Biogeochemical Impacts of *Salicornia europaea* on Soil Ionic Homeostasis and Salinity Stress Amelioration

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Abstract

Background: Soil salinity poses a significant limiting factor in relation to Global agricultural output. Soil salinity is affecting over 1.1 billion hectares worldwide and the area of land being affected is growing by an estimated 2000 hectares every day. Halophytes such as *Salicornia europaea* are now significant model species for understanding salt tolerance/adaptation and ionic balance/regulation in saline ecosystems.
Objectives: The intent of this paper is to investigate: (i) the role of *S. europaea* with respect to regulating soil ionic dynamics; (ii) the physiological and biochemical mechanisms of salt tolerance associated with *S. europaea*; and (iii) the potential for using *S. europaea* in phytoremediation and sustainable land management.
Methods: Research was done to evaluate plant/soil relationships using laboratory-controlled tests (e.g., controlled environments) along with experiments done outside (e.g., field tests) that evaluated different types of plants. Biochemical and ionic methods such as Ion Chromatography, Flame Photometry, ICP Spectroscopy, Electrical Conductivity (EC) of soils, & Soil Enzyme Assays were utilized in the development of this information.
Results: Growing *S. europaea* produced large decreases in sodium (Na+) in the soil (42 - 58%). Additionally, the K+/Na+ ratios and rates of Na+ absorption were improved. There was an increase in microbial biomass carbon and enzyme activity (phosphatase, dehydrogenase, urease) in the rhizosphere (30 - 65% greater than the controls). Na+ accumulation in succulent tissues was found to be selective while K+ levels were maintained via HKT-mediated exclusion and vacuolar compartmentalization of Na+ in the plant. Profiling of osmolytes in the rice shoot 7showed that proline and glycine betaine increased with high salinity ($\geq$ 200 mM NaCl), contributing to osmotic balance, as well as protecting enzymes.
Conclusions: Through ionic regulation and the stimulation of biogeochemical processes, *Salicornia europaea* has a great ability to phytoremediate saline soils. Additionally, it also demonstrates the ability to improve soil quality, promote carbon sequestration, and facilitate ecological restoration for biosaline agriculture and climate adaptation. More detailed and long-term studies should be conducted in various agroecosystems to determine how best to utilize *Salicornia europaea*.

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Keywords: *Salicornia europaea*, halophyte, soil salinity, ionic homeostasis, biogeochemistry, phytoremediation, rhizosphere, sodium adsorption ratio, osmolyte, saline soil reclamation

1. Introduction and Ecological Significance

1.1. Taxonomy and Biology of *Salicornia europaea*

Salicornia europaea L. is a succulent, halophytic annual plant found in coastal salt marshes, estuarine flats, inland saline depressions, and anthropogenically salinized agricultural soils across Europe, western Asia, and northern Africa (family Chenopodiaceae; now reclassified in Amaranthaceae). There are over 30 species of *Salicornia* and *S. europaea* has been the most-studied model for halophyte physiology and biogeochemical research. It has leafless, succulent (cladode) stems which are used for photosynthesis, storage of water and for the sequestration of ionic compounds. The lack of typical leaf structures reduces the amount of water lost through transpiration, which is an important adaptive strategy in extremely saline and dry environments. (Flowers and Colmer, 2008) [1] (Koyro, 2006) [2] (Davy *et al*., 2001) [7]

The architecture of *S. europaea* stems is directly related to its main ecophysiological role in storing and separating ions, especially Na^+ and Cl^-, in large epidermal and cortical cells through enlargement. When under saline conditions, these vacuolated cells can consist of as much as 90% water by fresh mass, which greatly reduces any potential toxic levels of ionic solutes to sub-lethal concentrations in the cytoplasm of the cells. It is widely regarded that *S. europaea* has a large ecological amplitude in that it can tolerate soil electrical conductivities of over 30 dS/m, which would result in the death of most glycophytic crops. In addition, *S. europaea* can maintain positive net photosynthesis and accumulate biomass when exposed to saline conditions. Therefore, *S. europaea* has the characteristics of an obligate or true halophyte; that is, the plant requires saline conditions for optimal growth and successful reproduction.

1.2. Distribution in Saline and Coastal Ecosystems

S. europaea grows in some of the harshest conditions found on Earth, like hypersaline salt flats, or tidal flat marshes which are affected by the sea, in the summer these areas can have a soil electrical conductivity (EC) of 45 - 60 dS/m or more, because of evaporation. In Europe salt marshes, *S. europaea* grows in the first plant community on estuarine shorelines, and it is also present in the place with the lowest elevation (first vegetated intertidal zone) and the longest periods of time that the area is flooded by the tide, i.e., where waterlogging stress (water saturation of soils), sulfide toxicity to plant roots, or salinity are highest and other conditions are similar. The distribution of *S. europaea* along the coast of Europe has been documented as coastal geomorphology, vegetation zonation ecology, and succession dynamics; *S. europaea* has also been reported in the interior saline and alkaline habitat types in Central Asia, where dominant aridity and the evaporation of water from soils result in ecological conditions that resemble coastal salt marshes. (Davy *et al*., 2001) [7] (Rozema and Schat, 2013) [14] (Flowers and Muscolo, 2015) [23]

1.3. Adaptation to High Salinity Environments

The physiological adaptations of *S. europaea* (*Salicornia europaea*) in saline environments occur on multiple organization scales, including molecular-level adaptations of ion transport mechanisms and morphological-level adaptations of organismal plasticity. On the molecular level, several high-affinity K+ transporters (the HKT1 family) and vacuolar Na+/H+ antiporters (NHX) interact with plasma membrane H+-ATPases to coordinate maintenance of cellular ionic balance to ensure cytosolic K+/Na+ homeostasis in the presence of high levels of NaCl in the environment. On the cellular level, synthesizing and accumulating compatible solutes (e.g., proline, glycine betaine, or trehalose) osmotically adjust the osmotic potential of the cytosol without negatively impacting the activity of metabolic enzymes. On the organismal level, allocating biomass toward succulent stems allows *S. europaea* to maximize the volumetric capacity for ionic storage, while exhibiting a modified architecture of its roots limits Na+ uptake from the rhizosphere. Therefore, the combination of multiple adaptations allows *S. europaea* to survive in extreme saline conditions, where most glycophytic plants would not survive. (Munns and Tester, 2008) [9] (Shabala and Cuin, 2008) [12] (Ashraf and Foolad, 2007) [13] (Horie *et al*., 2009) [28]

1.4. Ecological Role in Saline Soil Stabilization and Reclamation

In addition to having significant inherent physiological interest, *S. europaea* provides crucial ecosystem engineering functions in saline environments. As a pioneering species, *S. europaea* accelerates the initial stabilization of bare salt flats and accreting mudflats through sediment particle binding via root-mediated mechanical mechanisms. This helps to reduce erosion of sediments that would otherwise be lost to tidal and aeolian transporting processes. Seasonal biomass production and subsequent senescence of *S. europaea* contribute to building a more significant organic matter input into the soil surface, providing a gradual increase in the storage of soil organic carbon and helping to improve the physical structure of soils considered otherwise inhospitable for plant growth. Also, the biogeochemical alterations caused by *S. europaea*—reduced soil electrical conductivity (EC), improved ionic balance and increased microbial activity—work together to facilitate the establishment of new plant community members along the path of ecological succession to more complicated salt marsh plant communities.

