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REVIEW ARTICLE

Sesuvium portulacastrum: A versatile halophyte for bioremediation and sustainable applications: A review

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Abstract

Plant *Sesuvium portulacastrum*, commonly known as sea purslane, is a pioneer plant species in coastal areas and belongs to the Aizoaceae family. It thrives in sandy and saline environments, making it highly resistant to abiotic stresses like salinity and drought. This plant can be used for the restoration of salt-contaminated soils due to its ability to tolerate high sodium (Na) concentrations. Even under extreme salinity, it continues to grow without visible damage. The plant also produces a variety of bioactive compounds, including 20-hydroxyecdysone, secondary metabolites and antibacterial compounds. It is also rich in essential nutrients, making it valuable for application in food, medicine, natural fertilizers and animal feed. Studies in its biochemistry, molecular biology and physiology has provided insights into the mechanisms underlying its abiotic stress tolerance. Furthermore, biotechnological studies suggest its potential for pharmaceutical application. In dry and semiarid regions, the large-scale cultivation of *S. portulacastrum* contributes to the remediation of soils by reducing heavy metal concentration and salt concentrations in soils. For instance, in experiment where Na was added to soil, it led to a decrease in electrical conductivity and Na content, with 77.8 % of the Na extracted over a period of ninety days. Due to its resilience under saline, drought-prone and heavy metal-stressed conditions, this species serves as an effective bio indicator for pollution detection and a predictive tool for forecasting soil salinity.

Keywords: abiotic stress tolerance; biotechnology research; salt-contaminated soil restoration; secondary metabolites; *Sesuvium portulacastrum*

Introduction

In recent years, the usage of modern technologies in agriculture has increased rapidly, contributing to the rising salinity of agricultural lands. Salinity represents a major abiotic stress, initially causing osmotic stress and subsequently inducing ionic stress during both early and later stages of plant development. These stresses impacts plant survival mechanisms at the cellular, tissue and physiological levels (1). The primary reason for the decline in plant growth and development is the salinization of soil (2).

According to report, 1381 M ha, or 10.7 % of the worlds' total land area, are damaged by salinity. This includes 10 % of irrigated agricultural land and 10 % of rainfed cropland. In India, 6.73 M ha are affected, with Tamil Nadu alone accounting for 354784 ha of alkali soils and 13231 ha of coastal saline soils, totalling 368015 ha salt-affected land.

Salt-affected soils are generally categorised as saline (due to high soluble salt content), sodic (due to the excessively high Na content in the soil exchange sites and the soil solution with alkaline reaction), or saline-sodic (due to the dual problems of high salinity and alkaline pH). Typical categories of saline soils have spatial existence. These soil types commonly occur in areas with long-standing waterlogging, irregular rainfall patterns, high evapotranspiration demand under arid to semi-arid conditions and poor-quality groundwater (saline, sodic, or both).

Various methods have been developed to manage and remediate saline soils, including chemical, physical, mechanical, microbial, organic and phytoremediation methodologies (Fig. 1). Among these, phytoremediation using plants is considered a crucial and sustainable method. While higher accumulation of salt can be toxic to glycophytes, it offers an advantage to halophytes (3). Higher accumulation leads to changes in physiological and morphological characteristics of halophytes at the tissue level. In contrast to glycophytes, halophytes have adaptations to overcome the high salt levels in the growth medium by accumulating excess

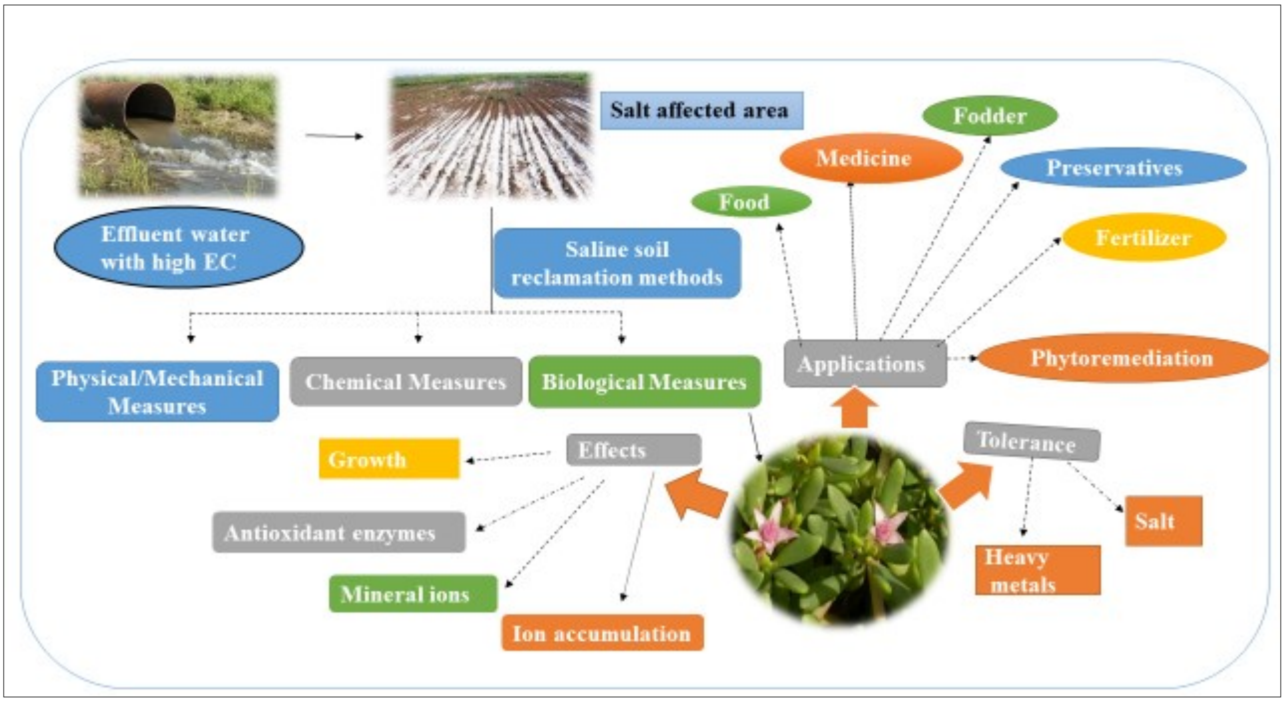

Fig. 1. Graphical abstract.

salt ions, which are then compartmentalized into the vacuoles. These plants also synthesize higher levels of osmolytes, such as proline, glycine betaine and soluble sugars and exhibit enhanced antioxidant enzyme activity, including catalase (CAT), ascorbate peroxidase (APX) and superoxide dismutase (SOD).

Sesuvium belongs to the Aizoaceae family, which has approximately eighteen species distributed across tropical and subtropical areas. They are divided into African and American species *via* phylogenetic research. The representative American species are *Sesuvium curassavicum, Sesuvium humifusum, Sesuvium maritimum, Sesuvium mezianum, Sesuvium rubriflorum* and *Sesuvium portulacastrum*, while representative African species are *Sesuvium congense, Sesuvium crithmoides, Sesuvium membryan-themoides* and *Sesuvioides.* The species *S. portulacastrum* is widely distributed globally.

The number of somatic chromosomes in *S. portulacastrum* varies by ecotype. An early study reported 2n = 36 chromosomes, while an ecotype with oblong-oblanceolate leaves was found to have 2n = 40 chromosomes. Other researchers have also reported 2n = 48 chromosomes for this species. Globally, *S. portulacastrum* is found in coastal regions of Australia, Africa, the Americas and Asia (4). Because of its broad distribution, it is known by various common names, including sea purslane and coastline purslane.

