertile land demands. Table 3 demonstrated the list of halophytes suitable for lignocellulosic biomass and bioethanol production. *Euphorbia*

**Table 2.** List of halophytes used as food and fodder commodities grown on saline lands.

Species	Plant parts	Nutritional values	References
<i>Chenopodium quinoa</i>	Seeds	Essential amino acid, proteins, lipids, vitamins, fibers and minerals	Pourshahidi et al., 2020; Vilcacundo & Hernández-Ledesma, 2017
<i>Sesuvium portulacastrum</i>	Leaf/stem	Rich in calcium and iron	Slama et al., 2017
<i>Crithmum maritimum</i>	Leaf	vitamins and minerals rich	Pereira et al., 2017
<i>Zostera marina</i>	Seeds	Starch, proteins and fats	Panta et al., 2014
<i>Prosopis glandulosa</i>	Seeds/ pods	40% protein content, lipids, carbohydrates and minerals	González-Montemayor et al., 2019; Setshogo et al., 2020
<i>Tetragonia tetragonioides</i>	Leaf	Amino acids	Neubauerová et al., 2020
<i>Cochlearia officinalis</i>	Leaf/stem	Vitamin C	Welcome & Van Wyk, 2019
<i>Batis maritima</i>	Root/stem	Amino acids and antioxidants	Boxman et al., 2018
<i>Pennisetum typhoidea</i>	Seeds	Rich in vitamin B, gluten free	Gadir & Adam, 2007
<i>Portulaca oleracea</i>	Leaf/ stem	Vitamin A, vitamin C, omega 3 fatty acids and rich in calcium	Uddin et al., 2014
<i>Distichlis palmeri</i>	Seeds	Fats, carbohydrates, proteins and fiber, higher than wheat.	Dagar, 2018
<i>Atriplex hortensis</i>	Leaf	Rich in proteins	Vila Roa, 2018

**Table 3.** List of halophytes used for lignocellulosic biomass cellulose, hemicellulose and lignin (%) for bioethanol production.

Species	Cellulose	Hemicellulose	Lignin	References
<i>Calotropis procera</i>	12.33	11.02	5.00	Radhaboy et al., 2019
<i>Suaeda monoica</i>	10.67	11.33	2.33	Patel et al., 2019
<i>Panicum virgatum</i>	45.01	13.02	12.01	Capecchi et al., 2016
<i>Suaeda fruticose</i>	8.67	21.05	4.67	Salem et al., 2019
<i>Phragmites karka</i>	26.15	29.02	10.33	Joshi et al., 2018
<i>Arthrocnemum indicum</i>	11.33	13.02	7.01	Nikalje et al., 2019
<i>Sporobolus ioclados</i>	15.33	30.60	2.01	Xu et al., 2011
<i>Desmostachya bipinnata</i>	26.67	24.68	6.67	Smichi et al., 2018
<i>Urochondra setulosa</i>	25.33	25.01	6.33	Atia et al., 2019
<i>Aeluropus lagopoides</i>	26.67	29.33	7.67	Naz et al., 2018
<i>Tamarix indica</i>	12.17	24.67	3.33	Sun et al., 2011
<i>Eleusine indica</i>	22.12	29.67	7.01	Abideen et al., 2011
<i>Salsola imbricate</i>	9.02	18.33	2.67	Oueslati et al., 2006
<i>Cenchrus ciliaris</i>	22.67	23.17	7.00	Encinas-Soto et al., 2016
<i>Lasiurus scindicus</i>	24.67	29.67	6.00	Abideen et al., 2011