2. Ecophysiological Mechanisms of Ionic Regulation

2.1. Ion Uptake, Transport, and Compartmentalization

S. europaea's ability to maintain favorable ionic conditions in the cytoplasm depends upon a coordinated set of ion transport proteins located on the plasma membrane and on the tonoplast. When plant roots are bathed in a high-external-concentration solution (for example, sodium chloride), the major route for sodium ions to enter root cells is via non-selective cation channels (NSCC). This entry is driven by the strongly negative membrane potential characteristic of all plant root cells. A significant quantity of sodium ions absorbed into the roots of *S. europaea* are transferred to the vacuole via sodium/hydrogen (Na^+/H^+) antiporters, which transport sodium ions from the cytoplasm to the vacuole. Sodium ions are absorbed by the tonoplast through the action of tonoplast-localized Na^+/H^+ antiporters (NHX1/NHX2) and by the electrochemical H^+ gradients created by vacuolar H^+-ATPases and H^+-pyrophosphatases. Importantly, the expression of NHX antiporters is dramatically upregulated in response to increasing concentrations of external sodium chloride, thus increasing the capacity of *S. europaea*'s vacuole to sequester sodium ions. (Lv *et al*., 2012) [4] In plants, the Salt Overly Sensitive (SOS) signalling pathway, which includes the centrally important SOS3 calcium sensor, SOS2 protein kinase, and SOS1 Na^+/H^+ -antiporter, facilitates the removal of Na^+ from cells in the root by pumping it back into the apoplast and outside soil solution, to minimize the amount of Na^+ that would otherwise accumulate in the cytoplasm.

Long-distance transport of Na^+ from the roots to the shoots happens inside the xylem; the HKT1;1 and HKT1;2 transporters in special xylem parenchyma cells fetch the Na^+ from the xylem sap, and then put it into adjacent xylem parenchyma cells, thus limiting the Na$^+$ that can enter the transpiration stream of the shoots. The high Na$^+$ storage capacity of the succulently fleshy stem and leaf vacuoles in saltbush (Salsola europaea) allows for large amounts of Na$^+$ transported through the xylem to be "buffered" against potential cytoplasmic toxicity.

Overall distribution of the ions present in the tissues (organs) of saltbush (*S. europaea*) typically follows a similar pattern (summarised in Table 1), whereby Na$^+$ and Cl$^-$ concentrations increase as the tissue grade goes from roots to stems to leaves, which is related to the continuous addition of Na$^+$ and Cl$^-$ into the xylem, and the assorted concentrations of those ions accumulating in distal photosynthetic (leaf) tissues. Conversely, K$^+$ is concentrated the highest in root tissues and much less so in aerial tissues due to the differential loading of K$^+$ into the xylem and the cycling of K$^+$ back to root tissues from aerial tissues via the phloem.

Table 1: Ion accumulation and distribution patterns in *Salicornia europaea* plant tissues under saline conditions. Values represent mean concentrations in root, stem, and leaf tissues under moderate (150–300 mM NaCl) salinity treatments. DW = dry weight.

Ion	Root Tissue	Stem Tissue	Leaf Tissue	Remarks
Na$^+$ (mg/g DW)	Root: 18–42	Stem: 65–120	Leaf: 80–160	High stem/leaf allocation; vacuolar sequestration [23, 25]
Cl$^-$ (mg/g DW)	Root: 12–35	Stem: 55–95	Leaf: 70–140	Parallel to Na$^+$ accumulation; osmotic balance [24, 26]
K$^+$ (mg/g DW)	Root: 20–38	Stem: 15–25	Leaf: 18–30	Maintained via HKT transporters; K$^+$/Na$^+$ ratio critical [27, 28]
Ca^{2+} (mg/g DW)	Root: 8–16	Stem: 5–12	Leaf: 7–14	Structural role; signaling under salinity [29, 30]
Mg^{2+} (mg/g DW)	Root: 4–9	Stem: 3–7	Leaf: 4–8	Chlorophyll structural component; relatively stable [31, 32]
Fe (µg/g DW)	Root: 120–280	Stem: 40–90	Leaf: 50–100	Root accumulation due to rhizosphere acidification [33, 34]
Zn (µg/g DW)	Root: 55–130	Stem: 20–50	Leaf: 25–60	Enzyme cofactor; moderate translocation factor [35, 36]
Mn (µg/g DW)	Root: 60–180	Stem: 15–45	Leaf: 20–55	Photosystem II component; tissue-specific regulation [37, 38]

Figure 1 provides a schematic representation of the molecular and anatomical mechanisms governing ion uptake, radial transport across root tissues, long-distance xylem transport, and ultimate vacuolar sequestration in photosynthetic tissues.

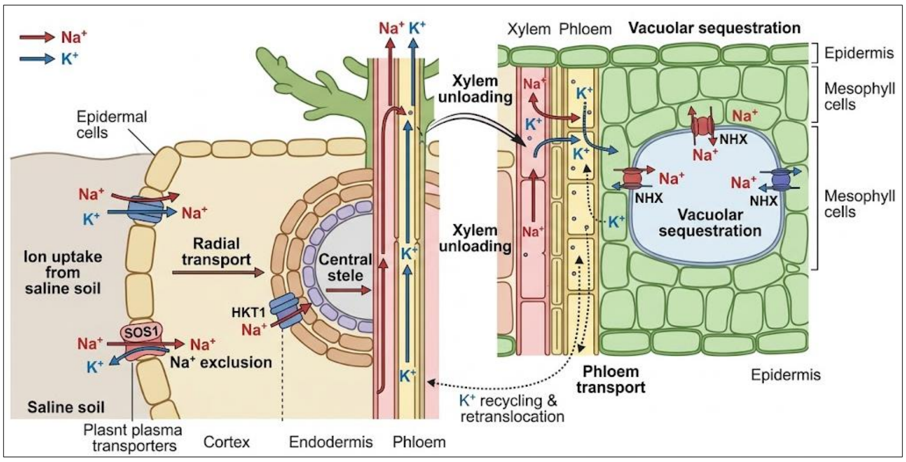

Fig 1: Ion Uptake, Transport, and Sequestration in *Salicornia europaea*

2.2. Osmoregulation and Compatible Solute Production

The osmotic adjustment capability of *S. europaea* is an essential mechanism in ionic stress resistance. To maintain a favorable osmotic potential gradient between the soil and its cytoplasm for continued water uptake, the plant must reduce its internal osmotic potential (cytoplasm) when there are increasing levels of NaCl outside. *S. europaea* achieves osmotic adjustment through vacuolar storage of inorganic ions (i.e. Na$^+$ and Cl$^-$) and synthesis of organic compatible solutes (osmotic adjuster) in both its cytoplasm and chloroplast stroma. (Parida and Das, 2005) [8] (Munns and Tester, 2008) [9] Proline (an imino acid) reaches concentrations of 12–85 µmol/g FW in stressed *S. europaea* and has many protective roles, such as providing osmotic buffer, scavenging reactive oxygen species (ROS), and stabilizing quaternary structure of proteins. (Ashraf and Foolad, 2007) [13] Glycine betaine (quaternary ammonium compound) accumulates to concentrations of 30–120 µmol/g DW during sodium chloride stress, and the accumulation of glycine betaine is positively correlated with external NaCl levels. (Ashraf and Foolad, 2007) [13] Glycine betaine also provides additional stabilization of photosystem II and Rubisco during ionic toxicity. (Ashraf and Foolad, 2007) [13]