Despite being a valuable halophyte, sea purslane remains relatively underexplored (Fig. 2). It is easily produced as a leafy vegetable in saline soils and has potential applications in the bioremediation of salt affected soils and water bodies. The objective of this study is to explore the potential of *S. portulacastrum* in restoring salt-contaminated soils, its abiotic stress tolerance mechanisms and its

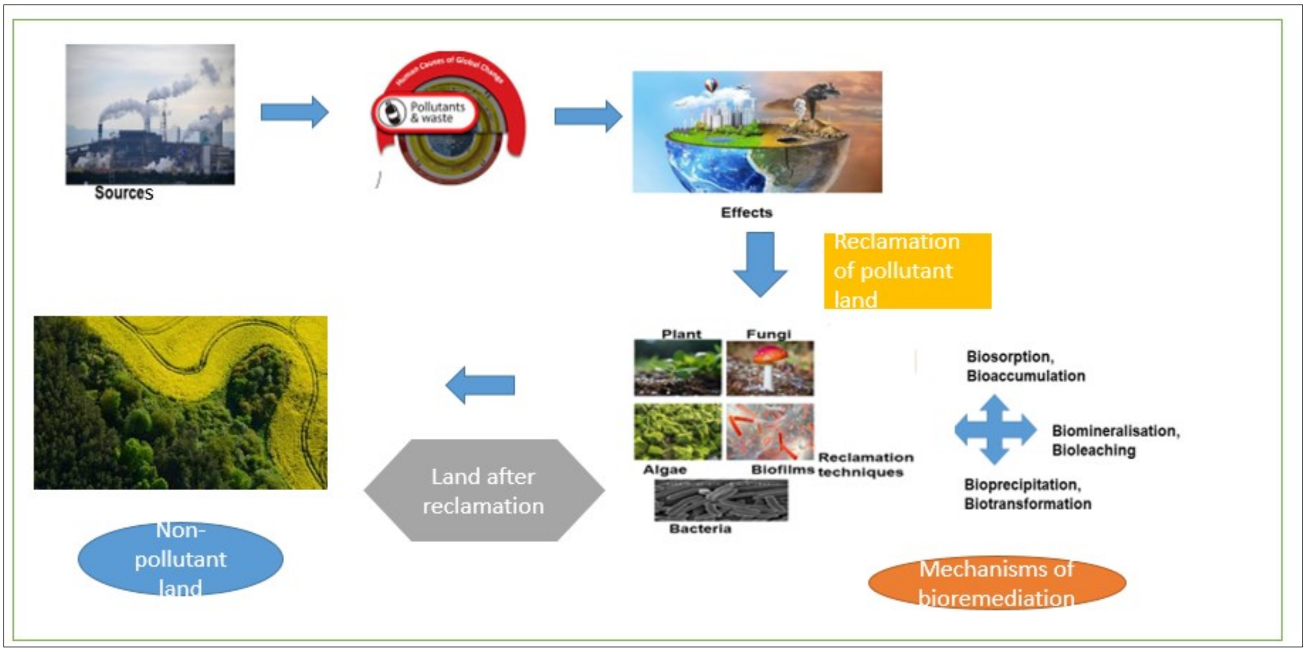

Fig. 2. Trends in bioremediation of pollutants and waste.

applications in food, medicine and biotechnology.

Methodology

The NOAA Central Library defines bibliometric analysis as "the quantitative examination of existing scholarly publications. Bibliometric analysis uses academic publications as a data source to shed light on the methods, structures and relationships involved in research production (4). It also assesses scholarly works based on the number of citations they have earned."

A systematic literature review was conducted using publicly accessible sources, such as Google Scholar, Web of Science, Scopus, Science Path, Springer and Wiley, to find relevant literature. Approximately 300 articles were collected using keywords such as *S. portulacastrum*, salt stress, salt tolerance mechanisms, heavy metal tolerance and the applications of *S. portulacastrum*. Among these, 80 articles focused on plants' bioremediation potential, 60 examined salt stress tolerance mechanisms and over 60 explored its morphology, growth and development. Additionally, 40 articles addressed its use as animal feed, 35 covered its medicinal properties and 25 investigated its potential as a preservative. Fig. 3 summarizes the literature pertaining to *S. portulacastrum,* particularly in the context of bioremediation.

A bibliometric analysis was then performed on peer-reviewed literature published between 2005 and 2024. The analysis focused on four key themes: (i) *S. portulacastrum*, (ii) bioremediation, (iii) stress mechanisms and (iv) applications. Open-source R software tools, bibliometric and its graphical interface biblioshiny were used. Bibliometric was particularly useful for processing the data and conducting scientific literature analysis.

The analysis found that over 300 publications have investigated salt accumulation in *S. portulacastrum*, emphasizing the need for further investigation into its bioremediation potential. The bibliometric circle, representing keywords used in bioremediation studies, grew as more specific terms were selected. The distance between keywords indicated topic similarity, with different circle colours representing distinct clusters. Furthermore, a three-field graph was created to show the connections between keywords, primary authors' keywords and sources. Rectangles representing these key elements varied in colour and height, with height corresponding to the number of relationships between elements.

The study also identified recent trends in bioremediation research, showing a significant increase in publications on *S. portulacastrum*. The annual growth rate of publications was calculated to be 103 %, with 2017 seeing the highest number of publications (147 articles) since 2005. Presents keyword occurrences, where larger circles represent more frequently co-selected keywords and distances between elements reflect topic similarity. The study also examined trends over time, revealing which subjects have been discussed more recently and which have persisted over time. The frequency of word usage in bioremediation research was also analysed, indicating that the most frequently used words are those that are most relevant to current research on the topic. Overall, the findings suggest that while substantial research has been conducted on the bioremediation potential of *S. portulacastrum*, there is a notable gap in its utilization as cattle feed.

Traits of salt-impacted soils

Electrical conductivity (EC), pH and the concentration of soluble ions specifically, Na^+, calcium (Ca^{2+}) and magnesium (Mg^{2+}) are the primary characteristics used to identify salt-affected soils, along with exchangeable sodium percent (ESP) and sodium adsorption ratio (SAR) (5). Salt-affected soil undergoes a slow and continuous pedogenesis, exhibiting distinctive characteristics over time (6). Globally, crop yields

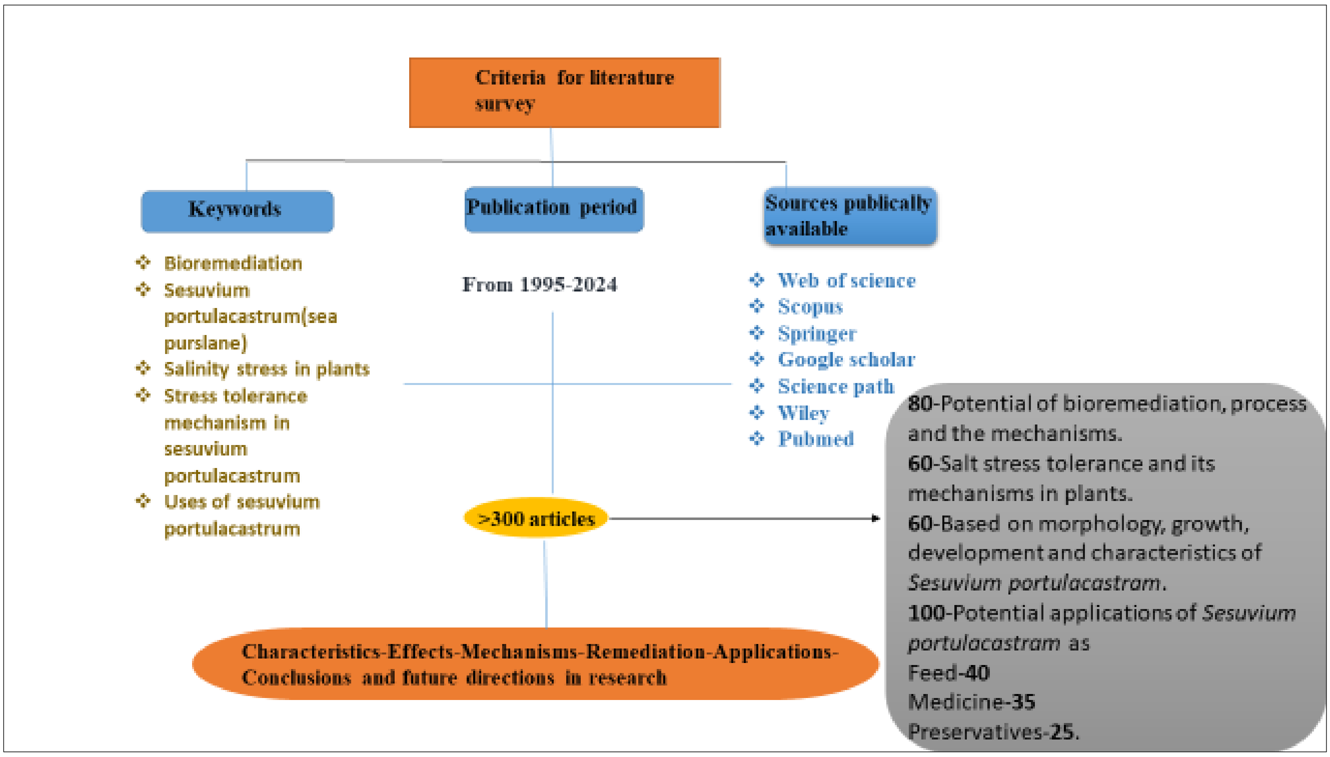

Fig. 3. Framework on literature collection and reviewing on bioremediation potential on *S. portulacastrum.*

are restricted by soils that are affected by salt. Understanding how salinity influences nutrient availability in plants is essential for developing effective management strategies to fulfil plant nutritional requirements and enhance yield, thereby meeting the demands of the growing global population.