*tirucalii* plants have been recommended for biofuel production by growing them on saline lands (Sharma et al., 2016). The values of lignocellulosic biomass makes species of *Phragmites*, *Cressa*, *Salicornia*, *Salsola*, *Panicum*, *Tamarix* extensively more promising candidates for bioethanol production (Kumar et al., 2018; Mukhtar et al., 2019). Many countries obtain biofuel from food crops which leads to food versus energy competitions. For the production of biodiesel, plant seed oil is a suitable resource. The biomass of these plants contains fatty acid methyl esters which can be used in conventional engines without any modifications (Table 4) (Duarte et al., 2017; Kumar et al., 2019). A number of *Suaeda* species have been investigated and it has been demonstrated that their oil seed is prospective with excellent engine performance parameters (Li & Song, 2019). *Salvadora* species rich in oil, lignin, cellulose and hemi-cellulose, which make it one of the best candidates for biofuel production as well as for cosmetic and soap production (Panta et al., 2014). *Ricinus communis* contains up to 40%, *S. bigelovii* 30%, *Kosteletzkya virginica* have 22% and *Kosteletzkya pentacarpos* accumulate about 20% seed oils of total dry weight and pose optimal engine value parameters for biodiesel production which could be used to replace other oil producing crops (Munir et al., 2020; Singh et al., 2019). Many halophytes which are suitable for the oil industry are presented in Table 4. Akinshina et al. (2016) reported *Karelinia caspia* as a most auspicious source of biomass yield and biogas production. *Panicum turgidum* is basically used as animal fodder in Pakistan but its chemical composition and multiple harvest in a season makes it promising candidate for biofuel production (Abideen et al., 2011).

### **Secondary metabolites and medicinal use of halophytes**

Under salt stress, the biosynthesis and accumulation of secondary metabolites with medicinal properties can be enhanced for plant protection against

**Table 4.** List of halophytes seed oil contents in (%) for biodiesel production.

Species	Oil %	References
<i>Suaeda fruticosa</i>	25.02	Zhao et al., 2018
<i>Halopyrum mucronatum</i>	22.70	Parida et al., 2019
<i>Alhaji maurorum</i>	21.90	Mohammadkhani & Servati, 2018
<i>Atriplex heterosperma</i>	15.80	Patel et al., 2019
<i>Arthrocnemum macrostachyum</i>	25.02	Kafi & Salehi, 2019
<i>Salicornia bigelovii</i>	30.02	Folayan et al., 2019
<i>Cressa cretica</i>	23.30	Al-Snafi, 2016
<i>Suaeda salsa</i>	22.02	Zhao et al., 2019
<i>Haloxylon stocksii</i>	23.20	Baber et al., 2018
<i>Kosteletzkya virginica</i>	30.02	Moser et al., 2016
<i>Atriplex rosea</i>	13.20	Toqeer et al., 2018
<i>Ricinus communis</i>	55.01	Roy et al., 2020
<i>Crithmum maritimum</i>	40.01	Alves-Silva et al., 2020
<i>Descurainia sophia</i>	44.17	Weber et al., 2007
<i>Suaeda torreyana</i>	25.27	Patel et al., 2019

oxidative injury (Table 5). Qasim et al. (2016) investigated 100 medicinal halophytes and non-halophytes plants and concluded that salt resistant plants have higher antioxidant capacity and total phenolic content than non-halophytes. *Rhizophora mangle* is used to cure diarrhea, *Chenopodium album* for constipation, *Portulaca oleracea* for stomach ache and *Zygophyllum simplex* for helminthiasis (Ferreira-Machado et al., 2014; Qasim et al., 2011; Qureshi & Bhatti, 2008). *Ziziphus nummularia* is used for skin infections. *Heliotropium curassavicum* is used for healing boils while a leaf paste of *Aerva javanica* and roots of *Cyperus rotundus* are used for skin infections as well as acne (Boestfleisch et al., 2017; Faustino et al., 2019). For the treatment of asthma, sore throat and cough, leaves of *Salvadora persica* and whole plants of *Leucas urticifolia* are used. Roots of *Zaleya pentandra* are used for influenza while *Aerva javanica* and *Capparis decidua* for chest infections (Nazir, 2019). *Aerva javanica* is used for headaches. *Suaeda glauca* has anti-neuroinflammatory and anti-oxidative effects. *Sonchus brachyotus* showed anti-bacterial activity. *Triglochin maritimum* has antioxidant and anti-fungal activity (Alnuqaydan & Rah, 2019; Kim et al., 2019; Nazar et al., 2018; Turcios & Papenbrock, 2019a).

### Bio-saline agriculture

Improper irrigation practices result in an increase of soil salinity which can be harmful for conventional crop growth and yield. To resolve this problem, salt tolerant plants can be exploited to reduce land competition and efficient resource utilization by deploying bio-saline agriculture (Blume et al., 2012; Brown & Funk, 2008). *Acacia ampliceps*, *Eucalyptus occidentalis*, *Prosopis juliflora* and *Casuarina equisetifolia* have been adapted in various saline regions of Pakistan for saline agriculture (Marcar et al., 2003). *Deplachne fusca* is an excellent crop to grow in waterlogged saline areas.