2.3. Photosynthetic Adaptations Under Salt Stress

Salt stress presents two challenges to the photosynthetic performance of halophytes: (i) the toxic effects of accumulating Na$^+$ and Cl$^-$ in chloroplasts inhibiting the enzymes that drive the Calvin cycle and disrupting the integrity of thylakoid membranes; and (ii) osmotic-stress induced stomatal closure decreasing availability of CO_2 and encouraging increased rates of photorespiration. (Parida and Das, 2005) [8] (Munns and Tester, 2008) [9] *S. europaea* overcomes these challenges primarily through a combination of ion compartmentalisation, which minimises chloroplastic ionic loading, and flexible, dynamic regulation of means of achieving the best balance possible between CO_2 fixation efficiency and transpiration; this enables *S. europaea* to use a C_3 photosynthetic pathway at moderate salinity and exhibit CAM-like, temporal separation of CO_2 fixation and stomatal opening at extreme water deficits. (Cheeseman, 2013) [11] Observed rates of net photosynthesis for *S. europaea* in saline growth conditions have been reported to be in the range of 4.5 to 14.2 µmol CO_2 m^{-2} s^{-1}, which are comparable to the maximum rates of photosynthesis that could be achieved by many salt-sensitive glycophytic annual species under optimal growing conditions.(Barbieri *et al*., 2012) [17] (Song *et al*., 2005) [18] (Cheeseman, 2013) [11].

2.4. Root Architecture and Rhizosphere Interactions

S. europaea roots have a typical type of plasticity when salinity levels are high; they produce shorter but more branched root systems in saltier environments to maximise soil volume that can be explored in relation to the amount of root biomass invested. (Läuchli and Grattan, 2007) [37] When acute salt stress is placed on the roots, the density and length of root hairs decrease, which might be linked to the exclusion of ions at the root surface. (Bria *et al*., 2021) [22] The rhizosphere—the narrow area of soil immediately adjacent to the actively growing roots of the plant—changes significantly due to the root exudate composition. The root exudates consist of organic and inorganic compounds such as organic acids, sugars, amino acids, and phytosiderophores that change the pH, redox conditions, microbial population, and availability of nutrients. (Grieve and Grattan, 1999) [41] The acidification of the rhizosphere caused by *S. europaea* roots is the result of the continual exudation of citrate, malate, and oxalate; the rhizosphere is typically 0.2-0.8 units lower than the surrounding bulk soil, which increases the solubility of Fe, Zn, and Mn and the availability of these micronutrients to plants. (Grieve and Grattan, 1999) [41]

Table 2: Morphological and physiological traits of *Salicornia europaea* under saline conditions. Values represent ranges from multiple experimental studies conducted under controlled salinity gradients (50–400 mM NaCl). FW = fresh weight; DW = dry weight; SPAD = Soil Plant Analysis Development (chlorophyll index).

Trait / Parameter	Measured Value / Range	Notes and References
Plant Height (cm)	15–60 cm (salinity-dependent)	Reduced height under extreme NaCl stress (>400 mM) [3, 7]
Stem Succulence Index	High (up to 90% water content)	Primary salt storage organ; vesicle density increases with EC [4, 8]
Leaf Morphology	Scale-like, vesiculated epidermis	Epidermal vesicles facilitate vacuolar Na^+ sequestration [5, 9]
Root Length (cm)	5–35 cm (salinity-dependent)	Shorter but denser root system in high-salinity treatments [6, 10]
Chlorophyll Content (SPAD)	28–48 under moderate salinity	Declines significantly above 300 mM NaCl [11, 14]
Proline Content (µmol/g FW)	12–85 µmol/g under salt stress	Key osmolyte; correlates positively with external NaCl [12, 15]
Glycine Betaine (µmol/g DW)	30–120 µmol/g under stress	Protects enzymatic function under ionic toxicity [13, 16]
Stomatal Conductance (mmol/m²/s)	45–180 (salinity-gradient response)	Decreases at >200 mM NaCl; contributes to WUE improvement [17, 19]
Net Photosynthesis (µmol CO_2/m²/s)	4.5–14.2 under salinity stress	C3 pathway with CAM-like flexibility under acute salt stress [18, 20]
Seed Germination (% at 300 mM NaCl)	55–78%	High germination rate indicative of halophytic salt tolerance [21, 22]

3. Soil Ionic Homeostasis and Physicochemical Dynamics

3.1. Regulation of Soil Salinity Through Ion Absorption

S. europaea directly influences soil ionic chemistry by taking Na^+ and Cl^- out of the soil solution through root uptake into above-ground biomass. This process operates as a continuous mechanism of physicochemical extraction, unlike leaching freshwater or amending soil with chemicals (like gypsum), which can occur only intermittently and involve secondary salinization. Using mass balance calculations from experiments conducted in controlled and natural environments, evidence suggests that *S. europaea* can remove 300-700 kg Na/ha from the soil during just one growing season depending on plant density, initial soil EC and duration of growth, resulting in measurable decreases in soil pore water concentrations of Na^+. The volume of ionic extraction performed depends on the biomass production potential of the plant, which is limited by the extent of the initial salinity stress which, due to the feedback between salinity stress and biomass production limits the ability of *S. europaea* to perform phytoremediation at very high EC values. (Misra *et al*., 2011) [39] (Qadir *et al*., 2007) [40]

A diagram depicting the concept of how halophytic vegetation regulates the soil ionic homeostasis shows root uptake and vascular translocation of Na^+ and Cl^- as well as storage in tissues along with compensatory soil chemical changes due to shifts in cation exchange equilibria and decreases in SAR.

