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Salts phytoremediation by halophytes in soil and aquatic environments: new mechanisms, promising species, and challenges

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Abstract

Excessive soluble salt accumulation in the soil or water reduces plant growth, renders land unusable, negatively impacts aquatic life, and limits water usage for various purposes. This paper explores the phytoremediation potential of halophytes and their ability to absorb salts from soil and aquatic environments. These plants offer numerous benefits, such as producing food, forage, oil, biofuels, and herbal medicines. They are useful in various sectors, including industry, pharmaceuticals, landscaping, and environmental reclamation. Halophyte farming, or biosaline agriculture, is successfully used for animal feed and biofuel production. Key challenges include identifying suitable varieties, improving yields, optimizing cultivation methods, and assessing economic viability for broader adoption. Phytoremediation is an eco-friendly and cost-effective method for cleaning up polluted environments, utilizing plants or algae to remove, detoxify, or stabilize contaminants in soil, water, or air. It offers several mechanisms, including phytoextraction, phytodegradation, phytostabilization, rhizofiltration, phytoaugmentation, and phytostimulation, as alternatives to traditional remediation techniques like excavation and removal of contaminated materials. Halophytes hold promise as a sustainable and cost-effective solution for mitigating soil and water salinity through salt phytoremediation, offering a hopeful prospect for the environment. However, more research is needed to refine halophyte cultivation, maximize their phytoremediation potential, and ensure economic feasibility.

Keywords:

Biosaline agriculture Haloculture Land reclamation Salinization Soil remediation

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1. Introduction

Salt-affected soils contain excessive amounts of soluble salts, high concentrations of exchangeable sodium, and a combination of both. They can be categorized into three types: saline, sodic, and saline-sodic (Richards, 1954). Saline soils have an electrical conductivity of saturation paste extract (EC_e) of > 4 dS m⁻¹, pH_e < 8.5, and exchangeable sodium percentage (ESP) < 15%, while sodic soils have EC_e < 4 dS m⁻¹, pH_e > 8.5, and ESP > 15%. Saline-sodic soils have EC_e > 4 dS m⁻¹, pH_e > 8.5, and ESP > 15%. They are primarily found in arid and semi-arid climates but can also occur in humid climates in coastal and inland areas (e.g. FAO, 2024; Hulisz et al., 2016; Witte et al., 2018). They can be formed due to *in situ* salt accumulation, shallow, highly

mineralized groundwater, seawater inundation, wind transport of salts, intensive irrigation agriculture, and industrial waste deposition (e.g. Pirasteh-Anosheh et al., 2023c; Stavi et al., 2021; Pindral et al., 2023). Soil salinization and sodification threaten agriculture, environmental sustainability, and ecosystem biodiversity. The FAO report reveals that over 85% of the world's topsoil and subsoil are salt-affected, with 85% being saline, 10% sodic, and 5% saline-sodic. Over 3% of topsoils and 6% of subsoils are affected by salinity or sodicity (FAO 2023). Over two-thirds of salt-affected soils are found in arid and semi-arid regions, 37% in deserts, and 27% in dry steppes (FAO, 2023).

Soil salinity imposes stress on plants and causes a reduction in growth by inducing a wide range of changes in molecular, biochemical, physiological, morphological, and phenological

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scales, which, in cases where the intensity of stress is higher than the plant's tolerance, can stop growth or even dies the plant (Pirasteh-Anosheh et al., 2016). This issue reduces the economic production of agriculture, destroys the sustainability of the environment, and threatens the biodiversity of ecosystems. Many common plants are sensitive to salinity, and low salt concentrations limit their growth. Halophytes have a higher tolerance to salt stress and can grow and complete their life cycle in higher soil salinities (Pirasteh-Anosheh et al., 2023a). Even some halophyte species grow more in moderate salinities than in non-saline conditions (Cárdenas-Pérez et al., 2022). However, it should be noted that halophyte growth also decreases in very high salinities (Glenn et al., 1991; Flowers, 2006; Cárdenas-Pérez et al., 2024; Ludwiczak et al. 2024).

The high exchangeable sodium content favors the peptization of soil colloids, which contributes to the destruction of the aggregate structure, clogging the soil pores and reducing water infiltration and aeration of the root zone. This effect is most spectacular in heavy (clay) soils of arid and semi-arid zones (Rengasamy et al., 2022). Sodic soils often have a pH higher than 8.5 due to the presence of sodium and potassium (hydrogen) carbonates. Strongly alkaline conditions (pH as high as 10-11) are toxic to plants (Abrol et al., 1988).

The plants that are placed in these conditions show different reactions. According to Prasad (2014), plants can be classified into four groups based on their response to salinity stress. The first group covers euhalophytes - plant species with a high salinity tolerance, whose growth is stimulated in medium salinity (e.g., Salicornia europaea and Suaeda maritima). The second covers facultative halophytes with high salinity tolerance but do not need salt to grow; however, they have little growth stimulation in low salinity conditions (e.g., Plantago maritima and Tripolium pannonicum). The third group collects non-halophytes with relatively good tolerance to salinity, like some of the most important field crops (e.g., Hordeum vulgare, Gossypium herbaceum, Asparagus officinalis, and Beta vulgaris) and tree species (e.g., Pistacia vera, Punica granatum, and Prunus dulcis). The fourth group covers halophobic plants that are sensitive to salinity and have a significant growth reduction in low salinities (e.g., Phaseolus vulgaris, Crocus sativus, and Solanum tuberosum).

A halophyte is a plant adapted to grow in environments with high salt concentrations. These plants have unique physiological and biochemical adaptations that allow them to tolerate and even thrive in saline conditions, which would be detrimental or lethal to most other plant species (Flowers and Colmer, 2008; Ghanem et al., 2021). Although there are various definitions for halophytic species, the most authoritative definition is attributable to Flowers and Colmer (2008): "Halophytes, plants that survive to reproduce in environments where the salt concentration is around 200 mM NaCl or more, constitute about 1% of the world's flora". Halophytes are found in different regions worldwide, including coastal areas (saltmarshes and mangroves), salt flats, and salt mines. They play an essential ecological role in these habitats by helping to regulate the balance of salt and water, providing habitat and food for various wildlife, and contributing to soil stabilization and erosion control (Flowers and Colmer, 2008; Pirasteh-Anosheh et al., 2022).

Ranjbar et al. (Ranjbar et al., 2018) stated that the halophytes adapt to saline conditions by reducing the entry of salt into the plant or reducing the salt concentration in the cytoplasm. They believed these mechanisms include excluding excess salts into the glands on the surface of leaves and stems, growing part of the epidermis and producing a bladder, compartmentalizing toxic ions into the vacuole, or preventing the entry of toxic ions into the roots. Halophytes have evolved various mechanisms to cope with high salt concentrations, including specialized root structures for salt uptake and excretion, salt gland or salt bladder formations for salt storage and secretion, and efficient water use strategies to minimize water loss in saline environments (Ghanem et al., 2021; Rahman et al., 2021). Some halophytes can also accumulate salts in their tissues, allowing them to maintain a favorable water balance and survive in saline soils (Rahman et al., 2021).

Different halophyte species have different behaviors in managing the excess of ion salts in the rhizospheres. Kefu et al. (2002) distinguished three groups using these strategies. First called recretohalophytes, groups of species that have salt glands on the outer surface of their organs, which secrete salt to the outside (exo-recretohalophytes, e.g., Acathus ebracteatus, Avicennia marina, and Ipomoea polymorpha) or naturally adapt to the ions released from the plant by producing salt bladders (endo-recretohalophytes, e.g., Atriplex spp., Chenopodium spp., and Salsola spp.). The second group, called euhalophytes covers species that accumulate salts in the juicy tissues of the green plant organs of the leaves (leaf succulent euhalophyte, e.g., Suaeda salsa, Suaeda lauca, and Salsola junatovii) or in the vacuole of the green organs and the vascular cylinders of the stem (stem succulent euhalophytes, e.g., Halostachys belangeriana, Kalidium schrenkianum, and Salicornia europaea). The third group - pseudo-halophytes collects species that accumulate salts in the parenchyma organs of the root (e.g., Phragmites australis).