**Table 5.** Tissues specific medicinal properties of halophytes which can be cultivated on saline lands.

Species	Parts use	Medicinal uses	References
<i>Amaranthus viridis</i> L.	Whole plant	Constipation	Faiz et al., 2019
<i>Chenopodium album</i> L.	Whole plant	Constipation	Jahan et al., 2019
<i>Cleome brachycarpa</i> Vahl.	Whole plant	Itching, inflammation, joint pain, skin diseases	Naeem et al., 2019
<i>Corchorus depressus</i> L.	Whole plant	Dysuria	Siringo et al., 2020
<i>Desmostachya bipinnata</i> L.	Root	Carbuncle	Sharma, 2019
<i>Glinus lotoides</i> L.	Whole plant	Blood purifier	Banerjee et al., 2019
<i>Ipomoea pes-caprae</i> L.	Whole plant	Diarrhea, vomiting, legs inflammation, pains, piles	Yakkala & Rao, 2019
<i>Cleome viscosa</i> L.	Whole plant	ear infection, deafness pain	Narsimhulu et al., 2019
<i>Rhizophora mangle</i> L.	Fruit/ root/whole plant	Diarrhea, diabetes	Rodríguez-García et al., 2019
<i>Salvadora persica</i> L.	Leaves/ fruit	Cough, asthma	Hammad et al., 2019
<i>Heliotropium curassavicum</i>	Root	Boils	Singh & Sharma, 2019
<i>Trianthema portulacastrum</i>	Leaves	Asthma	Falade et al., 2019
<i>Citrullus colocynthis</i> L.	Fruit/ root	Toothache, bleeding, piles, constipation, diabetes, leucorrhoea, Asthma	Ostovar et al., 2020
<i>Acacia nilotica</i> L.	Leaves/ grass/ bark	Asthma, demulcent, diarrhea	Kagne & Rajbhoj, 2019
<i>Cynodon dactylon</i> L.	Whole plant	Wounds, cuts	Fatima et al., 2019
<i>Gynandropsis gynandra</i> L.	Root/leaves	Stomach ache, skin inflammation	Govindappa, 2015
<i>Peganum harmala</i> L.	Whole plant/seed	Anti-microbial, Rheumatism, back pains, colic	Batyrbekov, 2018
<i>Portulaca oleracea</i> L.	Leaves/ fruit/seed	Gastric trouble, Stomachache	Farkhondeh et al., 2019
<i>Cyperus rotundus</i> L.	Root	Carbuncle, Acne	Jouybari et al., 2018
<i>Cressa cretica</i> L.	Leaf	Sores	El-Alfy et al., 2019
<i>Withania somnifera</i> L.	Fruit/leaves	Anthelmintic, tuberculosis, leucorrhoea	Umaarasu et al., 2019
<i>Heliotropium strigosum</i>	Whole plant	Boils, wounds, Ulcer	Singh & Sharma, 2019
<i>Leucas urticifolia</i> Vahl.	Whole plant	Cold, gastrointestinal problems, fever	Noronha et al., 2020
<i>Salsola imbricata</i> Forssk.	Whole plant	Vascular hypertension, Insecticidal	Ajaib et al., 2019
<i>Fagonia indica</i> Burm	Whole plant	Malarial fever, Skin eruption	Latif et al., 2019
<i>Zaleya pentandra</i> L.	Root	Influenza, phlegmatic cough, cancer	Mughal et al., 2020
<i>Digera muricata</i> L.	Whole plant	Constipation	Jain et al., 2019
<i>Tribulus terrestris</i> L.	Root	Urinary calculi, Kidney stones, spermatorrhea, general debility	Hamidi et al., 2019
<i>Zygophyllum simplex</i> L.	Leaves	Helminthiasis, asthma	Amaral-Machado et al., 2020