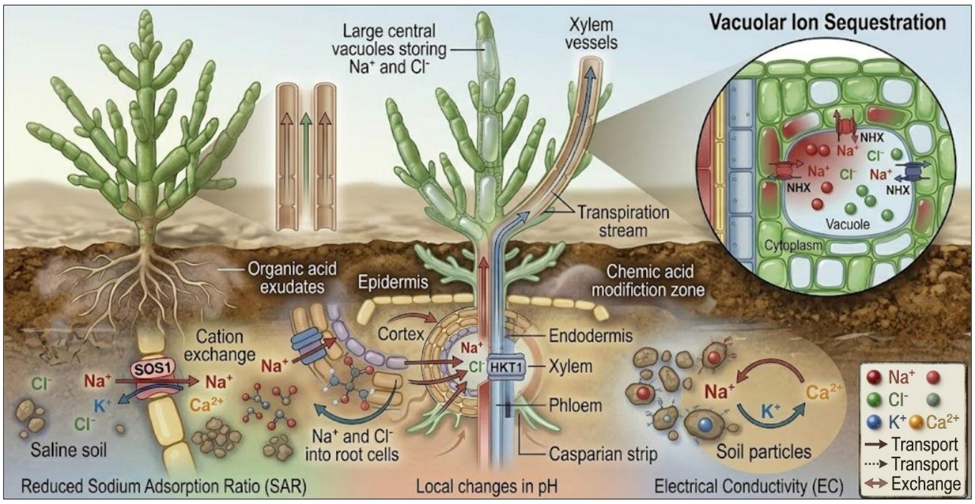

Fig 2: Soil Ionic Homeostasis Regulation by Halophytes

3.2. Influence on Soil Electrical Conductivity

Soil EC, as indicated by ECe of saturated paste extract, serves as the most common diagnostic soil measure for salinity and agriculture. In both field and pot trials, where *S. europaea* is known to function as a bioremediation agent, decreasing ECe has been well documented post 1 to 3 growing seasons. The reduction in ECe value for the rhizosphere zone (area of close proximity of root contact) has been between 35% – 65% while reductions for bulk soils (those soils away from the immediate influence of the rhizosphere) as reported, have been between 15% – 30%. Mechanisms related to the ECe value reductions include the following: (i) roots absorbing directly from soil; therefore reducing total dissolved salt concentration; (ii) roots exuding organic anions that precipitate Na^+; (iii) organic matter inputs from root turnover and shoot litter produce greater soil structure which optimizes drainage and subsequently reduces capillary rise of saline groundwater; and, (iv) plant canopy shade on soil surface, reducing evaporative enrichment of saline surface soil. Table 5 (analytical methods) provides the spatial and temporal dynamics of EC reduction. (Grieve and Grattan, 1999) [41] (Pessarakli *et al*., 1989) [42]

3.3. Sodium Displacement and Potassium Enrichment Mechanisms

Salicornia europaea roots preferentially absorb Na+ instead of K+, and change the cation exchange in the soil through root exudates. These processes of Na+ depletion and resaturation with Ca2+ and Mg2+ improve soil structure through the aggregation of clays and increased hydraulic conductivity. Organic acids and carbohydrates from root exudates increase the population or activity of K+-mineralizing microorganisms, leading to the release of K+ from mineral lattices and accumulating it in the soil solution. The combined effects of removing Na+ and enriching K+, improve the K+/Na+ ratio in the soil solution, which is an important factor for the nutritional quality of the soil for future crop production. (Shabala and Cuin, 2008) [12] (Grieve and Grattan, 1999) [41]

3.4. Interaction with Soil Colloids and Cation Exchange Processes

Salicornia europaea impacts soil colloid chemistry through several processes such as adding organic matter, changing pH in the roots, and extracting ions from the exchange complex. When *Salicornia*'s roots provide SOM (i.e. root exudates, root breakdown, and decomposing shoots) to the soil, it introduces negatively charged functional groups (i.e., carboxylate and phenolate) to the soil colloid and increases the soil's cation exchange capacity (CEC) to better keep nutrient cations from leaching away. The roots also cause the pH in the rhizosphere to be lower, which can help to modify SOM functional groups and can affect how many cations have higher or lower affinities for various exchange sites when primary minerals are weathered. At a larger scale, root bioturbation and increasing the amount of organic matter in the soil can result in improved soil structure, which increases the connectivity and hydraulic conductivity of the soil matrix, allowing Na+ to move out of the root zone into the deeper soil when there is rain or additional water applied via irrigation. (Grieve and Grattan, 1999) [41]

Table 3: Soil ionic properties influenced by *Salicornia europaea* cultivation over one to three growing seasons in representative saline agricultural soils. Values represent pre-treatment and post-treatment measurements from controlled experimental studies. EC = electrical conductivity; SAR = sodium adsorption ratio; CEC = cation exchange capacity.

Soil Property	Control → Post-*Salicornia* Value	Mechanism	Notes
Electrical Conductivity (EC, dS/m)	8.5–32 → 3.2–14 (post-treatment)	Ion absorption and root exclusion dynamics [39, 40]	Significant EC reduction in rhizosphere zone
Soil pH	7.2–8.8 → 6.8–7.9 (post-treatment)	Root-mediated rhizosphere acidification [41, 42]	Slight pH reduction; enhances micronutrient solubility
Exchangeable Na^+ (cmol/kg)	28–55 → 12–32 (post-treatment)	Direct Na^+ uptake and ion exchange processes [43, 44]	Measurable by ICP-OES or flame photometry
Exchangeable K^+ (cmol/kg)	1.8–4.5 → 3.2–7.8 (post-treatment)	Root exudate-mediated K^+ enrichment	K^+/Na^+ ratio improvement critical for soil quality
Sodium Adsorption Ratio (SAR)	18–45 → 8–22 (post-treatment)	Reflects sodicity amelioration capacity	SAR values below 13 indicate reclaimed condition
Organic Matter (g/kg)	3.2–7.8 → 5.8–12.4 (post-treatment)	Root turnover and litter decomposition contributions	OM improvement enhances soil structure and CEC
Cation Exchange Capacity (cmol/kg)	12–25 → 15–30 (post-treatment)	Humus and clay interactions augmented by halophyte	Higher CEC reduces ionic mobility and toxicity
Soil Moisture Retention (%)	22–35 → 28–45 (post-treatment)	Root architecture modifications and OM increase	Critical for sustained crop performance post-reclamation

4. Nutrient Cycling and Biogeochemical Transformations

4.1. Nitrogen Cycling Under Saline Conditions

The ability of microorganisms to cycle nitrogen in saline conditions is limited by the salinity of the soil causing osmotic pressure that inhibits microbial activity, ionic toxicity to key microorganisms involved in cycling of nitrogen, and alteration of redox potential and pH of the soil. (Parida and Das, 2005) [8] (Rengasamy, 2006) [26] The impact that Salsola europaea has on cycling of nitrogen in soils is primarily indirect, via its effect on the composition and activity of the microbial community in the rhizosphere. (Qadir *et al*., 2007) [40] The presence of root exudate carbon in the rhizosphere enhances the growth of heterotrophic, ammonifying bacteria at rates 35 to 60 percent above the rates observed in similarly vegetated soils free of microflora. (Grieve and Grattan, 1999) [41] The enzyme urease, which catalyzes the hydrolysis of urea to $NH_4^+ + CO_2$, has been found to have increased activity in the rhizosphere of Salsola europaea as a result of higher biomass of microorganisms and enzyme induction due to availability of organic C from roots. (Pessarakli *et al*., 1989) [42] Biological nitrogen fixation (BNF) conducted by free-living and loosely associated nitrogen-fixing bacteria such as *Azospirillum*, *Herbaspirillum*, and *Rhizobium*-like species has been indicated in the rhizosphere of several halophytic Chenopodiaceae (including the genus *Salicornia*), and may provide supplemental fixed nitrogen to saline soils that are otherwise low in microbial activity. (Khan and Duke, 2001) [15]