In saline environments, where non-essential nutrients are present at high concentrations, plants are often compelled to absorb essential nutrients from diluted sources. The efficiency of nutrient uptake and utilization in salt-affected soils is significantly reduced due to salt stress and unfavourable interactions with excessive cations and anions. Consequently, such soil generally requires enhanced nutrient supplementation. In legumes, biological nitrogen fixation is adversely affected under saline conditions. Additionally, high salt concentrations inhibit the activity of various enzymes essential for energy production, which in turn limits nutrient absorption.

Key soil and plant management techniques that improve nutrient uptake and use efficiency in salt-impacted soils include the application of soil amendments to reduce salinity, the application of farmyard manures to create favourable conditions for plant growth, leaching of salts from the soil profiles and cultivation of salt-tolerant crop species or genotypes within crop species. The application of fertilizer , particularly potassium, may also aid in reducing the impacts of salinity and enhance the efficiency of nutrient utilization (7). Increasing soil salinity remains a major contributor to reduce agricultural productivity due to its inhibitory effects on plant growth (8), photosynthesis, protein synthesis, lipid metabolism and numerous other metabolic processes (Table 1).

Techniques for reclaiming saline soils

Salinity poses a significant barrier to agricultural yield, particularly in arid and semi-arid areas. Saline soil, characterized by excessive soluble salts, inhibit water uptake and nutrient absorption by plants, ultimately stunting growth and reducing crop yields. Conventional reclamation techniques, including salt leaching through irrigation, have been widely employed; however, they frequently require a lot of water and might not be viable in areas with limited water supplies. Consequently, recent advancements have focused on more effective, economical and ecologically friendly methods to reclaim saline soils (Fig. 4). The use of soil amendments, including gypsum, charcoal and organic matter, has been shown to improve soil structure and increases water infiltration, thereby reducing salinity levels.

Physical methods

Physical methods are particularly employed to alter the boundary and/or soil profile conditions, which are closely linked to the physical characteristics of saline-alkaline soil, this can represent the pattern of mass and energy flow in the soil environment, ultimately influencing plant growth and microbiological activity (10). The main goal of these methods

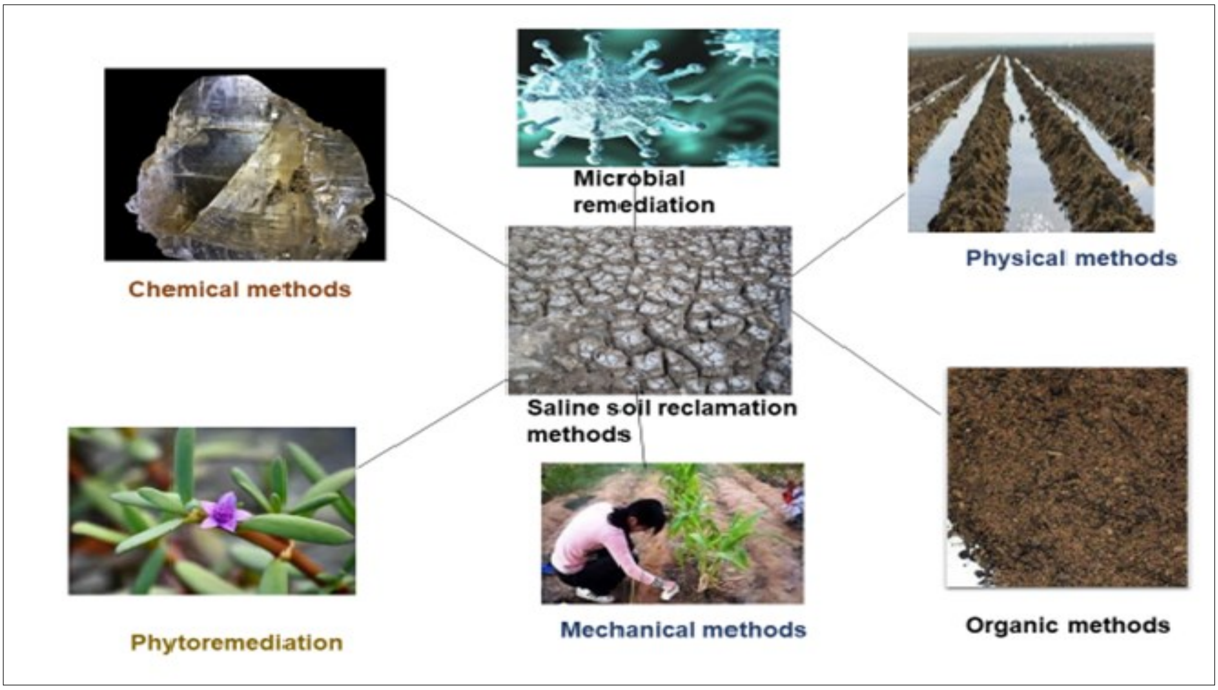

Fig. 4. Reclamation of soil salinity through various methods.

Table 1. Characteristics of various soils

Parameters	Saline soils	Sodic soils	Alkaline soils	Reference
Electrical conductivity (dSm^{-1})	>4	Variable	<4	
Sodium adsorption ratio (SAR)	<13	>13	>13	
Exchangeable sodium percentage (ESP)	<15	>15	Variable	(9)
P^H	6.5-8.5	8.5-10	>8.5	
Physical structure	Good (crusting)	Poor (dispersed)	Poor (compacted)	
Salt type	NaCl, $CaSO_4$	Na_2CO_3, $NaHCO_3$	Carbonate and bicarbonate	

is to alter the upper and lower boundary conditions in soil, which are connected to the soil water-gas characteristics.

Initially, the soil water and heat flow between the soil and the air was altered by the upper boundary conditions, which encompass drainage management techniques like drip and flood irrigation, together with agronomic measures like irrigation, buried layer and film mulching. Secondly, the cultivation layer conditions in the soil profile, such as agronomic practices (such as buried layer) and tillage (such as rotary tillage and deep vertically rotary tillage), are usually implemented to enhance the topsoil especially its physical characteristics.

The groundwater level is managed by the bottom boundary condition, which includes subsurface drainage canals, shafts and drainpipes. As technology has advanced, new techniques for the physical regulation of salinization have been introduced, including porous adsorption materials, biomass materials and degradable liquid films (11).

The most common irrigation methods include flood irrigation, drip irrigation, saline water and brackish water irrigation. Autumn irrigation is a traditional technique for reducing salt, which is influenced by the quantity and duration of water applied along with the freeze-thaw soil cycle (12). Drip irrigation, on the other hand, helps to mitigate water shortages and is employed to maintain optimal soil moisture levels in the root zone (13). Ploughing the layer plays a crucial role in the reclamation of saline-alkali soils. Deep vertical rotary tillage is a commonly used method in saline soils, as it effectively reduces pH, bulk density and EC while improving soil structure (14). In coastal saline areas, tillage techniques such as rotational tillage to a depth of 15 cm and deep tillage up to 25-30 cm are effective for enhancing soil properties, promoting plant growth and boosting economic benefits (15). Traditional methods like drainage ditches can also reduce salinity, open ditch drainage have been found to have a stronger desalination effect than subsurface pipe drainage, though certain studies suggest ditch drainage has only a moderate impact (16).

In general, physical measures play a key role in addressing saline-alkali related soil issues, demanding various types of agricultural machinery to manage water and salt movement, such as soil water infiltration, surface runoff and water–heat exchanges. These physical methods are widely used in soil reclamation to improve soil structure, infiltration rates and water retention capacity. Different regions affected by soil salinization require tailored physical strategies specific to that location, with one or two primary approaches, supplemented by additional techniques like water-saving irrigation, tillage, mulch and deep tillage (17).

Chemical methods

Saline-alkali soils contain variable quantity of soluble ions, which can be broadly classified into two groups based on the nature of the salt ions. The first group includes saline soils, which consist of ions like Na^+, potassium (K^+), chloride (Cl^-), sulfate ($SO4^{2-}$), etc. The second group is alkali soil, which primarily contains Na^+, bicarbonate (HCO_3^-) and carbonate (CO_3^-), with high pH levels. To improve ion exchange, neutralize acids and bases and balance ions, soil conditioners were applied. These are called as a chemical measures (18). Maintaining a proper K^+/Na^+ ratio in the soil is crucial for supporting crop growth (19). Common soil conditioners are calcium-based compounds, such as gypsum, which is particularly effective in alkali soils by reducing pH (20). Other acidic materials, like potassium dihydrogen phosphate, ferrous sulphate, aluminium sulphate and organic acids such as humic acid and furfural residue, are also used (21). The Ca^{2+} released by gypsum exchanges with Na^+ in soil colloids, lowering the sodium adsorbed by these colloids (22). Numerous studies have shown that gypsum application can enhance soil yield, although excessive gypsum use may hinder plant growth and decrease yield (23). Acidic materials are employed to enhance neutralization reactions, primarily affecting HCO_3^-, followed by Na^+ and Cl^-, which results in a 10-20 % reduction in pH (24).