Shoots of *Salicornia* can be used as a vegetable and the plants grow rigorously on extreme saline lands. Seeds of *Salicornia bigelovii* are rich in proteins and oils and have an exceptional phytochemical profile. High yields can be achieved by multiple harvesting in saline conditions. *Sesuvium portulacastrum* accumulates salts to high concentrations without toxic effects in leaves therefore it has been highly recommended for soil desalination (Lane et al., 2016; Muchate et al., 2016; Rahman et al., 2019). Atzori et al. (2017) claimed *Mesembryanthemum crystallinum* as a high value saline crop due to its medicinal properties. *Prosopis juliflora*, *Acacia nilotica* and *Tamarix articulata*, (tress) *Ziziphus mauritiana*, *Carissa carandus*, *Syzygium*

*cuminii* (fruiting tress), *Chloris gayana*, *Leptochloa fusca* and *Brachiaria mutica* (grasses) are recommended for saline soils revegetation (Dagar et al., 2006). *Vetiveria zizanoides* shows 72.6–78.7 Mg ha<sup>-1</sup> fresh shoot and 1.19–1.73 Mg ha<sup>-1</sup> root biomass yields when irrigated with saline water on calcareous saline soils (Akhzari & Aghbash, 2013; Dagar, 2005; Xia et al., 2000). Suthar et al. (2018) examined *Tecomela undulata*, *Prosopis cineraria*, *Salvadora oleoides* and *Acacia Senegal* under salt and drought stress and concluded that *Salvadora oleoides* has a dual potential to tolerate both stresses simultaneously and thus proved to be a potential candidate for bio-saline agriculture.

### **Revegetation and rehabilitation using halophytes**

Salinity and drought are the major stress factors which can be better tolerated by halophytes than most other plants. Establishment of plants on abiotic stress impacted areas (salinity and drought) involving native species is known as revegetation (Yan et al., 2020). These adaptive properties make halophytes valuable as good practice for revegetation and rehabilitation in order to maintain biodiversity. Growing halophytes on marginal lands is applicable and an environmentally friendly approach for rehabilitation, revegetation and phytoamelioration of the salt-affected soils. The rehabilitation of these salt-affected soil is necessary as these lands can be reused for agricultural resources, such as grazing and as turf grass for sports. Land rehabilitation is also useful as it enhance species biodiversity and limits erosion of soil by using land and water unsuitable for conventional crops. Soil effected due to secondary salinization can be reduce by many strategies to rehabilitate saline-sodic landscapes, such as scraping to remove salt crusts to allow plant establishment, drainage installation, and irrigation to leach Na<sup>+</sup> from the root zone (Siyal et al., 2002). Use of salt-accumulating plants which mostly belongs to family *Amaranthaceae*, can be suitable species for rehabilitation and revegetation for salt effected areas (Devi et al., 2008). Many halophytes including *Sclerolaena longicuspis*, *Atriplex halimus*, *Cenchrus ciliaris* and *Lotus creticus* *Tecticornia pergranulata* and *Frankenia serpyllifolia* are reported as promising species for arid rangeland rehabilitation, because of their adaptation and palatability (Shaygan et al., 2018). Biomass of plants for rehabilitation at saline degraded lands should be composed of a balanced ratio of total protein, nitrogen, neutral detergent fiber, acid detergent fiber, ash and lignin (Tlili et al., 2020). *Phlomis purpurea*, *Alternanthera bettzickiana* and *Limonium stocksii* have great ornamental uses due to the astonishing color of their leaves and flowers. They have the ability to survive under environmental stresses (Akhzari & Aghbash, 2013; Ozturk

et al., 2018). Most of the halophytes in Pakistan are usually herbs and shrubs which can grow in poor quality soils and brackish water to promote conventional irrigation system. Saline irrigation holds great potential for ensuring high pecuniary returns in saline prone areas (Panta et al., 2018).