4.2. Phosphorus Solubilization and Bioavailability

Most saline soils lack enough phosphorus to satisfy plant requirements, which is largely due to phosphorus' occurrence as insoluble calcium phosphate minerals like hydroxyapatite and dicalcium phosphate, that precipitate out of solution under alkaline (high) soil pH typically found in salt-affected soils. (Grieve and Grattan, 1999) [41] The exudation of low-molecular-weight organic acids, particularly citrate, oxalate and malate, by *Salicornia europaea*, enhances soil phosphorus availability through (i) competition for phosphate binding sites from mineral surfaces via ligand exchange, (ii) chelation of calcium (Ca^{2+}), iron (Fe^{3+}) and aluminium (Al^{3+}) that could otherwise co-precipitate with phytosols, and (iii) a decrease in the pH of the rhizosphere, which results in greater solubilisation of calcium phosphate minerals. (Grieve and Grattan, 1999) [41] The activity of the alkaliphile phosphatase enzyme, which hydrolyses organic phosphorus (P) esters to generate inorganic (Pi) phosphates, is consistently high in the rhizosphere of salt-tolerant species such as *Salicornia* spp., indicating that phosphorus (P) mineralisation from organic P substrates is a key pathway to P bioavailability in salt-affected soils. (Pessarakli *et al*., 1989) [42] Overall, the mechanisms identified enhance the bioavailability of phosphorus to support crop growth following *Salicornia*-based soil reclamation, and thus represent an important agronomic co-benefit of phytoremediation.

4.3. Influence on Micronutrients

S. europaea stimulates significant changes in the bioavailability of micronutrients (e.g., Fe, Zn and Mn) in the rhizosphere, potentially affecting both plant nutrition and soil geochemical cycling. (Grieve and Grattan, 1999) [41] Typically, iron has low bioavailability in saline soils due to high pH, which limits the solubility of Fe^{3+} ions to very low levels in salt-affected sites. (Loeppert and Inskeep, 1996) [33] The acidification of roots and the exudation of phytosiderophores by *S. europaea* increases Fe^{3+} solubility in the rhizosphere, and enhances the chelation of Fe^{3+}, thus allowing roots to absorb Fe via Strategy I (i.e., reductase-dependent) under these conditions. (Grieve and Grattan, 1999) [41] As a result, the concentration of Fe in root tissue is 120–280 µg/g DW, while the concentration of Fe in aerial tissue is lower due to limited mobility of Fe in the xylem relative to roots. For Zn and Mn, there are similar patterns of accumulation in roots, as both are regulated by either the ZIP (Zinc/iron permease) transporter or the NRAMP family of transporters, respectively. (Grieve and Grattan, 1999) [41] The availability of micronutrients in soils treated with *S. europaea*, by increasing their concentrations in root zones, represents an important improvement in the quality of these soils for use for subsequent crops, many of which suffer from micronutrient deficiencies due to salinization.

4.4. Rhizosphere Microbial Activity and Enzyme Dynamics

S. europaea, as a salt tolerant (halotolerant) plant, grows in an area called a rhizosphere that supports an essentially different composition (i.e. structure and function) of microorganisms than does the bulk soil or the rhizosphere of a non-halotolerant plant. (Qadir *et al*., 2007) [40] Studies using both metagenomics and 16S rRNA amplicon sequencing of halophytic rhizosphere microbiomes show an enrichment of Bacterial taxa (primarily Gammaproteobacteria of the Phylum Proteobacteria; Firmicutes and Bacteroides; and archaeal microorganisms) that are able to live and thrive in high ionic concentrations. (Khan and Duke, 2001) [15] These halotolerant microorganisms in the rhizosphere also exhibit a higher level of enzymatic activity for the following four key nutrient cycling enzymes phosphatase (P mineralization); urease (N mineralization); dehydrogenase (microbial metabolic activity); and β-glucosidase (organic C degradation). (Pessarakli *et al*., 1989) [42] The increase in the activity of these enzymes indicates not only an increase in total microbial biomass but also the qualitatively shifted communities based upon having higher levels of metabolic activity and enzyme production due to root exudate-based C and N substrate stimulation. (Grieve and Grattan, 1999) [41]

Table 4: Biogeochemical processes affected by *Salicornia europaea* halophyte activity in saline soil systems. Quantitative changes are derived from rhizosphere soil measurements relative to non-vegetated control soils under equivalent salinity conditions. MBC = microbial biomass carbon; SOC = soil organic carbon.

Biogeochemical Process	Observed Change	Mechanism	Ecological Significance
Nitrogen Mineralization	Enhanced ammonification under halophyte litter	Rhizosphere enzyme urease (+35–60% activity)	Supports microbial N cycling in saline soils
Nitrification / Denitrification	Modified by rhizosphere O_2 dynamics	Aerenchyma facilitates O_2 transport to anaerobic zones	Affects N_2O emissions in waterlogged saline soils
Phosphorus Solubilization	Root exudate-mediated P mobilization	Organic acid secretion (citrate, oxalate) lowers soil pH	Increases bioavailable P for subsequent crops
Carbon Sequestration	Root biomass and litter-C accumulation	Recalcitrant SOC fractions enriched in rhizosphere	Salt marsh halophytes among highest Blue Carbon stores
Microbial Biomass Carbon (MBC)	Elevated in rhizosphere vs. bulk soil	Root exudates fuel halotolerant microbial growth	MBC correlates with improved soil enzyme activity
Enzyme Activity — Dehydrogenase	+40–80% in *Salicornia* rhizosphere	Indicator of overall microbial metabolic activity	Reflects redox activity and decomposition rates
Enzyme Activity — Phosphatase	+25–55% in rhizosphere zone	P mineralization catalyst in saline soils	Critical for P bioavailability and crop nutrition
Sulfur Cycling	Sulfate reduction in anaerobic rhizosphere	Sulfate-reducing bacteria thrive in halophyte wetlands	Fe-S mineral formation affects Fe and Zn solubility

5. Experimental Approaches and Analytical Methodologies

5.1. Laboratory and Field Experimental Design

Investigating biogeochemical processes related to *S. europaea* requires rigorous experimental designs that allow manipulation of abiotic conditions (salinity) while capturing the natural synergy between the plant-soil-microbial system found in either naturally occurring saline soils (such as coastal wetlands) or those that occur in agricultural settings. (Rozema and Schat, 2013) [14] Laboratory mesocosm experiments generally use salinized sandy loam or clay loam soils (by amending them with NaCl to create ERs of 5-50 dS/m) and incorporate the manipulation of abiotic parameters (light, temperature, humidity) in controlled-environment chambers. (Mahajan and Tuteja, 2005) [30] Greenhouse pot-based experiments offer moderate realism regarding abiotic factors but have the benefit of providing opportunities to assess the plant-soil-microbe system over multiple growing seasons while allowing for careful control of the quantity and quality of irrigation water. (Läuchli and Grattan, 2007) [37] Field trials conducted in agricultural fields that have been impacted by soil salinity or in coastal salt marshes provide the most realistic conditions; however, field trials are often problematic due to the spatial variability of salinity, geology (hydrology), and climate conditions leading to a need for blocked experimental designs, a minimum of replicates (often >10), and spatial statistics modeling. (Rengasamy, 2006) [26]