A significant quantity of phosphate precipitate is formed in alkaline soil (25), but the addition of acid phosphate helps mitigate alkaline stress by facilitating neutralization in soil solution. Humic acid fertilizer influences the structure of soil bacterial and fungal communities, especially during harvest, when soil nutrient availability and root nutrient uptake are enhanced in saline soils (26). Biochar is a widely used soil conditioner for soils, improving soil structure and replacing excess exchangeable Na^+ by increasing soil organic carbon and cation levels, thereby reducing EC and salt content of soil (27). Biochars' functional groups, such as carboxyl groups, mitigate salt stress (14). It also alters the C:N ratio in saline-alkali soils (28). Low application rates reduce water evaporation, while higher doses enhance water retention, reduce surface salinity and lower SAR (29).

Chemical methods aim to alter soil chemistry, improve ion balance and decrease pH. However, their environmental impacts must be carefully assessed, as excessive application may lead to soil pollution. The choice of amendment depends on the soils' chemical and nutrient profile, with gypsum, humic acid and furfural residue being commonly used in low-organic matter saline-alkali soils (17).

Biological methods

Biological methods enhance salt tolerance and plant adaptation to saline-alkali soils. Root growth and exudation can improve the soils' physical and chemical properties of soil, boost plant dry matter accumulation and help salt removal from the soil through crop harvesting (30). These measures include three main components: improving salinity tolerance, enhancing soil fertility through plant growth and desalinating soil *via* during plant harvesting.

Several salt-tolerant plants, such as *Spartina anglica, S. portulacasturm, Australis Phragmites, Salicornia europaea, Sesbania cannabina, Suaeda salsa, Tamarix chinensis, Cynodon dactylon, Setaria viridis, Pennisetum alopecuroides* and *Imperata cylindrica* are found in various ecosystems and have been used for reclaiming saline-alkali soils, particularly those with high salinity levels (31). Plants like tamariz, Siberian white thorn and sand jujube can lower soil salinity, pH and bulk density (30). Their root exudates foster soil microorganisms and enhance soil enzyme activities such as cellulase, urease and dehydrogenase.

Planting salt-tolerant trees improves the soils' physical and chemical properties over a period of time. For instance, after planting, EC of the soil was reduced by 70-80 % and soil microaggregates contents improved by 5.0-5.9 %, while the soil particle size was reduced to 0.053 mm and EC was 1.65 dSm^{-1} (32). The concepts of dry salt discharge and plant salt accumulation focus on of saline-alkali soils alleviation. That demand excess irrigation water and high-salinity groundwater to accumulate in low-lying areas, where by the salt can be either absorbed by plants or left to accumulate (31). In dry salt discharge systems, halophytes help transport water and salt through transpiration, dispersing salt and improving salt accumulation efficiency (29). Although plant salt accumulation improves the biological adaptability of saline soils, long-term observations are needed to understand the frequent salt exchange between soil and groundwater in these areas. The saline-alkali soil primarily inhibits plant growth and development through its pH and ionic osmotic imbalances. Alkaline pH stress restricts root growth by lowering the levels of ethylene and auxin (33). Salt-tolerant plants are able to regulate osmotic pressure in their root and/or leaf cells, where root exudates act as shield themselves from salt stress (19). Additionally, metabolites like sucrose, amino acids, alkaloids, flavonoids and carotenoids help plants to cope with the stresses caused by saline-alkali soils. Metabolomic studies have shown that halophytes contain high levels of branched-chain amino acids, which pivotal enhance their ability to tolerate saline-alkali stress.

Soil microorganisms are vital for nutrient cycling and ecological stability in saline soils (13). The use of microorganisms for the reclamation of saline-alkali soils has been shown to be an effective approach (34). In the fertilizer industry, microbial fertilizers are categorized into three types: agricultural microbial agents, composite microbial fertilizers and bio-organic fertilizers (35). Agricultural microbial agents are fertilizers containing peculiar species and porous materials like peat (36). Bio-organic fertilizers are the fermentation products of beneficial bacteria with decomposed organic materials, such as animal manure, whereas composite microbial fertilizers are made up of two or more efficient bacterial strains (37). Microbial fertilizers enhance the excretion of Na^+ and uptake of K^+ by plants, thereby improving the K^+/Na^+ ratio in soil and boosting plant nutrient absorption (38). For example, microbial fertilizers produce extracellular polysaccharides (EPS) that form bacterial biofilms on plant roots, shielding them from sodium chloride (NaCl) stress. Additionally, volatile organic compounds (VOCs) released by microbial fertilizers induce physiological changes in plants, increasing their resistance to salt and alkali.

A sustainable and environmentally favourable approach has been proposed which is inoculation of native microalgae. Biological techniques are crucial for preserving or enhancing the health of saline-alkaline soils since they play critical role in the elimination of salt, plant growth and the general advantages of microorganisms. However, the implementation of biological methods remains limited due to challenges related to biological adaptability, environmental compatibility and efficiency (17).

Stress tolerance

Heavy metal tolerance

S. portulacastrum (sea purslane) exhibits tolerance to heavy metals, with mechanisms that vary depending on the specific metal. Heavy metal toxicity is one of the secondary stresses induced by salinity and sodicity. Studies have shown that *S. portulacastrum* accumulates significant amounts of various metals: 49.82 mg of chromium (Cr), 22.10 mg of cadmium (Cd), 35.10 mg of copper (Cu) and 70.10 mg of zinc (Zn) per kg of dry weight of the plant. The plant also accumulated 246.21 mg of nitrogen (N) per gram of dry weight.

Cd^{2+} accumulation in the vegetative parts of plants typically results in chlorosis, necrosis and growth inhibition. However, experimental data indicate that the roots of *S. portulacastrum* accumulate more Cd^{2+} than the shoots, suggesting the plant might function as a hyper-accumulator under certain conditions. Further research is needed to explore whether increased calcium (Ca^{2+}) concentrations in Cd-contaminated or saline soils could enhance the plants' ability to accumulate Cd. Additionally, reductions in K^+ absorption and translocation due to Cd^{2+} stress are linked to the complexation of ATP, reducing energy availability.

Comparative studies between *S. portulacastrum* and *Mesembryanthemum crystallinum* (another halophyte) have shown that *S. portulacastrum* had lower Cd concentration in its shoots but significantly higher K^+ and Ca^{2+} content. However, *S. portulacastrum* was not a hyper-accumulator of Cd or Cu, with metals primarily accumulating in the roots rather than the shoots. Research on *S. portulacastrum* treated with Cd (50 mM) and nickel (Ni, 100 mM) indicated that citrate concentrations in xylem and shoots increased, suggesting potential role for citrate in metal chelation to promote metal tolerance (17).

Salt tolerance

S. portulacastrum is highly tolerant to salinity, with plant growth steadily increasing when irrigated with nutrient solutions containing NaCl concentrations ranging from 100 to 500 mM. In hydroponic systems, plants grown with Na concentrations up to 500 mM exhibited growth comparable to or better than plants without Na. Na is more effective than K in promoting shoot development, leaf succulence and cell expansion, explaining why *S. portulacastrum* thrives in saline environments such as coastal beaches and mangrove areas.

This salt tolerance is primarily due to the plants' ability to absorb and translocate Na from roots to shoots, rather than by limiting Na uptake at the root level. As salinity increases, Na content also rises in *S. portulacastrum*, with concentrations typically higher in the shoots. The plants' ability to adapt to high salinity likely involves a coordinated mechanism, though the exact process remains unclear. Na uptake occurs via transporters like high-affinity potassium transporters (HKTs and HAKs) and non-selective cation channels (NSCCs) and is accompanied by the activation of antioxidant enzymes such as CAT, peroxidase and SOD, which mitigate the oxidative damage caused by reactive oxygen species (ROS).

Additionally, the plant also produces osmoprotectants such as proline, flavonoids and trehalose, which help reduce the effects of high Na concentrations. Key genes involved in Na transport, including the Na+/H+ antiporter (NHX3) and vacuole ATPase (V-ATPase), are activated during salt stress. Additionally, *S. portulacastrum* utilizes NHX and K+/H+ exchange mechanisms to compartmentalize Na in vacuoles, reducing cytosolic Na levels. The remaining Na in the cytosol is loaded into the xylem and transported to the shoots through the transpiration stream.