### **Phytoremediation and effluent purification**

In recent years, mine tailing, industrial waste, excess use of fertilizers and atmospheric deposition greatly affected saline areas. Metal storing capacity, uptake and detoxification of salts are specific mechanisms of halophytes that can be used for heavy metal and salt remediation (see Tables 6–8) (Nedjimi & Daoud, 2009). *Zygophyllum* genus are used for both polluted soils as well as for effluent purification. *Typha domingensis*, *Arthrocnemum macrostachyum*, *Dittrichia viscosa*, and *Prosopis juliflora* remediated heavy metals from effluents. *Phragmites australis*, *Phragmites karka*, *Tamarix smyrnensis*, *Medicago sativa* and *Glycine max* are suitable candidates to clean oil and gas polluted soils and water (Nie et al., 2011; Prasad & Tewari, 2016). Leaves of *Tamarix smyrnensis* have glands which excrete excessive salts and metal ions. Plants from the Brassicaceae family are considered vital phytoremediation agents. *Sesuvium portulacastrum* accumulates heavy metals and salts from effluents (Nguyen et al., 2017; Reginato et al., 2019). Zaier et al. (2014) used *Sesuvium portulacastrum* for remediation of lead polluted soils with addition of EDTA for enhancement of its phytoextraction activity. *Noccaea rotundifolium* and *Noccaea caerulescens* can store high concentrations of lead in their shoots. Hong and Chan (2002) investigated *Dianthus chinensis* and found high amounts of lead and cadmium in its shoots. *Suaeda salsa* is also used to remediate cadmium from contaminated soils (Paredes-Páliz et al., 2018). Manousaki et al. (2014) explored the phytoremediation potential of *Limoniastrum monopetalum* on lead and cadmium contaminated soils. Devi et al. (2016) examined many halophytes species and concluded that *Atriplex lentiformis* and *Suaeda fruticosa* were optimal metal accumulators. Li et al. (2019) claimed *Halogeton glomeratus* was an excellent candidate for phytoremediation of heavy metals as well as salt on contaminated soils. *Salicornia brachiata* can remediate nickel, cadmium and arsenic (Cabrita et al., 2019). Syranidou et al. (2017) reported that *Juncus acutus* had the ability to remediate Bisphenol-A from polluted water. Farzi et al. (2017) used *Salicornia europaea*, *Bienertia cycloptera* and *Salsola crassa* to reduce water salinity and they were recommended as a better option for salt remediation from wetlands. *Aster tripolium* stores copper and cadmium when grown in contaminated areas. *Atriplex marina* absorbs heavy metals via its roots and stores

**Table 6.** List of halophytes that accumulate heavy metals and can be a good source of bio-remediation of contaminated soils.

Specie	Heavy metals	Tolerance mechanism	References
<i>Halogeton glomeratus</i>	Chromium, nickel, zinc, cadmium, copper, arsenic	Osmoprotectants	Li et al., 2019
<i>Halopyrum mucronatum</i> , <i>Kosteletzkya pentacarpos</i>	Iron, zinc, chromium Cadmium, zinc	Excretion Osmoprotectants	Atia et al., 2019 Zhou et al., 2019
<i>Salsola imbricate</i>	Lead	Excretion	Mujeeb et al., 2020
<i>Atriplex halimus</i>	Zinc, cadmium, boron	Accumulation	Bankaji et al., 2019
<i>Avicennia marina</i>	Zinc, cadmium, lead	Exclusion	Dai et al., 2018
<i>Heliotropium bacciferum</i>	Lead, copper, zinc, manganese	Accumulation	Vicente et al., 2016
<i>Sesuvium portulacastrum</i>	Cadmium, arsenic, nickel	Phytoextraction	Fourati et al., 2019
<i>Bruguiera gymnorhiza</i>	Lead, cadmium, mercury	Exclusion	Sruthi & Puthur, 2019
<i>Tamarix smyrnensis</i>	Lead, cadmium	Excretion	Sghaier et al., 2019
<i>Atriplex undulate</i>	Lead, copper	Phytostabilization	Kumari et al., 2019
<i>Atriplex lentiformis</i>	Cadmium, copper, zinc	Phytostabilization	Eissa & Abeer, 2019
<i>Mesembryanthemum crystallinum</i>	Copper	Osmoprotectants	Tran et al., 2020
<i>Kandelia candel</i>	Cadmium	Antioxidant system	Xing et al., 2019
<i>Avicennia germinans</i>	Cadmium, copper	Metal binding molecules	Torasa et al., 2019

them in the leaves. For the monitoring of heavy metal pollution, *Ceriops decandra* is used as a biomarker because these plants show visible toxicity symptoms. For instance, in case of mercury, shoot tips become brown, leaves become yellow for lead and for cadmium toxicity show chlorosis. Activity assessment reveals the liner relationship between peroxidase activities and leaf tissue metal concentration which is associated with visible toxicity symptoms in *Ceriops decandra* (Gupta & Chakrabarti, 2013). *Tamarix smyrnensis* excretes cadmium via salts glands present on their leaves. In order to reduce metal load, these excreted metals can be collected before they reenter into the soil (Ali et al., 2019; Turcios & Papenbrock, 2019b).