Halophytes are also being explored for their potential use in agriculture in saline soils, as they may offer a sustainable solution for crop production in areas where traditional crops struggle due to the high salt concentrations in the soil (Cárdenas-Pérez et al., 2021). Furthermore, some regions have traditionally used halophytes for food, fodder, medicine, and other cultural uses. However, it's important to note that not all halophytes are suitable for human or animal consumption, as some may contain high levels of salt or other toxic compounds (Ibraheem et al., 2021). While halophytes show promise for phytoremediation, knowledge gaps remain regarding their effectiveness for salt remediation in real-world applications (Pirasteh-Anosheh et al., 2023a,b). Existing research often focuses on controlled environments, limiting our understanding of how these plants perform under field conditions with complex contaminant mixtures and fluctuating salinity levels. This review article addresses this gap by examining the phytoremediation abilities of halophytes across various studies. We aim to bridge the laboratory-to-field gap and suggest future research directions based on assessing their potential for saline soil reclamation and indicating promising species.

In selecting literature for this article, we prioritized relevance to the topic and ensured source quality by focusing on peer-reviewed articles and reputable authors. We considered publication dates to incorporate the latest findings while referencing seminal works that have significantly influenced the field. A diverse range of perspectives was targeted by balancing various study types and maintaining methodological rigor. We assessed citation frequency to identify influential works and explored interdisciplinary links for broader insights. Keywords used in the search included soil and water pollution, pollutants, soil and water contaminants, saline and hypersaline soils and waters, soil amendment, soil and water purification, soil improvement, soil reclamation, remediation, bioremediation, microbial remediation, phytoremediation, phytoextraction, phytodegradation, phytostabilization, rhizofiltration, phytoaugmentation, phytostimulation, halophytes, and salt-tolerant plants. The key databases searched for articles included Google Scholar, PubMed, JSTOR, Scopus, Web of Science, IEEE Xplore, PsycINFO, ScienceDirect, and SpringerLink.

2. Environmental remediation

Remediation refers to tending to or adjusting a problem, issue, or insufficiency in a specific region. The term can be connected to many areas, such as environmental remediation (Ferraro et al., 2023; Kensa, 2011). Environmental remediation includes the cleanup of contaminated land, water, and air, or discusses using different methods such as bioremediation, chemical treatment, thermal treatments, physical removal of contaminants, or mixed methods (Parnian et al., 2023). Environmental remediation could be performed in three types based on management strategies of resource management, ecological disruption, and location of remediation techniques application (Parnian et al., 2022a,b; Sharma et al., 2021; Saygal and Ahmed, 2021). The first type of environmental remediation is in situ, as the remediation process is applied to pollution occurrence with the lowest environmental disruptions. The second one is on situ; the remediation process applies to pollution with high environmental disruptions like soil excavation, deep soil tillage, etc. In the last type, the ex-situ, contaminated medium (soil/sediment/ water) is transported, and the remediation process is applied in a restricted area and controlled environment.

2.1. Bioremediation

Bioremediation is a natural and cost-effective method that uses living organisms to clean up polluted environments. It helps societies address pollution problems without harming the ecosystem. However, bioremediation faces challenges and limitations, particularly in the availability of essential nutrients for the growth of organisms. For example, algae and fungi require specific nutrients to survive and degrade pollutants in sediment, soil, water, and air (Parnian et al., 2022d; Rathankumar et al., 2022). There are various bioremediations, including bioventing, bioattenuation, biosparging, bioaugmentation, biostimulation, composting, landfarming, mycoremediation, microbial fuel cells, and phytoremediation. The availability of specific nutrients is crucial for practical bioremediation, as microorganisms require the nutrients to metabolize and break down pollutants (Bala et

al., 2022; Kuppan et al., 2024). Key nutrients include carbon (C) as an energy source, nitrogen (N) essential for amino acids and proteins, phosphorus (P) vital for energy transfer and nucleic acids, and sulfur (S) necessary for specific amino acids and vitamins. Additionally, trace elements like iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), and molybdenum (Mo) are required in small amounts for enzymatic processes. Providing a balanced supply of these nutrients can significantly enhance the growth and metabolic activities of microorganisms, improving the rates of pollutant degradation and overall remediation success.

Bioventing is a crucial in situ bioremediation method that uses microorganisms to degrade organic contaminants. It intensifies bacteria and archaea's activities, promoting hydrocarbon molecules in situ biodegradation with air, oxygen flow, and necessary nutrients (Gillespie and Philp, 2013). Oxygen is added to the soil during bioventing, helping to degrade adsorbed fuels and residuals of volatile organic compounds (Speight, 2020). Environmental bioattenuation involves natural pollutant biodegradation by adding nutrients, microbes, or other organisms, affecting the ecosystem's self-remediation and determining metabolic activity (Nguyen et al., 2021).

Biosparging is an in-situ remediation technique that uses indigenous microorganisms to biodegrade organic constituents in saturated zones, reducing petroleum hydrocarbon concentrations in groundwater, soil below the water table, and within the capillary fringe, by injecting air/oxygen and nutrients (USEPA 2004). Bioaugmentation is the addition of cultured microorganisms to degrade contaminants in solid or aquatic environments. It involves studying native microorganisms to determine if biostimulation is possible. If native microorganisms affect contaminants, more are added, while if not, exogenous microorganisms are introduced. Bioaugmentation improves efficiency and reduces site mitigation costs and time (Adams et al., 2015). Biostimulation is a technique that boosts bacteria's activity in a contaminated environment, enhancing their efficiency in degrading contaminants (Adams et al., 2015). Composting/co-composting involves mixing contaminated medium with bulking agents like wood chips, straw, rice hulls, or husks to increase porosity and aeration potential (Parnian et al., 2022c).

The land farming method is a full-scale bioremediation technology that usually incorporates liners and other techniques to control the leaching of contaminants. It requires excavation and placement of contaminated soils/sediments/ sludges. Contaminated medium is applied into lined beds and periodically turned over or tilled to aerate the waste (Yadav et al., 2021).

The mycoremediation approach uses fungi to break down or remove contaminants from soil or water. Mycoremediation techniques include using mushrooms and other fungi to break down pollutants. This technique is mainly used and incorporated into different bioremediation methods, such as phytoremediation, landfarming, composting, etc. (Cowan et al., 2022; Sharma et al., 2021). The microbial fuel cells approach uses microorganisms to generate electricity while breaking down pollutants in contaminated water (Verma et al., 2021). The phytoremediation approach uses plants and algae to control/stabilize/remove/detoxify contaminants from different environments, such as soil, sediment, water, and air (Parnian et al., 2022c).

These are just some examples of the different types of applied bioremediation techniques. The choice of technique depends on the specific type and extent of contamination, as well as the environmental conditions of the contaminated site. In this article, we focus on bioremediation, phytoremediation, and the ability of halophyte plants to rehabilitate saline soils.

2.2. Microbial remediation

Microbial remediation is a process of bioremediation that uses microorganisms, such as bacteria, fungi, or microalgae, to break down or remove pollutants from contaminated soil, water, or air. In bioremediation, microorganisms are introduced into a contaminated area to consume and break down the contaminants, converting them into harmless byproducts such as carbon dioxide, water, and biomass (Ferraro et al., 2023; Norris 1993; Parnian et al., 2022d).

Microbial remediation in salt remediation from soil/sediment and aquatic environments is primarily available for control, stabilization, and/or reduction of salinity side effects (reclamation/ restoration). The process is called by some scientists "biodesalination" (Patel et al., 2021), and this concept can also be extended to other uses of living organisms for salt control or remediation. Biodesalination of aquatic medium with microalgae (like Chlorella, Chlorococcum, Desmodesmus, Scenedesmus, and Monoraphidium) has great potential to remove chloride and nutrients (Figler et al., 2019). Also, there is great potential for sodium removal with cyanobacteria (Amezaga et al., 2014). Microbial remediation employs salt-tolerant microorganisms to alleviate soil and sediment salinity by enhancing the degradation of organic matter, producing organic acids that displace sodium ions, and fostering beneficial plant-microbe interactions, thus improving soil health and agricultural productivity. These microbes facilitate nutrient availability and can also degrade associated pollutants, offering a sustainable solution to the environmental challenges posed by salinization (Jariyal et al., 2022; Sharma et al., 2022).

Some microbes have synergism and another positive impact on plants' root systems. The soil fauna adds carbon-based molecules and nutrients to their environment through their exudates and body residue (Chen et al., 2016; Zhang et al., 2016; Li et al., 2019). These halo-tolerant microbes, such as Arthrobacter, Azospirillum, Alcaligenes, Bacillus, Burkholderia, Enterobacter, Flavobacterium, Pseudomonas, and Rhizobium, enhance soil fauna activity and improve plant growth and soil chemical, physical, and ecological quality (Arora et al., 2020). They add a high amount of carbon dioxide and active calcium (pedogenic carbonates) to the soil (Parnian et al., 2022d), which helps the soil to improve and drive the reclamation/restoration process. In this concept and similar situations, soil water and carbon dioxide turn into carbonic acid, and the active calcium can replace the sodium ions on the soil particle surface. This mechanism helps to increase sodium leaching and reduce sodium's harmful effects on soils (microbial-assisted salinity curing).