In transgenic models, overexpression of *S. portulacastrum* genes such as SpNHX1 (Na+/H+ antiporter) in yeast and *Arabidopsis* has been shown to enhance salt tolerance. Proteomic and metabolomic analyses revealed significant changes under salt stress, with overexpressed proteins linked to ion binding, photosynthesis, proton transport and ATP synthesis. Differentially expressed proteins (DEPs) in shoots and roots of salt-stressed plants further support the role of various metabolic pathways in salt tolerance (39).

Impact of growth changes under stress conditions

S. portulacastrum exhibits a remarkable ability to adapt to various abiotic stressors, such as salinity, drought and heavy metals, through a series of physiological, morphological and biochemical mechanisms. These adaptations are vital for the plants' survival and growth under stressful conditions. Several studies have shown that exposure to salt, drought and heavy metals, individually or in combination, leads to significant reductions in growth parameters such as root and shoot length, fresh and dry weight, root-to-shoot ratio, leaf number and leaf area (39, 40). However, under lower salt concentrations or when stress factors such as drought and heavy metals are balanced. *S. portulacastrum* shows improved growth, primarily due to its ability to maintain optimal water potential l, ion accumulation and metabolic adjustments.

Recent studies have also demonstrated that *S. portulacastrum* effectively employs osmotic adjustment strategies through the synthesis of osmolytes and by up regulating both enzymatic and non-enzymatic antioxidant activities (41). These physiological and biochemical responses enable the plant to recover many of its growth and functional parameters once the stress conditions are alleviated, indicating a high degree of resilience under both acute and chronic stress scenarios. The plants' capacity to lower its water potential and enhance water-use efficiency supports sustained growth and nutrient uptake even under unfavourable environmental conditions (40) .

Succulence and ion sequestration in response to salt stress

As a facultative halophyte, *S. portulacastrum* thrives in environments with high salinity levels (100-400 mM NaCl), even when nutrient availability is low. One of its key strategies for coping with salinity stress is the sequestration of ions and heavy metals into vacuoles, a mechanism that helps maintain osmotic balance between the vacuole and the cytoplasm (42). This process allows the plant to sustain its growth and protect its cellular structures. Halophytes like *S. portulacastrum* are known for "halo succulence," a phenomenon where high concentrations of salts in the vacuoles increase the succulence of vegetative tissues. This adaptation aids in reducing the toxic effects of excessive ion accumulation and helps stabilize cell turgor pressure, ensuring cellular integrity under high salinity (43).

Recent studies have shown that exposure to optimal concentrations of NaCl (100-400 mM) improves growth characteristics and enhances succulence in *S. portulacastrum*. In *in vitro* studies, plants exposed to 200 mM NaCl exhibited significant improvements in growth rate and halo succulence, further supporting the plants' ability to thrive under saline conditions. Moreover, *S. portulacastrum* is highly efficient at absorbing and distributing saline ions, as well as carbon resources, to different parts of the plant, thereby boosting its overall biomass, growth and net photosynthetic rate (44).

Impact of sodium on photosynthesis and growth

The plants ability to maintain high levels of succulence under salt stress (Fig. 5) is partly due to its efficient management of water and ion distribution. A study demonstrated that under NaCl concentrations ranging from 200 to 400 mM, the net CO_2 assimilation rate in *S. portulacastrum* initially increased up to first three weeks of treatment and then plateaued, stabilizing at levels comparable to untreated plants (45). This indicates that while the plant adapts to salt stress in the early stages, prolonged exposure may limit its photosynthetic capacity.

The rationale behind the plant's succulence trait involves two key mechanisms: (1) Na^+ help reduce the turgor pressure component of the water potential in cells, promoting cell expansion and (2) increased succulence effectively "dilutes" the ion content within cells, preventing toxicity from high concentrations of Na^+ (46). Interestingly, it has been hypothesized that absorbed Na^+ ions act as signaling molecules that trigger a cascade of salt-adaptation mechanisms in the plant; however, further research is needed to confirm this role in *S. portulacastrum*.

Studies also suggest that Na^+ is more effective than K^+ and Cl^- in promoting shoot development, leaf succulence and overall plant growth. When exposed to 200 mM Na^+, *S. portulacastrum* exhibited better growth and succulence than when exposed to equivalent concentrations of K^+ or Cl^-, further emphasizing the role of Na^+ in the plants' ability to cope with saline environments (20, 42).

Effects on osmolytes and mineral ions accumulation

Salt tolerance has several effects on plants where effects on osmolytes and mineral ions accumulation caused stress from salt greatly impacted the build-up of inorganic ions in *S. portulacastrum* stressed shoots. During salt stress, Na^+ concentration increased substantially in axillary shoots as salinity levels rose from 200 to 600 mM NaCl. At 600 mM NaCl, Na^+ concentration in treated shoots was approximately 2.6 times higher than that of the control. In contrast, K^+ accumulation did not show significant variation across different salt concentrations (200-600 mM). However, Ca^{2+} levels were drastically reduced at 200 and 400 mM NaCl treatments.

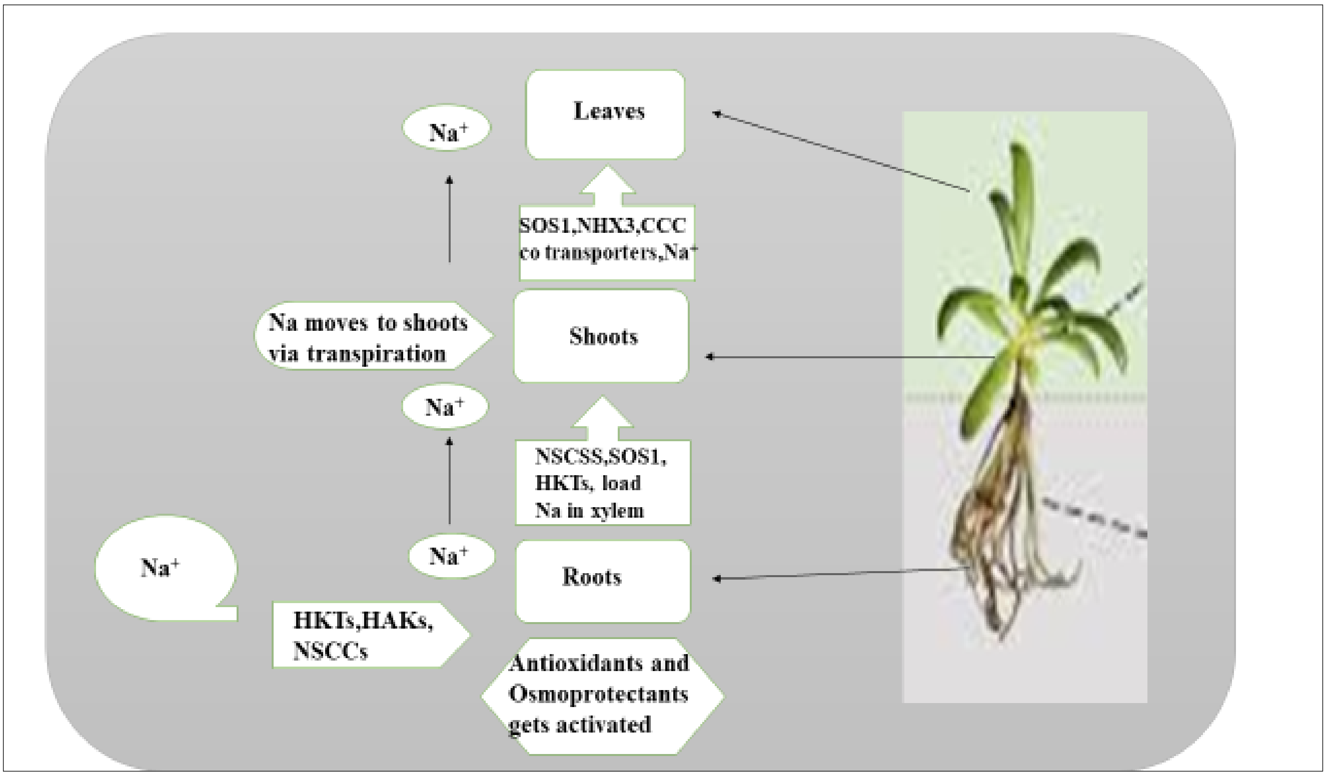

Fig. 5. Flow chart describing the transport of Na from roots to shoots.

Callus tissues developed under salt stress exhibited significantly higher levels of proline and glycine betaine content. When compared to control callus, the callus grown on MS medium supplemented with 200 and 400 mM salt exhibited the highest proline content (more than 12 and 7-fold respectively). A similar pattern was observed for glycine betaine accumulation. The concentrations of Ca^{2+}, K^+ and Na^+ in both salt-treated and untreated callus tissues showed notable differences. As salt levels increased, the accumulation of Ca^{2+} and Na^+ rose significantly-by about threefold and fourfold, respectively, compared to the control. In contrast, K^+ concentration decreased markedly under salt stress conditions (47).