### Removal of polycyclic aromatic hydrocarbons

Polycyclic aromatic hydrocarbons are the major contaminates of the atmosphere, marine and soil environments. Hydrocarbons impact very harmful effects on flora, fauna and humans. Polycyclic aromatic hydrocarbons accumulate in costal soils and plants grown in contaminated soil. Edible plants grown on such type of soils are enriched of these contaminants which is unsafe for consumption. Halophytes have the potential to remediate polycyclic aromatic hydrocarbons (Table 8). Xiao et al. (2015) describe the degradation of 90.67% fluoranthene, 93.27% pyrene, 100% benzo(a) anthracene, 100% chrysene, 100% benzo(b) fluoranthene, 100% benzo(k) fluoranthene, 99.53% benzo(a) pyrene and 100% by planting *Medicago sativa* for 150 days. Syranidou et al. (2017) used *Juncus acutus* for remediating Bisphenol-A from ground water. Ebadi et al. (2018) increased petroleum

**Table 7.** Metal accumulation capacity of halophytes grown under industrial waste water.

Species	Heavy metals	Metal Accumulation	References
<i>Arthrocnemum macrostachyum</i>	Lead	620 (mg/kg)	Lu et al., 2017
<i>Crucialia marina</i>	Zinc	390	Orescanin et al., 2006
<i>Dittrichia viscosa</i>	Lead	270	Abdallah et al., 2020
<i>Typha domingensis</i>	Selenium	30	Hadad et al., 2010
<i>Atriplex halimus</i>	Zinc	440	Bankaji et al., 2019
	Cadmium	606	
	Cadmium	830	
<i>Typha lotifolia</i>	Cadmium	210	Hejna et al., 2020
<i>Paspalum conjugatum</i>	Lead	150	Zhang et al., 2020
<i>Tamarix smyrnensis</i>	Lead	800	Sghaier et al., 2019
	Cadmium	800	
<i>Avicennia officinalis</i>	Copper	14.78 ( $\mu\text{g/g}$ )	Sarangi et al., 2002
	Zinc	107.8	
	Lead	23.21	
<i>Rhizophora apiculata</i>	Copper	10.25	Khan et al., 2020
	Zinc	16.8	
	Lead	12.23	
<i>Rhizophora mucronata</i>	Copper	19.90	Ganeshkumar et al., 2019
	Zinc	40.3	
	Lead	12.61	
<i>Excoecaria agallocha</i>	Copper	8.12	Yan and Tam 2013
	Zinc	76.6	
	Lead	27.35	
<i>Bruguiera cylindrical</i>	Copper	17.46	Sarangi et al., 2002
	Zinc	116.9	
	Lead	17.39	
<i>Ceriops decandra</i>	Copper	95.05	Gupta and Chakrabarti 2013
	Zinc	9.3	
	Lead	11.82	
<i>Aegiceras corniculatum</i>	Copper	13.39	Huang et al., 2020
	Zinc	12.8	
	Lead	12.91	
<i>Acanthus ilicifolius</i>	Copper	13.79	Shackria and Puthur, 2017
	Zinc	67.5	
	Lead	15.99	
<i>Arthrocnemum indicum</i>	Copper	10.89	Sghaier et al., 2020
	Zinc	67.2	
	Lead	10.83	
<i>Suaeda maritima</i>	Copper	10.81	Malik and Ravindran 2018
	Zinc	71.1	
	Lead	11.08	
<i>Suaeda monoica</i>	Copper	7.77	Joshi et al., 2020
	Zinc	19.0	
	Lead	10.57	
<i>Sesuvium portulacastrum</i>	Copper	10.47	Feng et al., 2018
	Zinc	62.4	
	Lead	16.95	
<i>Ipomoea pescaprae</i>	Copper	32.22	Cordova, 2020
	Zinc	44.9	
	Lead	13.38	

hydrocarbon degradation but 10-fold in *Salicornia persica* by adding *Pseudomonas aeruginosa* to the oil contaminated soil. *Salicornia fragilis* accumulate polycyclic aromatic hydrocarbons in shoot tissues after planting in contaminated soil (Abdollahzadeh et al., 2019). *Halimione portulacoides* accumulate polycyclic aromatic hydrocarbons in shoots from contaminated soil (Khan et al., 2019).