The process can be accelerated by adding nutrients and oxygen to the contaminated area to encourage the growth and activity of microorganisms. This branch of bioremediation is often

used to clean up contaminated sites polluted by hazardous substances, such as petroleum, pesticides, and heavy metals (Adams et al., 2015). It is considered a relatively cost-effective and environmentally friendly approach to environmental remediation, as it does not involve using harsh chemicals or excavating and removing contaminated soil (Saleem et al., 2022). However, the success of bioremediation depends on several factors, including the type and amount of contaminants present, the environmental conditions of the contaminated site, and the effectiveness of the microorganisms used (Saleem et al., 2022; Zhang et al., 2020). Therefore, careful assessment and planning are necessary before implementing bioremediation as a remediation strategy.

2.3. Phytoremediation and mechanisms

Phytoremediation is an eco-friendly method for cleaning polluted environments using plants or algae to remove, detoxify, or stabilize soil, water, or air contaminants. It is cost-effective compared to conventional methods like excavation (Garcia-Caparros et al., 2022). Key mechanisms of phytoremediation include phytoextraction, phytodegradation, phytostabilization, and rhizofiltration.

A phytoextraction technique uses green plants or algae to uptake and accumulate contaminants from the soil through their active organs, such as shoots or roots (Fig. 1). The plants or algae are then harvested and disposed of properly, along with the contaminants they contain. This mechanism is also active and particularly effective for removing heavy metals from soil, such as lead and cadmium (Garcia-Caparros et al., 2021; Govere, 2021). Salicornia fruticosa, Sesbania drummondii, Pteris vittata, Sedum alfredii, Commoelina communis, and Arundo donax are the species that utilize phytoextraction as one of the phytoremediation mechanisms (Kafle et al., 2022).

Phytodegradation uses plant/algae mechanisms to break down contaminants in the polluted environment through metabolic processes (Fig. 2). Plants may release enzymes into the soil that break down organic-based pollutants, such as petroleum products and pesticides, converting them into less harmful compounds (Gill et al., 2023; Govere, 2021). Nevertheless, this mechanism of phytoremediation is generally ineffective for mineral or inorganic contaminants, such as salts from the sodium-halogen group. This mechanism is found in *Blumea malcolmii*, *Pueraria thunbergiana*, *Erythrina crista-galli*, and *Pontederia crassipes* (Kafle et al., 2022). Furthermore, it seems that *Salicornia europaea*, *Distichlis spicata*, *Atriplex halimus*, *Atriplex nummularia*, *Suaeda maritima*, *Avicennia marina*, *Chenopodium quinoa*, and *Tribulus terrestris* also use phytodegradation to tolerate salinity.

Phytostabilization uses plants to immobilize contaminants in the soil, preventing them from spreading to other areas (Fig. 3). The plants absorb the pollutants and deposit them in their roots or leaves, reducing their mobility and preventing them from leaching into groundwater or another area (Garcia-Caparros et al., 2022; Gill et al., 2023). Nevertheless, this mechanism of phytoremediation is often ineffective for soluble salts that are more soluble than gypsum and for elements or molecules that do not adequately interact with the active surfaces of plants or algae (such as the root systems of terrestrial plants and the root-leaf

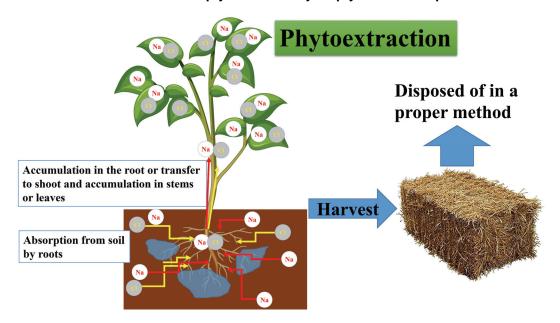


Fig. 1. Schematic phytoextraction in a halophyte, where the plant absorbs salts from the soil and accumulates them in the root, stem, or leaf. Designed by the authors based on information from Govere (2021) and Garcia-Caparros et al. (2022)

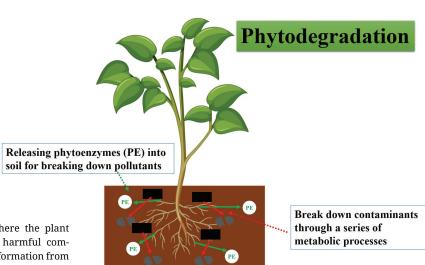


Fig. 2. Schematic phytodegradation in a halophyte, where the plant breaks down contaminants (black rectangle) into less harmful compounds (gray pieces). Designed by the authors based on information from Govere (2021) and Garcia-Caparros et al. (2022)

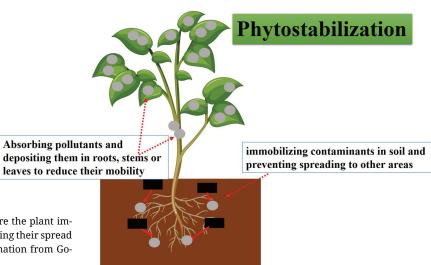


Fig. 3. Schematic phytostabilization in a halophyte, where the plant immobilizes contaminants in soils (black rectangle), preventing their spread to other areas. Designed by the authors based on information from Govere (2021) and Garcia-Caparros et al. (2022)

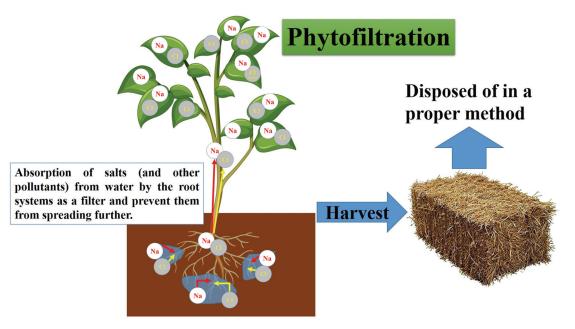


Fig. 4. Schematic phytofiltration (rhizofiltration) in a halophyte, where roots of the plants act as filters and absorb salts from water. Designed by the authors based on information from Govere (2021) and Garcia-Caparros et al. (2022)

systems of aquatic macrophytes). An example of such elements is salts from the sodium-halogen group. Interestingly, most phytostabilizer halophytes such as *Avicennia alba*, *Phragmites australis*, *Phragmites karka*, *Aeluropus lagopoides*, and *Sporobolus virginicus* are native to the coastal marshes (Aziz and Mujeeb, 2022).

The rhizofiltration technique (also known as phytofiltration) uses plants with large root systems to absorb contaminants such as salts from water (Fig. 4). The roots of the plants act as filters, trapping the pollutants and preventing them from spreading further (Elizareva et al., 2020; Govere, 2021). *Phragmites australis* can also be an example of a plant applying rhizofiltration.

Phytoremediation using halophytes has the potential to be a cost-effective and environmentally friendly approach for remediating saline environments contaminated with pollutants. However, further research is needed to optimize the technique and determine the long-term effect of using halophytes in phytoremediation.

2.4. Phytoremediation by halophytes

This novel branch of bioremediation harnesses the unique properties of halophytes, a relatively new approach, to remove or detoxify pollutants in a saline environment. Phytoremediation can be an effective remediation strategy for many contaminants, including heavy metals, organic pollutants, and radioactive substances in saline environments, e.g., salt-affected soils and saline agricultural drainage (Cristaldi et al., 2020). However, the technique's effectiveness depends on several factors, including the type and extent of contamination, the type of plants used, and the environmental conditions of the contaminated site. Additionally, phytoremediation can be a slow process, and it may take several growing seasons for the plants to remove or detoxify contaminants from the ecosystem (Cristaldi et al., 2020; Singh et al., 2022). The use of halophytes in phytoremediation has several

advantages over traditional phytoremediation techniques. Halophytes are adapted to saline environments to grow in highly saline soils and water, which is intolerable for most other plants (Aziz and Mujeeb, 2022; Garcia-Caparros et al., 2022). This makes them an ideal choice for remediating saline environments that are contaminated with pollutants.