Effect on antioxidant enzymes

Soil catalase (S-CAT), a common antioxidant enzyme, serves as an indirect indicator of soil biomass (Fig. 6). Soils with higher microbial biomass typically exhibit elevated catalase activity (48).

Under salt stress, catalase activity in *S. portulacastrum* declined significantly-by 7.8-fold at 200 mM NaCl and 6.09-fold at 400 mM NaCl compared to the control-and was almost completely suppressed at 600 mM NaCl. In contrast, APX activity increased progressively with salt levels up to 400 mM, but declined under 600 mM salt stress, indicating a threshold beyond which antioxidant defenses may become compromised.

Stress tolerance mechanisms

Avoiding cytosolic salt accumulation is a fundamental principle for mitigating salinity stress toxicity and it requires substantial energy input to operate efficiently. The growth and productivity of several commercial crops, such as rice, wheat, maize and cotton, are in danger due to drought stress (49). The similarity in H^+ in the plasma membrane can be explained by the physiological adaptation to salinity, which causes intrinsic tension to reduce the passage of toxic ions to the leaves. Salinity stress affects ATPase activity in different organelles and compartments, including salt-sensitive ATPases in the plasma membrane, F-ATPase in mitochondria and chloroplasts and vacuolar ATPase in vacuoles (Fig. 7) (50).

Although the regulation of enzymatic activity under persistent stress conditions remains complex, it is hypothesized that elevated concentrations of sulpholipids contribute to the stabilization of F-ATPase in thylakoid protein complexes (51). Sulpholipids have been found to be essential for the synthesis of ATP in chloroplast membranes and for the stabilization of photosystems. Since salt stress management is an energy-demanding (Fig. 8) process in plants that requires a high amount of ATP production to maintain the osmotic balance (52). Surprisingly, the increased concentration of sulpholipids and sulpho quinovosyl diacyl glycerol (SQDG) in the salt-stressed shoots of *S. portulacastrum*, which primarily contain palmitic acid, γ-inolenic acid and trace amounts of linoleic acid, suggested their active involvement in salt stress tolerance (47). These sulpholipids, which are present in thylakoid membranes, are known to stabilize protein complexes in photosystem II and other chloroplast membranes. Additionally, it has been noted that changes in the length and intensity of salt stress impact the unsaturation of SQDG (47). The presence of unsaturated fatty acids in membrane lipids improves salt stress tolerance by enhancing the resistance of photosystem II.

Excessive salinity disrupts the metabolism of nitrogen, which in turn impacts its protein synthesis and accumulates free amino acids (48). Interestingly, it was discovered that as NaCl concentrations increased, the amounts of amino acids

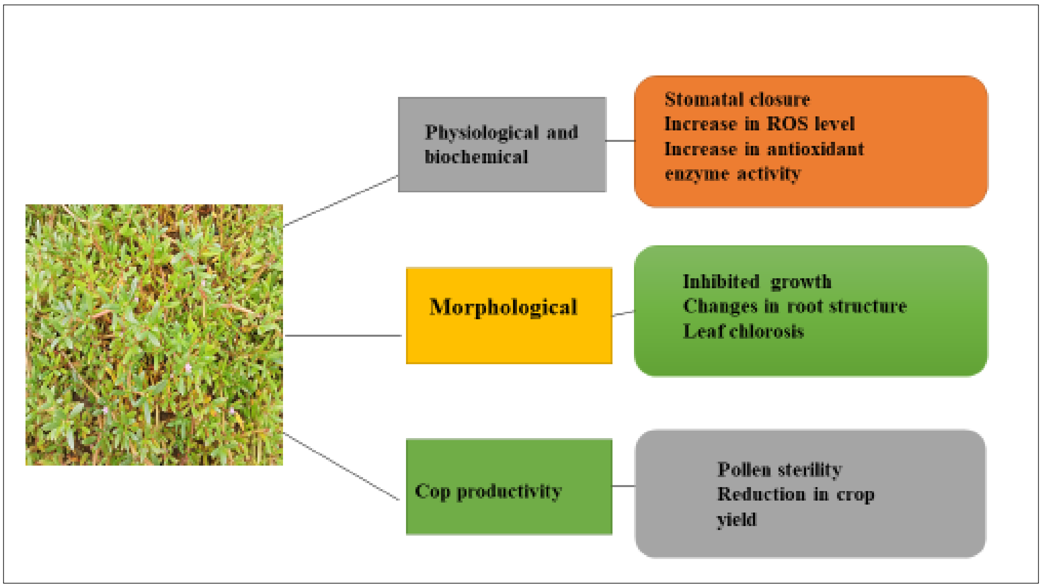

Fig. 6. Changes occurring in plant during salt tolerance.

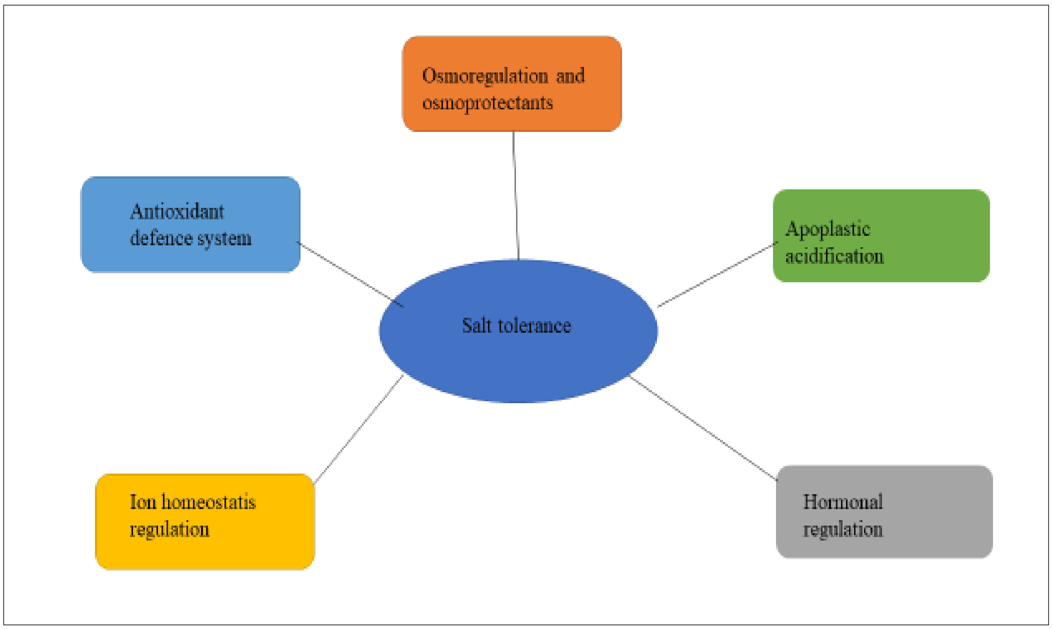

Fig. 7. Depicts the salt tolerance in plants.

and proteins in *S. portulacastrum* initially decrease under salt stress. However, these levels tend to recover with prolonged exposure (53). The succulent stem and leaves of *S. portulacastrum* have been found to contain elevated levels of amino acids such as proline, aspartic acid, glutamic acid, alanine, serine and glycine (49). Moreover, the amino acid pools of various plant components have also shown notable seasonal fluctuations, with an overall quantity of amino acids in the leaves decreasing in the summer, while stems exhibit an increase. Notably, proline levels decrease in summer, in contrast to higher concentrations of aspartic acid, glutamic acid, alanine, valine and leucine (2). Under salt stress, whether alone or combined with drought, *S. portulacastrum* accumulates higher levels of proline, which helps the plant resist osmotic stress. However, seasonal influences on proline accumulation remain difficult to fully explain. A strong correlation has been observed between proline content, tissue hydration and growth maintenance under osmotic stress (54).