**Table 8.** Halophyte used for phytoremediation of polycyclic aromatic hydrocarbons from contaminated saline soils.

Halophytes	Contaminants	Degradation (%)	References
<i>Spartina densiflora</i>	Phenanthrene	43-78	Mesa-Marín et al., 2019
<i>Cakile maritima</i>	Phenanthrene	75	Arbelet-Bonnin et al., 2019
<i>Juncus maritimus</i>	Total petroleum hydrocarbons	12	Tang, 2019
<i>Phragmites australis</i>	Total petroleum hydrocarbons	16	Fadhil & Al-Baldawi, 2020
<i>Halimione portulacoides</i>	Total petroleum hydrocarbons	10-64	Khan et al., 2019
<i>Scirpus maritimus</i>	Total petroleum hydrocarbons	13-79	Gorbatiuk & Pasichnaya, 2019
<i>Juncus maritimus</i>	Total petroleum hydrocarbons	0-48	Tang, 2019
<i>Aeluropus littoralis</i>	Total petroleum hydrocarbons	32	Sima et al., 2019
<i>Iris dichotoma</i>	Total petroleum hydrocarbons	19-30	Capuana, 2020
<i>Setaria viridis</i>	Total petroleum hydrocarbons	24-52	Ponce-Hernández et al., 2020
<i>Salicornia persica</i>	Total petroleum hydrocarbons	55-57	Abdollahzadeh et al., 2019
<i>Juncus roemerianus</i>	Total petroleum hydrocarbons	48-66	Ogheneruemu et al., 2020
<i>Suaeda salsa</i>	Total petroleum hydrocarbons	43	Li & You, 2020
<i>Iris lactea</i>	Total petroleum hydrocarbons	19-30	Capuana, 2020

### Use of halophytes for landscaping

Biological systems are greatly influenced by directly deposited saline contaminations. To minimize the salinity problem, it is essential to assess halophytes for landscaping and for fixation of sand dunes. Species capable of tolerating 0.5% NaCl or more are potential candidates for landscaping, for recreational purposes for instance (Sağlam & Önder, 2018). *Camphorosma* species are highly preferred in landscaping because they have the ability to convert soils from erosion, grow in highly salty areas and also have high nutritional values (Zamin et al., 2019). *Phragmites karka* and *Typha domingensis* are both excellent stabilizer of erosions due to their ability to grow and survive in flooded areas. *Maireana sedifolia*, *Iresine rhizomatosa*, *Cakile maritima* and *Arthrocnemum halocnemoides* are very effective desert landscape species and extensively used in landscaping. Tolerance to high salinity and other environmental stresses established *Callistemon citrinus* and *Callistemon laevis* as candidates for landscaping in saline and arid areas (Cassaniti & Romano, 2011; Ortiqova, 2019). Plant responses to the salt stress depend on the duration and intensity of salt exposure (Ventura et al., 2015). Species like *Halimione*, *Plantago*, *Frankenia*, *Camphorosma*, *Halocnemum* and *Acantholimon* are used as ground cover and are highly preferred in high salt lands and can be used as turf grasses (Ungar, 1987).

### Conclusions

Halophytes are getting attention in the world due to their ability to grow and complete their life cycle under harsh environment. The main adaptation of halophytes includes strict control of the water/ion fluxes which helps in maintenance of proper osmotic adjustment under saline conditions. Halophytes can prevent themselves from lethal oxidative burst by producing metabolites such as antioxidants and osmoprotectants which

have a close association with protecting photosynthesis and biomass production. Halophytes can compete with other conventional crops for multiple economic benefits as they are outside the human food chain, and contain a variety of metabolites which can convert directly into biofuel, can be used for medicinal application, and are a source of edible oil. Increasing population and calories demands calls for increased food production by using halophytes which will reduce our food crises while achieving sustainable environmental goals set by UNO. Utilization of halophytes in revegetation and rehabilitation for landscaping are closely associated with phytoremediation and effluent purification which can be established and implemented in developing countries to improve economic potential and agro-management systems to feed the growing populations. Cultivation of halophytes for industrial purposes can be recommended due to their ability to grow on saline degraded lands thus leading to an economic and environmental benefit for our society.

### Disclosure statement

No potential conflict of interest was reported by the authors.

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