Halophytes also have a high capacity for accumulating certain pollutants, such as heavy metals, in their tissues. This means they can remove these pollutants from the soil or water more efficiently than other plants (Mushtaq et al., 2020). Additionally, some halophytes such as *Halocnemum strobilaceum* and *Salicornia spp.*, and non-halophytes such as *Salix viminalis* have been found to have the ability to break down certain organic pollutants, such as petroleum products, through metabolic processes (Schmidt, 2003; Al-Mailem et al., 2010). This allows them to remove these pollutants from the soil or water and convert them into less harmful compounds.

Research on phytoremediation using halophytes is ongoing, and several studies have shown promising results (Aziz and Mujeeb, 2022; Cowan et al., 2022; Kefu et al., 2002; Mushtaq et al., 2020; Parnian et al., 2022c,d). Halophytic species have several mechanisms that make them effective for phytoremediation in saline environments (Aziz and Mujeeb, 2022; Pirasteh-Anosheh, et al. 2016; Rahman et al., 2021). Among others, there are salt tolerance, high ion exchangeability, salt excretion, salt hyperaccumulation, and specific metabolic processes. Salt tolerance allows them to grow in saline environments contaminated with pollutants. High ion exchangeability and a high capacity for absorbing ions, such as sodium and chloride, will enable them to reduce the concentration of these ions in the environment and reduce the toxicity of the contaminated soil or water. Some halophytes such as Alhagi maurorum, Atriplex polycarpa, Suaeda maritima, and Tamarix chinensis can excrete excess salt through specialized structures, such as salt glands or bladders, which allow

them to balance salt and water in their tissues, even in highly saline environments. Some halophytes (e.g. *Atriplex halimus, Arthrocnemum macrostachyum, Chenopodium quinoa, Crucianella maritima, Dittrichia viscosa,* and *Salicornia europaea*) can hyperaccumulate certain pollutants, such as heavy metals, in their tissues. This enables them to eliminate these contaminants from the soil or water more effectively than other plants.

The following are some examples of the use of halophytes to improve saline soils around the world using halophyte species:

- a. Salicornia europaea in the Netherlands. Salicornia europaea has been used in large-scale reclamation projects. The cultivation of Salicornia not only improves soil structure and reduces salinity but also provides economic benefits through the production of edible products. Studies have shown that Salicornia can significantly lower soil salinity levels while enhancing soil fertility over time (Stienstra, 1987; Radulovich and Umanzor, 2021).
- b. *Limonium bicolor* in China. *Limonium bicolor* has been utilized for the reclamation of saline-alkali soils, particularly in coastal regions. This species is known for its high salt tolerance and ability to improve soil conditions. Large-scale planting of *Limonium bicolor* has been implemented to stabilize soil, enhance biodiversity, and promote ecological restoration. The plant's root system helps to improve soil structure, which facilitates better water infiltration and reduces surface salinity (Liu and Wang, 2021).
- c. Atriplex spp. in Australia. Atriplex species, particularly Atriplex nummularia, can be used for the reclamation of saline lands. These plants are well-adapted to arid conditions and can thrive in high-salinity environments. Large-scale projects should be done to demonstrate that Atriplex can reduce soil salinity and improve soil health, making it suitable for subsequent agricultural use. The deep root systems of Atriplex species help to draw down saline groundwater, thereby mitigating salinity issues in the soil (Radulovich and Umanzor, 2021; Christiansen et al., 2022).
- d. Chenopodium quinoa in South America. Quinoa (Chenopodium quinoa) has been explored for its potential to reclaim saline soils, particularly in regions affected by salinization due to irrigation practices. Quinoa is a halophyte that can tolerate saline conditions and has been shown to improve

- soil quality while providing a nutritious crop. Large-scale cultivation of quinoa in saline areas has been linked to enhanced soil fertility and reduced salinity levels, making it a viable option for sustainable agriculture in affected regions (Bilalis et al., 2019; Liu and Wamg, 2021).
- e. Haloculture pilot, Iran. Various species of halophytes, including *Salicornia spp.*, *Atriplex spp.*, quinoa, and *Tamarix aphylla*, were cultivated in the haloculture pilot in the Jofair region of Khuzestan Province in southwestern Iran to sustainably utilize highly saline soil and water resources. Improved biodiversity, stabilization of dust centers, and improved soil conditions were among the tangible results of this pilot (Hasheminejad et al., 2017; Pirasteh-Anosheh et al., 2021).

Therefore, the salt tolerance and ion exchange mechanisms in halophytes not only enable them to thrive in saline environments contaminated with pollutants but also hold the potential to revolutionize phytoremediation. Additionally, their hyperaccumulation and metabolic processes enhance their ability to efficiently remove or detoxify contaminants from the soil or water compared to other plants (Mohammadi et al., 2022; Parnian et al., 2022b). These unique abilities make halophytes well-suited for phytoremediation in saline environments affected by pollutants, offering a promising solution to the global challenge of environmental pollution.

3. Salt phytoremediation in soil and aquatic environments (potential of halophytes)

Halophytes have good potential for salt phytoremediation in both soil and water environments. These plants can be used in phytoremediation to remove excess salt from soil or water, making them suitable for agriculture, urban and interurban green space, pasture and forest, or industry, and other uses (Jesus et al., 2015; Nouri et al., 2017). By absorbing excess salt from soil or water, halophytes can reduce salinity levels (Imadi et al., 2016; Rahman et al., 2021), making the environment more suitable for other plants or organisms (Fig. 5). This process is a cost-effective and environmentally friendly method to mitigate tainted sites. However, it's crucial to note that further research is needed to



Fig. 5. The ability of *Alhagi camelorum* to grow in hypersaline lands. Around the *A. camelorum* plants marked with a red circle are desalinated; it is possible that the *A. camelorum* plants absorbed a significant part of the soil salts, although there may be other reasons

determine the most effective halophytes for different phytoremediation applications and the optimal conditions for their growth and remediation potential. This underscores the importance of ongoing research in this field and the potential for future advancements in phytoremediation using halophytes.

3.1. Salt phytoremediation in soil

Salt phytoremediation in the soil is a process of using plants to remove excess salts from saline or sodic soils, making them more suitable for plant growth (Mushtaq et al., 2020). Mechanisms of salt phytoremediation using halophytes may be different. Saline soils have high levels of soluble salts, while sodic soils have high levels of sodium that can cause soil structure problems, such as compaction and reduced water infiltration. Both types of soil can be challenging for agriculture (Pirasteh-Anosheh et al., 2022), and phytoremediation can help to restore them to a healthier state. Growing halophytes could help the soil recover its structure and increase its porosity, water infiltration, and water permeability. Further, growing halophytes might increase soil organic matter, soil fauna (both quantity and quality), and biodiversity, leading to salt-affected soil recovery. This mechanism, which is new compared to other phytoremediation mechanisms, is called phytoaugmentation (Fig. 6). Phytoaugmentation is regarded as a promising technology for remediating contaminated soil and wastewater (Kumar et al., 2021).

Phytoextraction has already been mentioned. Plants used in salt phytoremediation can absorb salts from the soil through their roots and accumulate them in their tissues. Once the plants have absorbed the salts, they can be harvested and removed from the site, effectively removing the salts from the soil. Alternatively, the plants can be left on the site to decompose, returning the absorbed salts to the soil in a less harmful form (Imadi et al., 2016; Nouri et al., 2017).

Plants that grow in saline soils have active root systems like other plants. These plants add carbon-based molecules

and nutrients to their environment through root leakage and exudates (Heuermann et al., 2023). Moreover, halophytes grow residues added to the soil, providing carbon and bioavailable nutrients. These leakages, exudates, and residues provide soil fauna with carbon and other nutrients. Therefore, halophyte enhances soil fauna activity, and alongside these plants, they add a high amount of carbon dioxide and active calcium (pedogenic carbonates) to soil (Khalidy et al., 2022, Parnian et al., 2022d). Concerning soil water, carbon dioxide turns into carbonic acid, and calcium can replace the sodium ions on the soil particle surface. This mechanism enhances sodium leaching and reduces its harmful effects on soils. It is referred to as phytostimulation, which includes enhanced rhizosphere biodegradation, rhizodegradation, or plant-assisted bioremediation (Ortiz-Castro and López-Bucio, 2019).

The effectiveness of salt phytoremediation depends on several factors, including the type of plant used, the level of salinity in the soil, and the length of time in which the plants are left to grow. Some plants are more effective at absorbing salts than others, and the salinity level in the soil can affect plant growth and salt uptake (Jesus et al., 2015). The length of time in which the plants are left to grow also affects the amount of salts removed from the soil (Mushtaq et al., 2020).