Proline functions as an antioxidant in order to prevent denaturing of protein quaternary structures, stabilizing cell membranes through interactions with phospholipids and provided energy and nitrogen (49). Exogenous proline also mitigates salt stress effects by boosting plant uptake of K^+, decreasing Na^+ and Cl-uptake and translocation and increasing antioxidant activities (55). Proline synthesis under water stress is aided by increased ornithine-aminotransferase activity in *S. portulacastrum*, but protein catabolism is facilitated by decreased proline dehydrogenase activity. Proline is synthesized through either glutamate or ornithine pathways. A deeper understanding of the mechanisms sustaining proline production and accumulation in response to osmotic stress is still needed. These adaptive responses likely involve increased activity of proline-synthesis enzymes like pyrroline-5-carboxylate reductase, reduced incorporation of certain amino acids into proteins limiting their conversion to glutamate and arginine and inhibition of pyrroline-5-carboxylate dehydrogenase caused by salt stress. (56). Protein biosynthesis such as Δ^1-pyrroline-5-carboxylate synthetase, takes place when removal of inhibition of enzymes happens. (51, 52). To fully comprehend the metabolic plasticity and stress physiology of this plant under

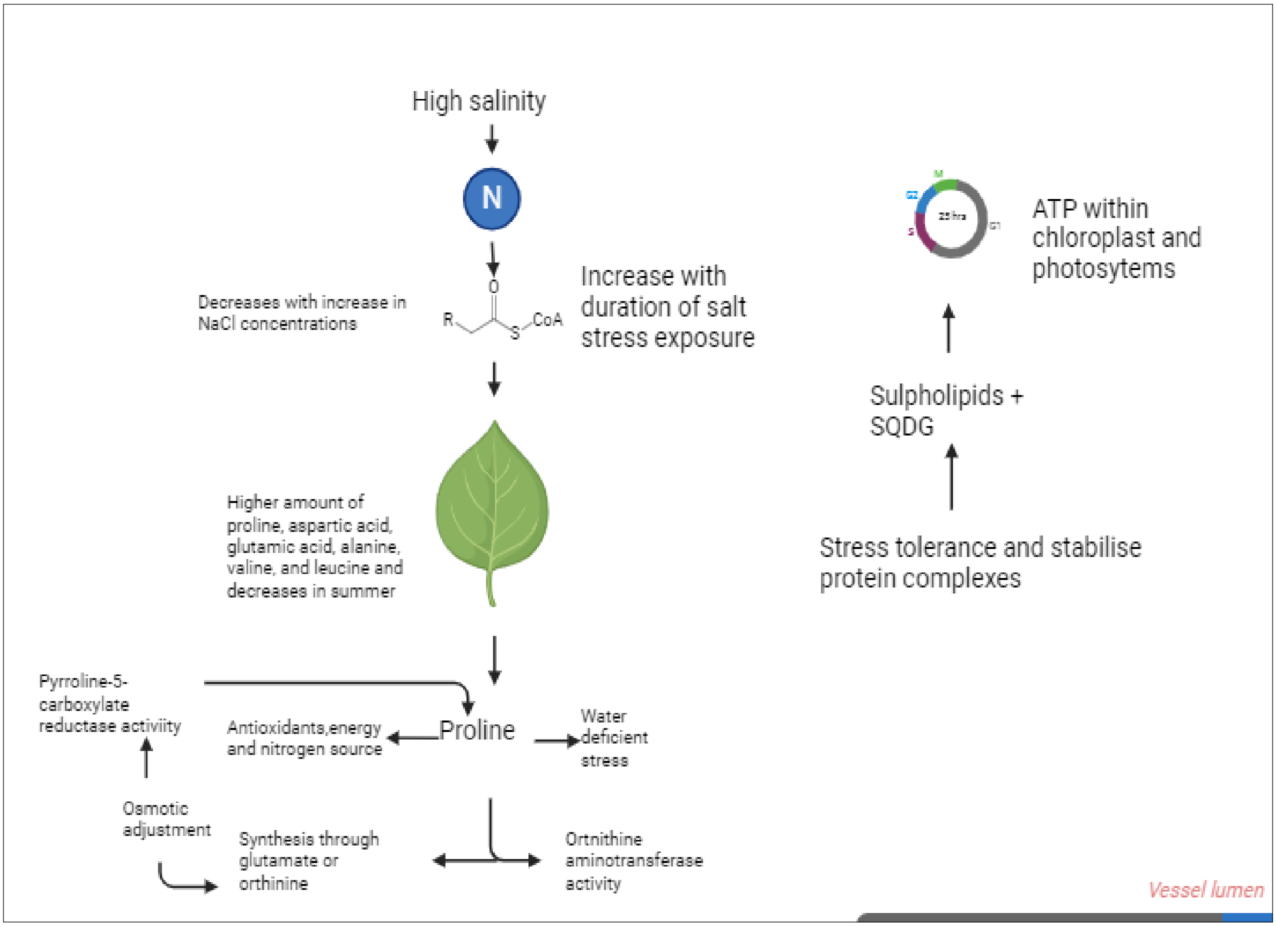

Fig. 8. Mechanism involved in salinity induced anti-stresses reaction.

osmotic and ionic stress, further detailed investigation is warranted.

In addition to amino acids, the fatty acid profile revealed that the leaves had significant concentrations of campesterol, stigmasterol and sitosterol as important sterols and myristic, palmitic, stearic, oleic, linoleic and linolenic acids as essential fatty acid components.

Uses of *Sesuvium portulacastrum*

Medicine

The ethanolic extract of *S. portulacastrum* has demonstrated promising activity against nosocomial infections and major pathogens associated with various gastrointestinal disorders, including dysentery, diarrhoea, indigestion and even neurodegenerative conditions such as Alzheimers' disease (57). It has been used as an antibacterial agent to treat a variety of conditions, including epilepsy, dermatitis, conjunctivitis, haematuria, leprosy and purgative.

Rich in bioactive secondary metabolites, *S. portulacastrum* holds considerable potential as a natural alternative to synthetic raw materials for applications in the food, fragrance, cosmetic and pharmaceutical industries, offering both medicinal and commercial value (56). In traditional medicine, it is used as a remedy for fever, kidney disorders, and scurvy by indigenous populations in regions of Latin America, Africa and Asia, including countries such as China, Japan, India and Pakistan (58).

The therapeutic properties of the essential oil derived from *S. portulacastrum* are largely attributed to its high content of monoterpenes, primarily composed of hydrocarbon compounds such as o-cymene, β-pinene, α-pinene, 1,8-cineole, limonene, α-terpinene, α-terpinolene and camphene. The antimicrobial efficacy of these compounds is associated with their ability to compromise the integrity of bacterial and fungal cell membranes, thereby exerting cytotoxic effects on the pathogens (59).

It has been demonstrated that the fatty acid methyl esters (FAME) extract from *S. portulacastrum* leaves had more saturated fatty acids than unsaturated fatty acids. Additionally, the extract exhibited antibacterial action against both *Aspergillus fumigatus* and *Aspergillus niger* (60).

Food and fodder

Due to its pungent flavour and fleshy like texture, it has a high as potential nutritional substrate and is also grown as a wild vegetable crop in southern India (61). In India and Southeast Asia, *S. portulacastrum* is sporadically grown as a vegetable for cooking. Typically, the stem sections are thoroughly washed and then boiled in two to three changes of water to remove excess salt before consumption.

In the coastal region, the plant is also utilized as a feed for cattle and domestic animals like goats and sheep, as its nutritional composition closely aligns with the recommended values for livestock feed. Additionally, crabs are particularly attracted to this plant, making it useful as bait in crab traps (62).

Given its nutritious makeup in Table 2, this plant can be utilized in the coastal region as a vegetable substitute. As represented in the table, the comparison of available and recommended nutrients in *S. portulacastrum* enables it to use as both feed and fodder for cattle.

Natural fertilizer

A noticeable increase in both growth and biomass output was observed when the oilseed crop *Arachis hypogaea* (groundnut) was cultivated in soil amended with phosphate-solubilizing rhizobacteria, farmyard manure and compost derived from halophytic plants such as *S. portulacastrum*, *Suaeda maritima* and *Ipomoea pes-caprae*. It was found that compost prepared from halophytic plants significantly enhanced the activities of key soil enzymes, including urease, alkaline phosphatase and dehydrogenase, along with improving the population of beneficial soil microflora such as bacteria, fungi and actinomycetes.

As an alternative to chemical fertilizers, the use of organic compost derived from vigorously growing halophytes has been recommended to improve crop productivity and soil fertility, thereby increasing the agronomic value of halophytes (63).

Preservatives

The quality of goatskins preserved using a paste made from the dried plant powder of *S. portulacastrum* was comparable to that of skin preserved in salt (64). Hence, *S. portulacastrum* can be used instead of salt in the curing process of goatskins. Because *S. portulacastrum* is a "salt hyper accumulator," it has created new avenues for the regulated preservation of fish, beef and other foods by using halophytic species as an inexpensive supply of preservative instead of salt.