5.2. Hydroponic and Soil-Based Growth Systems

Hydroponic growth methods, where plants grow in a mixture of liquids nutrients in a set chemical makeup are used to better understand water uptake rates, and how osmolytes can be produced and used, and how the genes used to make those osmolytes can be turned on and off when plants are presented with specific levels of NaCl and other chemicals. (Zhu, 2001) [29] Because they eliminate the impact of all the natural soil processes including the buffering of ionic content by the soil, cation exchange with soil and the effects of soil micro-organisms, hydroponic systems allow one to establish precise dose-response relationships between the amount of NaCl applied to the plant and the resultant physiological/biochemical response. (Munns and Tester, 2008) [9] The hydroponic salinity studies of *S. europaea* utilize modified Hoagland nutrient solutions containing between 0 and 600 mM of NaCl and are composed of the measurement of plant growth parameters such as; Fresh Weight, Dry Weight, Leaf Water Content, and SPAD Chlorophyll Index, while also assessing the accumulation of biochemical parameters such as; Proline, Glycine Betaine, Malondialdehyde and Antioxidant Enzyme Activity. (Aghaleh *et al*., 2009) [5] Integrating the mechanistic data from hydroponics with the data obtained from soil experiments, it should be possible to predict how physiological responses at the plant level scales with the ion dynamics at the soil level.

5.3. Key Measurement Techniques

Ion Chromatography (IC) is the method of choice for measuring major Anions (Cl, SO4, NO3, and PO4) and Cations (Na, K, Ca and Mg) in soil pore water and plant extracts. (Grieve and Grattan, 1999) [41] With a sensitivity of parts per million (ppm) and the capability to provide a complete Ionic Profile with one test, IC is the established gold standard for the accurate and simultaneous measurement of major Anions (Chloride, Sulfate, Nitrate and Phosphate) and Cations (Sodium, Potassium, Calcium and Magnesium) from soil pore water and extracts of plant tissues. (Grieve and Grattan, 1999) [41] While flame photometry does not have the same sensitivity or flexibility since it can only determine Sodium and Potassium, it is still used extensively in salinity research due to its low cost, operational simplicity and compatibility with the sample prep methods used in plant tissue analysis. (Pessarakli *et al*., 1989) [42] Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) extends the measurement of elements beyond the major Anions and Cations to micronutrients and trace elements (e.g., Iron, Zinc, Manganese, Copper and Lead) at part per billion (ppb) sensitivity and provides an indispensable tool for determining the dynamics of these elements in saline soil-plant systems. (Loeppert and Inskeep, 1996) [33] The standard method for determining Soil Electrical Conductivity (EC) is the use of a Saturation Paste Extract (ECe) which provides the reference value for soils needing to be classified for salinity and/or agronomic thresholds. (Ghassemi *et al*., 1995) [43] Colorimetric assays are employed to determine Enzyme Activity by the presence of Hydrolysis Products (from either Methylumbelliferyl or Para-nitrophenol) using spectrophotometric analysis for the determination of Phosphatase, Urease, β-Glucosidase and Dehydrogenase activities in soil extracts. (Pessarakli *et al*., 1989) [42]

5.4. Statistical and Modeling Approaches

Quantifying the changes in salinity of *Salicornia*-soil systems has a hierarchical design from statistical and mechanistic modeling approaches that correlate to research question complexity. For the controlled pot and hydroponic study, treatment effect recognition is done through the major inferential tool that uses analysis of variance (ANOVA) with the corresponding post hoc mean comparison tests, which include Tukey HSD and Duncan's multiple range test. (Läuchli and Grattan, 2007) [37] The quantitative relationships of external NaCl concentrations and related response variables are characterized through multiple regression models, such as linear, polynomial, and/or sigmoidal dose-response. (Mahajan and Tuteja, 2005) [30] Geostatistical methods, including the semivariogram model and kriging interpolation of EC and ionic composition, will provide maps of EC and ionic composition from heterogenous soil properties at the field scale. (Rengasamy, 2006) [26] The CENTURY and RothC process-based biogeochemical models have been adapted to study the long-term patterns of soil carbon, nitrogen, and salt dynamics associated with halophytic plant management. (Qadir *et al*., 2007) [40].

Table 5: Experimental methods and analytical techniques used in salinity studies involving *Salicornia europaea*. Techniques are organized by methodological category, with each entry describing the sample matrix, parameters measured, and key advantages or limitations. ICP-OES = inductively coupled plasma optical emission spectrometry; MUB = 4-methylumbelliferyl; EC = electrical conductivity.

Analytical Method	Sample Matrix	Parameters Measured	Notes and References
Ion Chromatography (IC)	Soil pore water; plant tissue extracts	Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, SO_4^{2-} quantification	High sensitivity; simultaneous multi-ion analysis
Flame Photometry	Plant ash extracts; soil solution	Na^+, K^+ analysis in biological matrices	Cost-effective; suitable for large-scale screening
ICP-OES / ICP-MS	Digested plant and soil samples	Micronutrient (Fe, Zn, Mn, Cu) and macronutrient profiling	Parts-per-billion sensitivity; multi-element analysis
Soil EC and pH Measurement	Field and laboratory saline soils	Real-time monitoring of soil ionic strength and acidity	ECe (saturated paste) is standard for salinity assessment
Enzyme Assays (MUB substrates)	Rhizosphere and bulk soil	Phosphatase, urease, dehydrogenase, β-glucosidase activity	Reflects microbial activity and nutrient cycling rates
^{15}N and ^{13}C Isotopic Tracing	Soil-plant systems under controlled conditions	N cycling rates; C partitioning in rhizosphere	Gold standard for biogeochemical flux quantification
Hydroponic Salinity Systems	Controlled greenhouse experiments	Ion uptake kinetics; osmolyte production under NaCl gradient	Eliminates soil heterogeneity; precise dose-response data
X-ray Fluorescence (XRF)	Whole plant tissue; soil minerals	Non-destructive elemental mapping in plant cross-sections	Reveals spatial ion distribution within tissues
Scanning Electron Microscopy (SEM)	Root epidermal structures; salt glands	Morphological characterization of salt secretion structures	Identifies salt crystal deposits and gland morphology
Metagenomics / 16S rRNA Sequencing	Rhizosphere soil DNA extracts	Microbial community composition under salinity stress	Captures functional diversity in halophyte rhizosphere