Salt phytoremediation in the soil is a promising method for restoring saline and sodic soils to a healthier state, making them more suitable for plant growth. It is an environmentally friendly and cost-effective method of soil remediation that does not require heavy equipment or chemicals, making it suitable for areas where other methods are not feasible (Nouri et al., 2017; Jesus et al., 2015; Mushtaq et al., 2020).

Some of the halophytes that are effective in soil remediation are suggested in Table 1. These halophytes can absorb and accumulate excess salts and other contaminants (e.g., heavy metals, organic compounds, etc.) from the soil through their root systems and leaves and can also help to improve soil structure and fertility (Shaygan et al., 2018; Shekhawat et al., 2006).

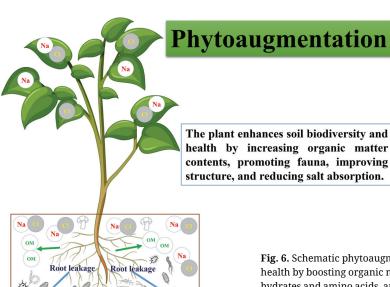


Fig. 6. Schematic phytoaugmentation in a halophyte, where plants improve soil biodiversity and health by boosting organic matter (OM), releasing dissolved organic matter (DOM) such as carbohydrates and amino acids, and developing soil fauna. This improves soil structure and permeability, salt leaching, and reduces Na and Cl absorption through increased biological Ca availability. Designed by the authors based on information from Kumar et al. (2021)

Table 1Some halophyte species with phytoremediation potential for soil improvement

Species	Family	Life Form	Maximum tolerance	Photosynthetic pathway	Habitat	Distribution
Acacia auriculiformis (Benth.) Pedley	Fabaceae	Tree	12 dS m ⁻¹	C3	Coastal habitats, geophyte, woodland, forest	China, India, Vietnam, Palau
Acacia stenophylla (Benth.) Pedley	Fabaceae	Tree	61 dS m ⁻¹	C3	Inland arid & sub-arid regions in warm temperate to tropical zones	Australia, USA
Alhagi maurorum Medik.	Fabaceae	Herbaceous perennial	30 dS m ⁻¹	C3	Agricultural land, sandy hills, inland salt marshes disturbed lands	Eurasia, Middle East
Astragalus laxmannii Jacq.	Fabaceae	Herbaceous	50 dS m ⁻¹	C3	Rocky slopes, grasslands, meadows, Alpine zones	China, North America
Atriplex lindleyi Moq.	Amaranthaceae	Herbaceous	60 dS m ⁻¹	C4	Dry areas	Tunisia, USA
Atriplex nummularia Lindl.	Amaranthaceae	Shrub	60 dS m ⁻¹	C4	Hemicryptophyte, inland unvegetated or sparsely vegetated habitats	USA, India, Australia
Atriplex paludosa R.Br.	Amaranthaceae	Shrub	62 dS m ⁻¹	C4	Upper saltmarshes	Australia, Iraq
Atriplex patula L.	Amaranthaceae	Annual herbaceous	72 dS m ⁻¹	C3	Continental inland salt steppes, saltmarshes	Canada, USA, Slovakia
Calotropis procera Aiton	Apocynaceae	Tree, Shrub	54 dS m ⁻¹	C3	Inland saline lakes, ponds, pools	Pakistan, Saharo-Arabian regions, Australia
Phragmites australis Cav.	Poaceae	Perennial grass	-	C3	Pristine wet areas: wetlands, marshes, rivers, lakes	Middle East, America
Limonium iranicum (Bornm.) Lincz.	Plumbaginaceae	Shrub	31 dS m ⁻¹	C3	Inland unvegetated or sparsely vegetated habitats, Hemicryptophyte	Iran, Middle East
Lotus pedunculatus Cav.	Fabaceae	Herbaceous perennial	34 dS m ⁻¹	C3	Ditches, wet pastures, bogs, marshes	Brazil, North Africa, Turkey
Lycium chinense Mill.	Solanaceae	Chaemaephyte	51 dS m ⁻¹	C3	Slopes, roadsides, disturbed areas, wastelands	China, southern Africa, America
<i>Prosopis articulata</i> S. Watson	Fabaceae	Shrub	18 dS m ⁻¹	C3	Stony & sandy mesas, plains, along washes and valleys, desert, desert grassland	Mexico, USA
Prosopis juliflora (Sw.) Raf.	Fabaceae	Tree	57 dS m ⁻¹	C3	Woodland, forests, geophyte	America, India, UAE
Salicornia brachiata Roxb.	Amaranthaceae	Annual herbaceous	60 dS m ⁻¹	C3	Coastal saltmarshes, saline reedbeds	India, southern Africa
Salicornia europaea L.	Amaranthaceae	Annual herbaceous	50 dS m ⁻¹	C3	Coastal sands, mudflats, saltmarshes	Europe, North Africa
Salsola kali L.	Amaranthaceae	Weedy	80 dS m ⁻¹	C4	Inland saltmarshes	Old World, Turkey, Wales
Schoenoplectus californicus (C.A. Mey.) Steud.	Cyperaceae	Herbaceous	27 dS m ⁻¹	C3	Coastal saltmarshes, saline reedbeds	USA, Chile, Bolivia
Schoenus nigricans L.	Cyperaceae	Herbaceous	14 dS m ⁻¹	C3	Moist & wet dune slacks, coastal saltmarshes, saline reedbeds	Western Europe, UK, Spain, Montenegro

Table 1 – continue

Species	Family	Life Form	Maximum tolerance	Photosynthetic pathway	Habitat	Distribution
Scirpoides holoschoenus (L.) Soják	Cyperaceae	Herbaceous perennial	94 dS m ⁻¹	C3	Psammophile	Spain, Montenegro, Australia
Sesbania cannabina (Retz.) Poir	Fabaceae	Herbaceous perennial	20 dS m ⁻¹	С3	Agricultural area, domestic habitats	China, Iran
Sonneratia apetala Banks	Lythraceae	Tree	40 dS m ⁻¹	C3	Marine mud shores, coastal habitats	South America, Old World, China, Indian subcontinent
Sophora alopecuroides L.	Fabaceae	Herbaceous perennial	$20~dS~m^{-1}$	C3	Hemicryptophyte, inland unvegetated or sparsely vegetated habitats	China, Pakistan, Eastern Europe
Spinifex littoreus Merr.	Poaceae	Perennial grass	-	C4	Coastal saltmarshes and dunes, saline reedbeds, sandy shores	India, Taiwan, Indonesia
Sporobolus maritimus (M.A. Curtis) Fernald	Poaceae	Perennial grass	51 dS m ⁻¹	C4	Marine mud shores, inland saline and brackish lakes, ponds, & pools	England, Portugal, Spain, South Africa
Suaeda calceoliformis (Hook.) Moq.	Amaranthaceae	Marine habitats	43 dS m ⁻¹	C3	Inland saltmarshes	USA, Canada
Suaeda monoica Forssk. ex J.F.Gmel.	Amaranthaceae	Shrub	85 dS m ⁻¹	C4	Coastal saltmarshes, saline reedbeds, Mediterranean inland salt steppes	Sudanian region, Saudi Arabia, India, Philistine
Suaeda nigra (Raf.) J.F.Macbr.	Amaranthaceae	Shrub	54 dS m ⁻¹	C4	Chaemaephyte	Mexico, USA, Iran
Suaeda stellatiflora G.L.Chu	Amaranthaceae	Herbaceous	-	C4	Marine habitats	China
Suaeda salsa L.	Amaranthaceae	Herbaceous	-	C3	Coastal salt flats, tidal wetlands	Europe, Asia, and North Africa
Suaeda vera Forssk. ex J.F.Gmel.	Amaranthaceae	Nano- chamaephyte	54 dS m ⁻¹	C3	Inland saline lakes, ponds, saltmarshes, coastal dunes, sandy shores	Jordan, Mediterranean region, Morocco, Egypt, Portugal, Spain
Sulla coronaria (L.) Medik.	Fabaceae	Biennial herbaceous	20 dS m ⁻¹	C3	Subtropical biome	Tunisia, Mediterranean region
Tamarix arceuthoides D. Don	Tamaricaceae	Tree, Shrub		C3	Saline areas of deserts & semi- deserts	Turkmenistan, Iran
Tamarix chinensis Lour.	Tamaricaceae	Tree, Shrub	54 dS m ⁻¹	C3	Phreatophyte	Mongolia, China, Japan
Tamarix indica Willd.	Tamaricaceae	Tree	112 dS m ⁻¹	C3	Riverbanks, floodplains, coastal areas	India, Sri Lanka, Pakistan
Tamarix smyrnensis Bunge	Tamaricaceae	Tree	9 dS m ⁻¹	C3	Coastal areas, riverbanks, and saline wetlands	Turkey, Iran, Pakistan
Trianthema portulacastrum L.	Aizoaceae	Annual herbaceous	24 dS m ⁻¹	C4	Coastal dunes, sandy shores	Mexico, India, Venezuela, Pantropical