Remediation

Over the course of Earths' evolution, both large and small organisms have acquired genetic traits and specific biochemical capabilities to cope up with its unfavourable conditions and environments. These capabilities were achieved through adaptation or detoxification by enzymes or (bio) chemical reactions to extract energy from certain substances, leading to the development of a coexistence with toxic chemicals that can withstand their toxicity. The resistant and active efflux pump system is one of the defence mechanisms against toxicity caused by high concentrations of salts, since it prevents adverse effects on the regular life cycle (2). The scientific and labour-intensive process of bioremediation needs to be focused on a condition specific to the site (57). Plants that are planted in saltwater soil that are physiologically dried out may improve soil fertility, which in turn increases crop output. In comparison to other species, *S. portulacastrum* was reported to accumulate approximately 26 % of the original Na present in the soil over a period of 170 days, identifying it as a highly suitable species for remediation of salt-affected soils in arid and semi-arid regions (Fig. 9) (57). As a specialized salt accumulator, *S. portulacastrum* can accumulate up to 2507 kg of sodium per ha within 170 days. Based on this accumulation rate, it is estimated that sedimentation could remove around 14 % of the salt from the 0–1 m soil horizon in a medium with 10 % water content and over 200 mM NaCl concentration (39).

In the present study, *S. portulacastrum* showed the highest bioaccumulation of Na^+ and Cl^-, while the soil showed a sharp decrease in these ions. Although K is a necessary element for plant growth and development, too much of K can cause many different activities in plants to become distorted (55) .

Table 2. Nutritional value of *S. portulacastrum* leaves

Main class	Sub class	Available	References
Proteins	Proline	41.6 mg/100g	(5)
	Threonine	23 mg/100 g	
	Valine	35 mg/100g	
	Lysine	40 mg/100g	
	Isoleucine	26 mg/100g	
	Leucine	50 mg/100g	
	Phenylalanine	29 mg/100g	
Vitamins	b-carotene	680 mg/100g	(32)
	Vitamin C	6.95 mg/100g	
	Vitamin K	164 mg/100g	
	Vitamin B_1	0.02 mg/100g	
	Vitamin B_2	0.06 mg/100g	
	Folate	17.4 mg/100g	
	Niacin	0.24 mg/100g	
	Pantothenic acid	0.17 mg/100g	
	Vitamin E	1.08 mg/100g	
Essential oils	O-Cymene	32.61%	(46)
	a-Pinene	14.12%	
	2-b-Pinene	13.55%	
	1-Transcaryophyllene	8.31%	
	8-Transcaryophyllene	8.31%	
	Cineole	6.79%	
	Limonene	6.40%	
Mineral nutrients	Potassium	3.4%	(43)
	Calcium	0.3%	
	Magnesium	49.7 mg/100g	
	Phosphorous	87.0 mg/100g	
	Sulfur	85.0 mg/100g	
	Sodium	808 mg/100g	
	Iron	13.5 mg/100g	
	Iodine	955.0 mg/100g	
	Selenium	63.0 mg/100g	
	Zinc	1,490.0 mg/100g	
	Vanadium	579.0 mg/100g	
	Chromium	204.0 mg/100g	
Proximate compositions	Fat	4-6%	
	Protein	5-6%	
	Ash	2-3%	
	Crude protein	20-30%	

Several halophytes have been tested in the past in an attempt to potentially restore salt-affected soils. It was found that *Suaeda glauca* (46), *Suaeda altissima* (40), *Suaeda monoica* (41) and *Apera intermedia* (42), *S. portulacastrum* (43) displayed higher Na content when the salinity of NaCl increased. In halophytes, a progressive increase in NaCl concentration led to a greater buildup of NaCl in the leaves as compared to the shoots or roots. It is well known that dicotyledons require a certain osmotic adjustment, which is mostly provided by Na and Cl ions. Halophyte cells also need

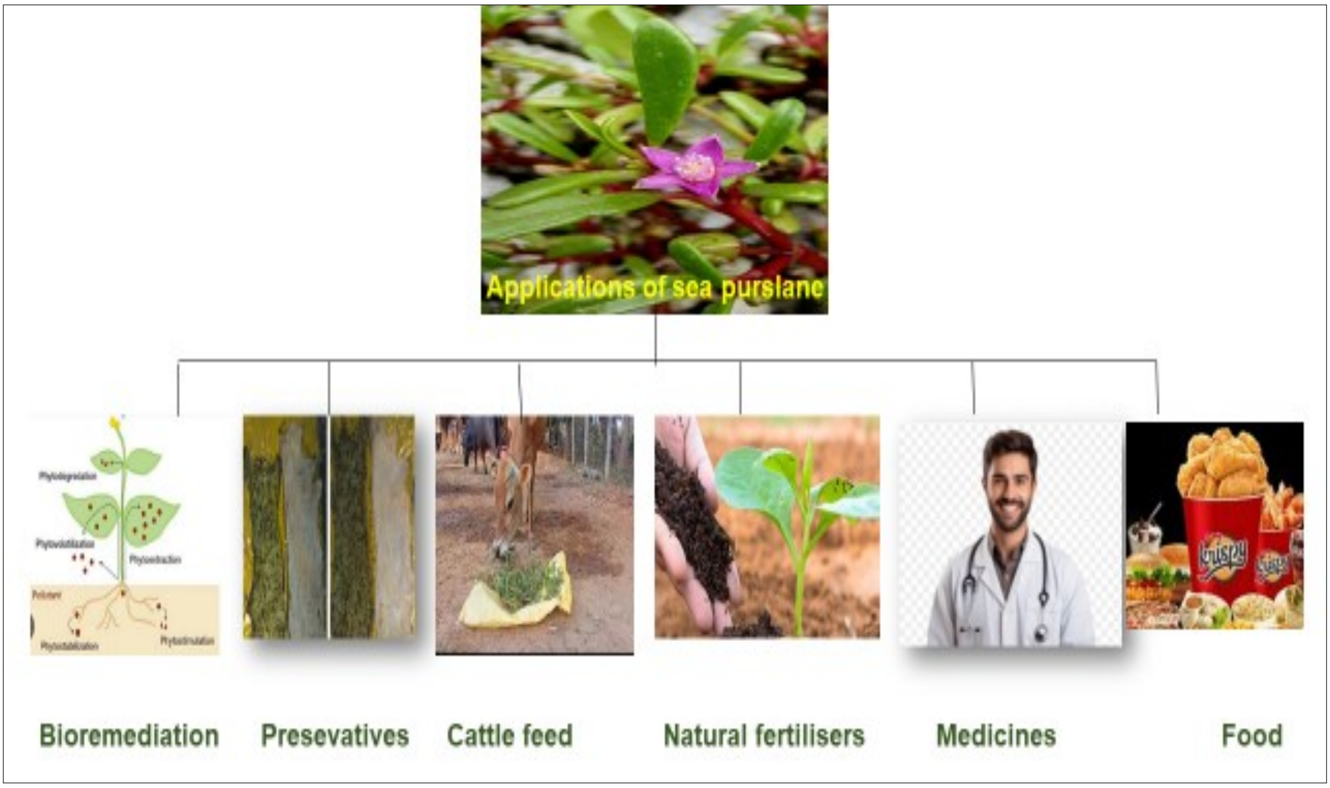

Fig. 9. Applications of *S. portulacastrum.*

lower potentials inside than outside the plasmalemma to maintain cellular water (65, 66).

Conclusion

S. portulacastrum is a hyperaccumulating halophyte that effectively regulates ion accumulation, especially Na^+, K^+ and Ca^{2+}, by compartmentalizing toxic ions into vacuoles, aiding its survival in saline environments. This species exhibits significant potential as a pioneer plant for environmental conservation, owing to its array of adaptive mechanisms that enable it to withstand various abiotic stresses. Although its physiological and biochemical responses to stress are relatively well understood, further research at the molecular level is crucial to fully elucidate its tolerance mechanisms and to potentially enhance the stress resilience of other crop species. Comprehensive genome sequencing and advanced tissue culture techniques may provide valuable insights into its adaptive biology and facilitate the large-scale propagation of this plant for applications in environmental restoration, such as greening barren lands and ameliorating saline soils. Furthermore, the plant holds considerable biotechnological promise, particularly as a "biofactory" for the production of valuable secondary metabolites with potential applications in the pharmaceutical industry. In addition to its ecological and industrial uses, *S. portulacastrum* possesses high nutritional value, making it a viable fodder resource for livestock in arid and semi-arid regions, thereby contributing to food security. Its salt-accumulating ability can also be strategically employed to reduce soil salinity in agricultural lands, improving soil health and crop productivity. Future research should prioritize advancing genomic and transcriptomic studies, optimizing a cultivation practices and exploring the full range of its biotechnological applications to promote sustainable agriculture and industrial use.

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Authors' contributions

PN carried out the overall preparing of review, participated in the sequence alignment and drafted the original manuscript. PD carried out the overall correction work. KS and SSR participated in the bioremediation part. MT and KN participated in mechanism part. MRB and NS prepared the tables. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies

The authors hereby declare that generative AI and/or AI-assisted technologies (Quilbot, Chatgpt) were utilized during the preparation of this manuscript. These tools were employed solely to improve the clarity, grammar and overall presentation of the text. All scientific content, data interpretation and conclusions remain the authors' original work. The authors take full responsibility for the content of the publication.

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