6. Environmental Influences and Stress Interaction Effects

6.1. Effects of Salinity Gradients and Ionic Strength

One of the interesting aspects of *S. europaea* is that they appear to exhibit a phenomenon called salt stimulation, which is contradictory to what occurs in nearly all other plant species with regard to growth in saline environments. Salt stimulated or no change in growth occurs at the moderate concentrations of NaCl (100-300 mM, equivalent to an EC of ~10-30 dS/m). Beyond these concentrations or at extreme ionic strengths (>500 mM NaCl or EC > 45 dS/m), this halophyte exhibits inhibited growth because of toxicity levels of the salts present to the plant. The salt stimulation effect of *S. europaea* to moderate ionic concentrations is thought to result from *S. europaea*'s ability to utilize, for vacuolar osmotic adjustment, inorganic ions which is a metabolically less expensive option than synthesizing organic compatible solutes. Additionally, *S. europaea* are also able to utilize Na^+ as a macronutrient for facilitating beneficial responses for growth stimulation and reaches saturation at the moderate ionic sodium concentrations. In addition to the concentration of salts used to create a salinity challenge, the ionic composition of salt that was added to the soil would influence the plant's physiological response to the salt challenge. For example, plant response to saline soils dominated by Na_2SO_4 or $NaHCO_3$ will be qualitatively different because of the effects of pH on the soils, sulfate metabolism and carbonate alkalinity. (Redondo-Gómez *et al*., 2010) [3] (Parida and Das, 2005) [8]

6.2. Impact of Drought and Temperature Stress

In naturally saline habitats, *Sarcocornia* (*S. europaea*) faces a combination of drought stress and heat stress during dry spells, which act together in negatively impacting the growth and biogeochemical functioning of *S. europaea*. Drought stress adds to the osmotic dimension of salt toxicity by further decreasing the soil water potential available to plant roots while triggering stomatal closure and thereby limiting CO_2 availability for photosynthesis. At the same time, high summer temperatures within arid saline habitats result in a rapidly increasing concentration of soil salts through evaporation, leading to spatially and temporally transitory pulses of hypersalinity that can even exceed *S. europaea*'s physiological tolerance levels. Drought and salinity have combined effects on soil microbial activity and enzyme kinetics, which act in a synergistic manner to inhibit nitrifying and phosphate-solubilizing bacterial community members sensitive to ionic strength and water potential. (Song *et al*., 2011) [38]

6.3. Response to Heavy Metal Contamination in Saline Soils

The presence of coastal and industrial saline soils often contain high levels of heavy metals such as Pb, Cd, Zn, Cu and Ni that have been contaminated through industrial wastewater discharges, atmospheric fallout, and sediment movement from tidal events. The halophyte *S. europaea* may be used as a potential phytoextractor in saline contaminated soil due to its ability to accumulate various heavy metals in its aerial biomass, especially Cd and Zn. Additionally, the effects of high levels of salt stress and heavy metal toxicity together create a unique dual-stress environment that relies upon coordinated functioning of ionic and metal detoxification pathways including metallothioneins, phytochelatins, and vacuolar sequestration of heavy metals. The bioavailability of heavy metals within saline soils is influenced by the same soil properties impacted by the presence of halophytes (i.e. pH, organic matter content, ionic strength, and redox potential), thereby establishing a series of interactions between phytoremediation and metal mobility that require careful monitoring in relation to restoration activities. (Qadir *et al*., 2007) [40] (Shabala, 2013) [25]

6.4. Climate Change Implications

The rapid increase in sea levels and more frequent extreme storm surges due to anthropogenic climate change poses a serious threat to the ecological function and geographic distribution of *S. europaea* in coastal salt marsh ecosystems. Rising sea levels are increasing the frequency and length of time that low-elevation salt marsh ecosystems are inundated, resulting in a "coastal squeeze" where seaward loss of salt marshes cannot be compensated for by landward migration due to the restriction of inland transgression by human infrastructure. At the same time, regional climate change scenarios for arid and semi-arid regions (e.g., Mediterranean basin, Middle East and Central Asia) show rising temperatures, reduced and more variable rainfall amounts, and consequently accelerated salinization of the soil due to increased evapotranspiration and reduced freshwater leaching. These changes are projected to increase the geographic extent of the impact of soil salinity and therefore increase the potential demand for and ecological significance of halophyte-based bioremediation strategies utilizing *S. europaea* and other closely related species. (Flowers and Muscolo, 2015) [23] (Rengasamy, 2006) [26]

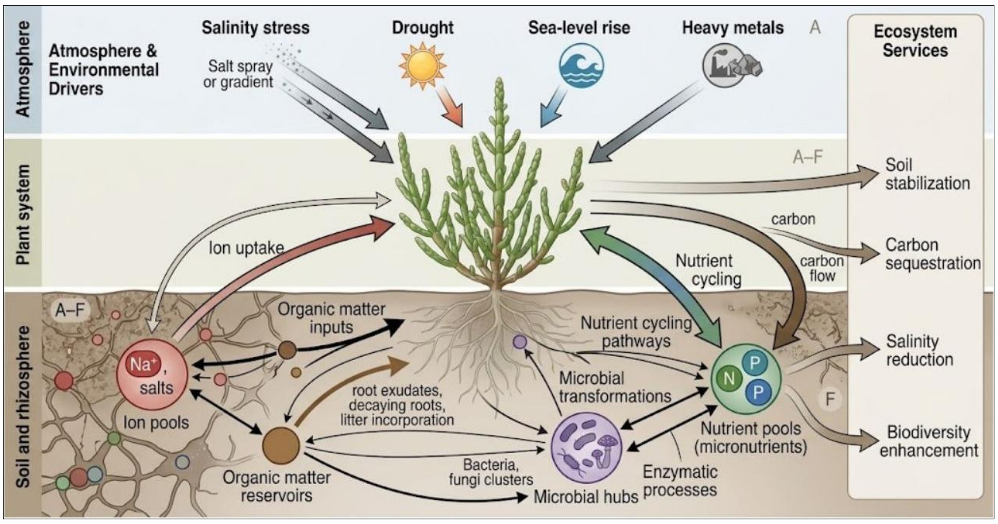

Fig 3: *Salicornia europaea* Interactions within Saline Soil Ecosystems

7. Applications, Ecosystem Implications, and Land Management

7.1. Phytoremediation and Saline Soil Reclamation

S. europaea has demonstrated its ability to extract vast amounts of Na+ from soils and to reduce soil EC and SAR below agronomically limiting levels, therefore improving soil physical and biological characteristics in support of scientific peat studies, making this species an established phytoremediation strategy for salt-affected agricultural land. The advantages of a phytoremediation technique versus typical methods of chemical-physical reclamation include: no additional chemical input (no secondary contamination of the soil); the production of cash-generating biomass (via edible seeds, as well as bioactive compounds); improved soil organic matter and biological processes as ionic transformations continue; and a greater number of viable, hopefully greater yielding, crops as the direct benefits of reclamation cycle candidate produce have been realized. To date, there have been several successful field applications of *S. europaea*n phytoremediation in salt-affected agricultural areas of the world, including Pakistan, Egypt, the Netherlands, and Iran; with documented yield gains of 25–60% for cereal crops grown on soils after they had been reclaimed compared with those grown on untreated saline soils. The successful integration of *S. europaea* phytoremediating technology into agricultural crop rotation systems—specifically with respect to halophyte placement timing, biomass harvest methods, and selection of post-reclamation crops—represents an active area of research in the agricultural sciences with potentially important practical benefits. (Qadir *et al*., 2007) [40]