Table 1 - continue

Species	Family	Life Form	Maximum tolerance	Photosynthetic pathway	Habitat	Distribution
Trifolium fragiferum L.	Fabaceae	Herbaceous perennial	42 dS m ⁻¹	СЗ	Extractive industrial sites	Europe, Middle East, Iran, Australia, Netherlands, Argentina
Typha angustifolia L.	Typhaceae	Herbaceous perennial	22 dS m ⁻¹	C3	Inland saline and brackish lakes, ponds, and pools, surface standing waters	China, Jordan, Spain, USA
Typha domingensis Pers.	Typhaceae	Herbaceous perennial	30 dS m ⁻¹	C3	Coastal habitats, permanent inland saline lakes, ponds, and pools	Mexico, Argentina, USA, Spain, Pakistan, Iraq
Typha latifolia L.	Typhaceae	Herbaceous perennial	29 dS m ⁻¹	C3	Inland saline lakes, ponds and pools, coastal saltmarshes and saline reedbeds	Jordan, Canada
Vigna marina (Burm. f.) Merr.	Fabaceae	Herbaceous	40 dS m ⁻¹	C3	Coastal dunes and sandy shores	Pantropical, India, Japan, Australia, USA

Data primarily extracted from the eHALOPH database (Flowers et al., 2024) and supplemented with the authors' experiences.

However, the effectiveness of halophytes in soil remediation depends on several factors, including the type and level of contamination present in the soil, the local climate and soil conditions, careful selection of the appropriate plant species, proper soil and plant management, and the specific characteristics of the halophyte species being used (Sakai et al., 2012; Shaygan et al., 2018).

3.2. Salt phytoremediation in aquatic environments

In aquatic environments, salt phytoremediation involves using plants to clean up contaminated water bodies with salts, heavy metals, and other harmful substances (Ferraro et al., 2023; Parnian et al., 2022a). Aquatic plants can absorb and accumulate large amounts of salts and other dissolved minerals from water. This ability is due to specialized transporters in their root cells that can actively take up ions from the surrounding water (Gill et al., 2023; Sharma et al., 2021).

The process of salt phytoremediation in aquatic environments involves the selection of suitable plant species that can tolerate high levels of salt and other contaminants in the water (Sharma et al., 2021). The mechanism in the aquatic environment is related to phytoextraction. Once these plants are established in the contaminated water body, they can start to uptake and accumulate the excess salts and other harmful substances. Over time, accumulating these substances in the plant tissues can reduce contamination levels in the water. The plants can subsequently be harvested and disposed of properly, or the contaminated plant material can be treated further to extract valuable minerals or other useful substances (Nguyen et al., 2021; Yasseen and Al-Thani, 2022).

Salt phytoremediation is a promising approach for cleaning up contaminated water bodies in areas where conventional remediation methods may not be feasible or cost-effective. However, the success of this process depends on several factors, including the selection of appropriate plant species, the availability of nutrients and other resources, and the level and type of contamination in the water (Gill et al., 2023; Yasseen and Al-Thani, 2022). Several plant species are suitable for phytoremediation in aquatic environments, as presented in Table 2. These plant species effectively remove excess salts, heavy metals, and other contaminants from aquatic environments. The suitability of a particular plant species for phytoremediation depends on the plant species used, water stream rate, specific type and level of salts and contamination present in the water, as well as the local climate and other environmental factors (Nguyen et al., 2021; Sharma et al., 2021; Parnian et al., 2022a; Gill et al., 2023).

The ability of halophytes for salt phytoremediation can differ between soil and aquatic environments. In soil, halophytic plants can assimilate salts from the soil through their roots and amass them in different organs and organelles. Once a halophyte uptakes the salts, they can be collected and expelled from the location, successfully expelling them from the soil. On the other hand, the plants can be cleared out of the location to break down, returning the accumulated salts to the soil in a less destructive way. On the other hand, halophytes can absorb and accumulate an excess of salts and contaminants from aquatic environments through their roots. These plants can thrive in brackish or saline water, and after they have absorbed the salts and contaminants, they can be harvested and removed from the water.

 $\begin{tabular}{ll} \textbf{Table 2} \\ \textbf{Some halophyte species suitable for phytoremediation in aquatic environments} \\ \end{tabular}$

Species	Family	Life Form	Maximum tolerance	Photosynthetic pathway	Habitat	Some recorded distribution
Althenia cylindrocarpa (Körn. ex Müll.Berol.) Asch.	Potamogetonaceae	Aquatic, Seagrass	54 dS m ⁻¹	C3	Low-mid saltmarshes	Australia
Amphibolis antarctica (Labill.) Asch.	Cymodoceaceae	Aquatic, Seagrass	98 dS m ⁻¹	C4	Coastal stable dune grassland, Seagrass beds on littoral sediments	Australia
Amphibolis griffithii (J.M.Black) Hartog	Cymodoceaceae	Seagrass, Aquatic	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia
Halodule bermudensis Hartog.	Cymodoceaceae	Aquatic, Seagrass	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	West Indies
Halodule uninervis (Forssk.) Boiss.	Cymodoceaceae	Aquatic, Seagrass	50 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia, India, Malaysia, MENA
Halophila australis Doty & B.C.Stone	Hydrocharitaceae	Aquatic, Seagrass	54 dS m ⁻¹	С3	Seagrass beds on littoral sediments	Australia
Halophila baillonis Asch.	Hydrocharitaceae	Seagrass, Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Amazon rainforest, Caribbean marine
Halophila beccarii Asch.	Hydrocharitaceae	Seagrass, Aquatic	54 dS m ⁻¹	С3	Seagrass beds on littoral sediments	China, Vietnam, Bangladesh, India
Halophila capricorni Larkum	Hydrocharitaceae	Aquatic, Seagrass	_	C3	Seagrass beds on littoral sediments	Australasia
Halophila decipiens Ostenf.	Hydrocharitaceae	Seagrass, Aquatic	46 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia, Thailand, China
Halophila engelmannii Asch.	Hydrocharitaceae	Seagrass, Aquatic	40 dS m ⁻¹	C4	Seagrass beds on littoral sediments	North America
Halophila gaudichaudii J.Kuo	Hydrocharitaceae	Aquatic, Seagrass	-	C3	Seagrass beds on littoral sediments	Japan, Marshall Islands
Halophila hawaiiana Doty & B.C.Stone	Hydrocharitaceae	Aquatic, Seagrass	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Pacific-West Archipelago
Halophila major Miq.	Hydrocharitaceae	Seagrass, Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Thailand
Halophila mikii J.Kuo	Hydrocharitaceae	Seagrass, Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Japan
Halophila minor (Zoll.) Hartog	Hydrocharitaceae	Aquatic, Seagrass	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	East Asia, Australia
Halophila nipponica J.Kuo	Hydrocharitaceae	Seagrass, Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Korea, Japan
Halophila okinawensis J.Kuo	Hydrocharitaceae	Aquatic, Seagrass	-	C3	Seagrass beds on littoral sediments	Japan
Halophila ovalis (R.Br.) Hook.f.	Hydrocharitaceae	Seagrass, Aquatic	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	USA, Australia, China
Halophila spinulosa (R.Br.) Asch.	Hydrocharitaceae	Seagrass, Aquatic	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia, Malaysia
Halophila stipulacea (Forssk.) Asch.	Hydrocharitaceae	Seagrass, Aquatic	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Red Sea, Persian Gulf, Indian Ocean

Table 2 – continue

Species	Family	Life Form	Maximum tolerance	Photosynthetic pathway	Habitat	Some recorded distribution
Halophila tricostata M.Greenway	Hydrocharitaceae	Aquatic, Seagrass	_	C4	Seagrass beds on littoral sediments	Australia
Hydrilla verticillata (L.f.) Royle	Hydrocharitaceae	Aquatic	10 dS m ⁻¹	C3	Atlantic communities	USA, China, Iran
<i>Posidonia angustifolia</i> Cambridge & J.Kuo	Posidoniaceae	Seagrass, Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Australia
<i>Posidonia denhartogii</i> J.Kuo & Cambridge	Posidoniaceae	Aquatic, Seagrass	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Australia
<i>Posidonia kirkmanii</i> J.Kuo & Cambridge	Posidoniaceae	Aquatic, Seagrass	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Australia
<i>Posidonia robertsoniae</i> J.Kuo & Cambridge	Posidoniaceae	Aquatic, Seagrass	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Australia
Posidonia australis Hook.f.	Posidoniaceae	Seagrass, Aquatic	75 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia
<i>Posidonia coriacea</i> Cambridge & J.Kuo	Posidoniaceae	Aquatic, Seagrass	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Australia
Posidonia ostenfeldii Hartog	Posidoniaceae	Aquatic, Seagrass	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia
<i>Posidonia sinuosa</i> Cambridge & J.Kuo	Posidoniaceae	Aquatic, Seagrass	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia
Ruppia megacarpa R.Mason	Ruppiaceae	Seagrass, Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments, inland saline lakes, ponds	Australia, New Zealand
Ruppia polycarpa R.Mason	Ruppiaceae	Aquatic, Seagrass	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments, inland saline lakes, ponds	New Zealand, Australia
Ruppia cirrhosa (Petagna) Grande	Ruppiaceae	Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	America, Europe
Ruppia maritima L.	Ruppiaceae	Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	USA, Brazil, Netherlands, UK, MENA
Sagittaria montevidensis Cham. & Schltdl.	Alismataceae	Aquatic	54 dS m ⁻¹	C3	Prairie wetlands, lakes, ponds, marshes, streams, rivers	North & South America
Stuckenia pectinata (L.) Börner	Potamogetonaceae	Aquatic	18 dS m ⁻¹	C3	Permanent inland lakes, ponds, pools, marine habitats	GB, USA, Russia, Netherlands, Baltic coast, Spain, South Africa
Syringodium isoetifolium (Asch.) Dandy	Cymodoceaceae	Aquatic, Seagrass	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia, Indonesia, Philippines, India, Indian and Pacific Oceans
Thalassia hemprichii (Ehrenb.) Asch.	Hydrocharitaceae	Aquatic, Seagrass	31 dS m ⁻¹	C4	Coastal habitats, Marine habitats	Indonesia, China, India, Australia, Palau
Thalassia testudinum K.D.Koenig	Hydrocharitaceae	Aquatic	42 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Belize, Cuba, USA, Canada

Table 2 - continue

Species	Family	Life Form	Maximum tolerance	Photosynthetic pathway	Habitat	Some recorded distribution
Thalassodendron pachyrhizum Hartog	Cymodoceaceae	Seagrass, Aquatic	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia
Zannichellia palustris L.	Potamogetonaceae	Aquatic	9 dS m ⁻¹	C3	Surface running waters, industrial sites, brackish water tidal rivers	Africa, Europe, USA, Chile, MENA
Zostera angustifolia Loser	Zosteraceae	Aquatic, Seagrass	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	UK, Norway
Zostera asiatica Miki	Zosteraceae	Seagrass, Aquatic	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Korea, Japan, USA
Zostera caespitosa Miki	Zosteraceae	Aquatic, Seagrass	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	Korea, Japan, China
Zostera capensis Setchell	Zosteraceae	Aquatic, Seagrass	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Africa - south and east
Zostera japonica Ascherson & Graebner	Zosteraceae	Aquatic, Seagrass	27 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia, East Asia, USA
Zostera muelleri Irmisch ex Ascherson	Zosteraceae	Seagrass, Aquatic	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia, New Zealand
Zostera polychlamys (J.Kuo) S.W.L.Jacobs & Les	Zosteraceae	Seagrass, Aquatic	54 dS m ⁻¹	C3	Seagrass beds on littoral sediments	South & Western Australia
Zostera tasmanica Martens ex Ascherson	Zosteraceae	Seagrass, Aquatic	54 dS m ⁻¹	C4	Seagrass beds on littoral sediments	Australia, New Zealand, Tasmania

Data primarily extracted from the eHALOPH database (Flowers et al., 2024) and supplemented with the authors' experiences.

4. Suitable characteristics for salt phytoremediation

4.1. Capacity to salt absorption

It is important to note that not all halophytic plants are suitable for salt phytoremediation, and different plant species may have varying levels of effectiveness in various environments. Among more than 1200 halophyte species listed in the eHALOPH database, only 22.4% (269 species) have bioremediation potential (Flowers et al., 2024). The effectiveness of salt phytoremediation can also depend on the management of the plants and the environment in which they are grown.

Both glycophytes and halophytes have a limited capacity to absorb and store salts in their tissues. In glycophytes, the absorption of salts is limited as they are not adapted to high salt concentrations in the soil or water (Himabindu et al., 2016; Pirasteh-Anosheh et al., 2016). When exposed to high salinity levels, glycophytes experience salt stress, negatively affecting their growth, development, and productivity. The limited capacity of glycophytes to absorb and store salts is one of the main reasons why they are unsuitable for phytoremediation of saline soils or waters (Assaha et al., 2017; Himabindu et al., 2016). Hasanuzzaman et al. (2014) believed that even salt-tolerant crops do not remove the salt from saline environments, and they

emphasize halophytes for remediation. Using salt-tolerant crops does not remove the salt; hence, halophytes that can accumulate and exclude the salt can be effective. However, halophytes also have a limited capacity to absorb and store salts more than glycophytes (non-halophytic plants). Once the plants, whether halophyte or glycophyte, have reached their maximum capacity for salt accumulation, they will need to be harvested and removed from the site, and the process may need to be repeated periodically to maintain the desired level of salt removal.

The capacity of halophytes to absorb salts from soil or water can vary depending on several factors, such as the species, the salinity level of the soil or water, and the environmental conditions in which the plant is grown (Flowers and Colmer, 2008; Kefu et al., 2002; Pirasteh-Anosheh et al., 2023c). The accumulation of salts in the tissues of halophytes can only occur up to a certain threshold beyond which the plant will experience salt toxicity (Ranjbar et al., 2018). Halophytes such as *Salicornia europaea*, *Salicornia brachiata*, *Atriplex canescens*, *Limonium sinuatum*, *Suaeda maritima*, *Mesembryanthemum crystallinum*, and *Halimione portulacoides* can accumulate salt concentrations that can reach up to 10% (and even more) of their dry weight, indicating a high capacity for salt uptake and accumulation (Flowers and Yeo, 1995; Shabala and Mackay, 2011; Loconsole et al., 2019). The capacity of halophytes to absorb salts from water can

depend on several factors. However, some halophytic plants can remove up to 90% of the salt from saline water (Hasanuzzaman et al., 2014; Nguyen et al., 2021).

4.2. Essential features

Plants suitable for phytoremediation should possess specific characteristics that enable them to remove or stabilize contaminants from the environment effectively. Some of the characteristics of a plant suitable for phytoremediation include (Aziz and Mujeeb, 2022; Parnian et al., 2022b,c):

- Tolerance to high levels of contaminants: Phytoremediation plants should be able to tolerate high levels of contaminants, such as heavy metals, high alkalinity, or petroleum and organic pollutants, without suffering from toxicity or other adverse effects.
- Ability to absorb and accumulate high amounts of contaminants: Phytoremediation plants should be able to absorb and accumulate contaminants from the soil or water in their tissues, where they can be safely stored or degraded.
- Fast growth and high biomass: Plants with fast growth rates and high biomass production can efficiently remove large quantities of contaminants from the environment within a relatively short period.
- Deep root system: Plants with deep root systems can effectively reach and remove contaminants from the deeper layers of soil or groundwater.
- Low maintenance requirements: Phytoremediation plants should have low maintenance requirements and be easy to grow and propagate.
- 6. Non-invasive: Phytoremediation plants should be non-invasive and not pose a risk of spreading beyond the intended remediation area.
- 7. Compatibility with the remediation technology: The choice of a phytoremediation plant should be compatible with the specific remediation technology used, such as phytostabilization or phytodegradation.

Overall, a plant's suitability for phytoremediation depends on its ability to effectively remove or stabilize contaminants from the environment and other practical considerations such as its growth rate and maintenance requirements.

5. Challenges

As stated above, halophytes have a good potential for reclamation and remediation of saline soils and waters. However, this approach undoubtedly has some crucial challenges, which of them are summarized below:

5.1. Agronomic aspects

Although halophytes grow well in their natural habitats and produce seeds and propagate after completing the growth cycle, their cultivation in new environments always faces important problems. One of the most essential agricultural aspects that is the main challenge of halophyte cultivation is seed germination

and seedlings establishment of halophytes. Usually, the seeds of halophyte species have deep physiological and physical dormancy, which require special protocols to break them. Furthermore, creating a uniform and pure cover of a halophyte species is challenging due to genetic impurity and the production of heterogeneous seeds (Pirasteh-Anosheh et al., 2022).

From an ecological point of view, producing heterogeneous seeds is a strategy to ensure the survival of the next generation, as a single plant may produce heterogeneous seeds in terms of dormancy, dispersal, and persistence in the seed bank (Matilla et al., 2005). In addition, other agricultural aspects such as time, density, method of sowing or planting, water (irrigation), and nutritional (fertilization) requirements are generally unknown in these plants. Of course, superior agricultural characteristics such as quick adaptation, low demand for water and nutrients, high competition ability with weeds, and tolerance to biotic and abiotic stresses are among the positive aspects of these species for their domestication (Liu et al., 2021).

Furthermore, the effective remediation of saline environments through the cultivation of halophytes necessitates extensive research into the specific soil conditions, microbial associations, and climatic factors that impact halophyte growth. Additionally, the formulation of effective agricultural practices, such as optimizing irrigation and fertilization regimes, can significantly improve the establishment and productivity of halophytes, thereby enhancing the success of phytoremediation projects.

5.2. Invasiveness

The next problem is the possibility of these species becoming aggressive. Due to the fast growth, low demand for water and nutrients, and highly competitive capacity of this species against common agricultural species, there is a possibility that this species will act as an invasive species in a new area. An invasive species (synonymous with exotic, non-indigenous, introduced, or newcomer) is a plant not native to a region. When it enters that region, it grows and develops a lot, usually out of control, and can cause a lot of economic and environmental damage to the new area (Ievinsh, 2023).

Invasive species are generally defined as alien species that can spread aggressively outside their natural range, which can be dangerous for the environment, economy, or human health (Al Hassan et al., 2016). Some examples of invasive plant species outside the domestic location are Alhagi maurorum, Alternanthera philoxeriodes, Ambrosia psilostachya, Ambrosia psilostachya, Azolla filiculoides, Bassia indica, Carpobrotus edulis, Centaurea solstitialis, Cortaderia jubata, Dittrichia viscosa, Hedera helix, Hydrocotyle vulgaris, Lantana camara, Lepidium latifolium, Opuntia spp, Parthenium hysterophorus, Phragmites australis, Pontederia crassipes, Portulaca oleracea, Pueraria montana, Retama monosperma, Reynoutria japonica, Salsola kali, Salsola tragus, Spartina patens, Spartina patens, and Tamarix ramosissima.

The uncontrolled use of invasive halophyte species in phytoremediation projects can significantly disrupt surrounding ecosystems. These invasive plants may outcompete native species for essential resources such as water, nutrients, and light,

disrupting local food and altering animal habitat structures, including the potential proliferation of pests and diseases. Consequently, this disruption can lead to a decline in biodiversity, potentially resulting in the extinction of certain native plant and animal species (Zainab et al., 2023).

Additionally, invasive plants/algae can affect the whole ecosystem's environment through soil chemistry alteration and hydrology, further impacting native plant/algae communities and the animals that depend on them (Szumańska et al., 2021). The economic costs associated with managing invasive species and mitigating their impacts can be substantial, often requiring significant resources for control and restoration efforts (Heringer et al., 2024). Consequently, understanding and addressing the threats posed by using invasive plant/algae species in environmental remediation is essential for preserving biodiversity and maintaining healthy ecosystems.

5.3. Adaptability

Another issue related to the effective use of halophyte plants for rehabilitating saline soil and aquatic environments is using the appropriate species. A limited number of suitable species can be considered for each region. For example, according to the eHALOPH database, about 27 halophytic and other salinity-tolerant species with bioremediation capabilities are economically efficient for soil improvement (Garcia-Caparross et al., 2023; Flowers et al., 2024). For each region, a suitable species compatible with the climatic properties, agricultural resources (especially soil and water), and social and economic conditions of that region should be selected. Secondly, it should not act as an invasive species. Species adapted to one area can behave like invasive species in other areas. Therefore, detailed research on a large scale as on-farm is needed to investigate the adaptation and domestication of halophyte species in a region.

5.4. Economic aspects

The economics of using halophyte species for phytoremediation can be drawn from two perspectives. First, reaching one or more suitable species for remediation in a saline environment requires conducting research and implementing pilot studies. Implementing research and pilot studies sometimes needs a huge budget, which does not necessarily always bring successful results and may need to be repeated consecutively. Second, the economic value of phytoremediation. Is the use of halophytes economically efficient? Halophytes are believed to have potential economic value as grain, vegetable, fruit, medicine, animal feed, and biofuel feedstocks, and in greening and coastal protection; however, a few halophytes are cultivated for economic purposes at present, and most halophytes are still found in the wild (Cárdenas-Pérez et al., 2021; Liu and Wang, 2021). This issue depends on labor costs and other consumption items in each area, on the one hand, and the value of the target land for rehabilitation, on the other hand. The possibility of consuming grown halophytes can also play a role in this financial balance (Barkla et al., 2024).

6. Conclusions and future prospects

Halophytes offer a promising ecological solution for mitigating soil salinity. Their unique ability to absorb and tolerate high salt concentrations makes them ideal candidates for phytoremediation. They can potentially function as biofilters in saline environments, accumulating salts in their tissues and improving soil conditions. Furthermore, the possibility of utilizing halophytes for biofuel, fodder, or other commercial purposes adds economic value to this approach. However, significant research gaps remain unclear. The efficiency of salt phytoremediation varies greatly between halophyte species regarding salt uptake and overall remediation capacity. Factors like watering regime, temperature, and plant maturity are known to influence this efficiency, but more robust predictive models are needed to optimize these factors for specific applications. Despite the challenges, several strengths underline the potential of halophyte-based phytoremediation. It represents a natural solution that avoids harsh chemicals. Additionally, research on genetic modification holds promise for enhancing salt uptake rates. Moreover, the economic benefits of utilizing halophytes for various purposes offer a compelling incentive for large-scale implementation. However, significant knowledge gaps require further investigation. The long-term environmental impacts of large-scale halophyte use remain unclear. Determining the most effective halophyte species for specific environments and developing robust predictive models are crucial for successful implementation. Understanding the internal mechanisms of salt uptake in halophytes is critical for optimizing this technology. Further research in this area will pave the way for its effective and sustainable application.

Conflict of interest

The authors declare no conflict of interest.

Author Contributions

Hadi Pirasteh-Anosheh – Conceptualization, Data curation, Methodology, Writing – original draft. Amir Parnian – Data curation, Investigation, Methodology, Writing – original draft. Abolfath Moradi – Conceptualization, Investigation, Writing – original draft. Pedro Garcia Caparros – Data curation, Investigation, Methodology, Writing – original draft. Agnieszka Piernik – Data curation, Investigation, Methodology Writing – review & editing. Piotr Hulisz – Conceptualization, Investigation, Supervision, Writing – review & editing.

All authors read and approved the final manuscript.

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Zastosowanie halofitów do fitoremediacji zasolonych gleb i wód: nowe mechanizmy, obiecujące gatunki i wyzwania

Słowa kluczowe

Rolnictwo biosalinowe Halokultury Rekultywacja terenów Zasolenie Remediacja gleb

Streszczenie

Nadmierne zasolenie gleb skutkuje ograniczeniem wzrostu roślin, powoduje wyłączenie gruntów z produkcji rolniczej, negatywnie wpływa na ekosystemy wodne, a także ogranicza wykorzystanie zasobów wodnych w rolnictwie, przemyśle i życiu człowieka. W niniejszej pracy dokonano oceny potencjału fitoremediacyjnego roślin słonolubnych (halofitów) i ich zdolności do absorpcji soli z gleby i środowiska wodnego. Uprawa halofitów, czyli rolnictwo biosalinowe, jest z powodzeniem stosowane do produkcji żywności, pasz dla zwierząt, oleju, biopaliw i farmaceutyków. Kluczowe wyzwania obejmują identyfikację i selekcję odpowiednich odmian roślin, poprawę plonowania, optymalizację metod uprawy oraz ocenę opłacalności ekonomicznej w celu szerszego zastosowania. Wykazano, że halofity są grupą roślin, które mogą być stosowane jako zrównoważone i opłacalne rozwiązanie łagodzące problem zasolenia gleb i wód. Potrzebne są jednak w tym zakresie dalsze badania.