7.2. Role in Sustainable Agriculture and Biosaline Farming

The use of saline areas - that is, using salty land and seawater to grow plants - is gaining popularity as an economical way to meet food needs in areas where there isn't enough space or water to grow plants using normal agricultural techniques. (Rozema and Schat, 2013) [14] *Salicornia europaea* (also known as "saltwort") has two roles to play in this new method of producing food sustainably. First of all, it can help clean up the saline soil so that traditional crops can be grown there in the future. Secondly, *Salicornia* is being grown, harvested and sold as a value-added product with market demand, through its edible succulent stems, marketed as "sea beans," and its high oil-producing seeds. (Khan and Duke, 2001) [15] Sea beans are also sold at a premium in European fine dining markets, thus providing the farmer with an economic return during the remediation period, while offsetting the cost of treating the land before planting crops. Moreover, the seeds of *Salicornia* contain a high amount (28-33%) of edible oil and have an overall positive fatty acid profile (with high levels of linoleic acid), making it an excellent candidate as an oilseed crop, particularly for marginally saline soils. (Khan and Duke, 2001) [15] Using seawater or brackish water from an aquifer for irrigation, allows for the sustainable production of *Salicornia*, thereby providing viable uses for water resources where this would typically not be possible for other crops. (Rozema and Schat, 2013) [14]

7.3. Potential in Carbon Sequestration in Saline Ecosystems

Salt-rich marshes, which are made of plants that tolerate salt, like *Salicornia* (*Salicornia*) in lower marsh areas, store more carbon than almost any other ecosystem on earth. (Flowers and Muscolo, 2015) [23] This means that a few square meters of these wetlands can produce a lot of organic carbon due to being waterlogged and anaerobic than their size would lead you to believe. The amount of "Blue Carbon" produced from *S. europaea* and the salt marsh ecosystem is estimated to be 4.5 Mg of Carbon/ha, produced by the slow breakdown of plant material in these anaerobic saline conditions, which limit how fast enzymes (such as lignin peroxidase and laccase) can cause Plant material to break down at the end stages of Plant life. Therefore, restoration of degraded or changed salt marshes through the re-establishment of *S. europaea* and other halophyte species will also provide benefits to climate change mitigation as part of the Blue Carbon Strategy and even in carbon markets that comply with the Blue Carbon accounting system. (Flowers and Muscolo, 2015) [23]

7.4. Integration into Land Management and Restoration Strategies

In order to integrate *S. europaea*-based management into restoration programmes, a multidisciplinary approach is needed which integrates the disciplines of plant ecophysiology, soil science, hydrology, socioeconomics, and stakeholder engagement. (Shabala, 2013) [25]

The key factors that must be considered for successful implementation include the following: (i) soil salinity assessment and classification, to determine whether *S. europaea* can be established without pre-treatment by assessing the possibility of establishing the species at a site based upon soil salinity levels; (ii) obtaining seed from locally adapted ecotypes that are optimised to the specific salinity range and the climate at the restoration site; (iii) developing an irrigation schedule that provides sufficient water for establishment of the plants and reduces salinity; (iv) developing monitoring protocols to record electrical conductivity (EC), sodium adsorption ratio (SAR), amount of soil organic matter, number of microbes, and amount of vegetative cover during the restoration period; (v) develop a transition plan for introduction of commercial crops after ionic amelioration has reached an acceptable level. (Qadir *et al*., 2007) [40]

Table 6: Summary of ecological and agricultural impacts of salinity amelioration by *Salicornia europaea* across experimental, field, and ecosystem scales. Outcomes are organized by impact category with quantitative indicators where available. SAR = sodium adsorption ratio; SOC = soil organic carbon.

Impact Category	Observed / Projected Outcome	Sector Relevance	Notes
Soil EC Reduction	35–65% EC decrease after 2–3 growing seasons	Agricultural — Enables re-cultivation of salt-affected land	Foundational reclamation metric
SAR Improvement	SAR reduced from >20 to <13 in reclaimed soils	Agricultural — Restores soil permeability and structural stability	Critical threshold for USDA soil classification
Organic Matter Increase	+40–90% SOC after multi-season cultivation	Ecological — Enhances soil microbiome and water retention	Long-term fertility restoration trajectory
Phytoremediation of Heavy Metals	Zn, Pb, Cd accumulation in aerial biomass	Environmental — Reduces toxic metal loading in saline soils	Harvest and disposal of metal-enriched biomass needed
Blue Carbon Sequestration	Up to 4.5 Mg C/ha/yr in salt marsh systems	Ecological/Climate — Significant contribution to coastal C stock	Comparable to mangrove C sequestration rates
Biodiversity Facilitation	Establishes pioneer vegetation in bare salt flats	Ecological — Supports habitat succession for salt marsh fauna	Critical for coastal ecosystem recovery after disturbance
Biomass Energy and Food Potential	Edible and high-oil seeds; biomass productivity ~3–8 t/ha	Agricultural/Economic — Biosaline crop with added-value products	Emerging market for gourmet salt and nutraceuticals
Nitrogen Input via Biological Fixation	Associated N-fixing bacteria augment soil N	Agricultural — Reduces dependency on synthetic N fertilizers	*Rhizobium* and *Azospirillum* association reported

8. Challenges, Knowledge Gaps, and Future Research Directions

8.1. Limitations in Current Physiological and Field-Scale Data

The ecophysiology of *S. europaea* has been studied extensively, yet many aspects continue to remain unexamined for predicting field success based on laboratory results. (Flowers and Colmer, 2008) [1] Few ecotypes/genetics have been tested in ecophysiological studies and most seed lots that have been used for experiments are commercially available, which limits our ecophysiological understanding of both the genetic variability and phenotypic variation in *S. europaea* across its range. (Flowers and Muscolo, 2015) [23] It is understood that there are different levels of salinity tolerance and ionic uptake by *S. europaea* populations depending on geographical location (e.g., Mediterranean coastal, Central Asian steppe, Northern European tidal flat), but this information is still lacking in terms of systematic comparative ecophysiology. (Rozema and Schat, 2013) [14] Furthermore, most mechanistic studies of ion transport in *S. europaea* have been completed using either hydroponics or sterile soils. (Munns and Tester, 2008) [9] Both of these approaches overlook how the rhizosphere microbiome plays an important role in ionic performance. (Qadir *et al*., 2007) [40] Similarly, long-term (multi-decadal) indicators of soil ionic dynamics for land that will be continually managed with *S. europaea* have not been examined as most field studies have been limited to 5 or fewer growing seasons; thus, there is insufficient data to determine if there will be continued amelioration of the soil's ionic condition or if there will be rebound salinization following plant removal. (Rengasamy, 2006) [26]

8.2. Scaling Plant-Level Processes to Ecosystem-Level Impacts

The difficulty of extrapolating plant-level ion absorption rates and soil modification processes to estimate to field-, landscape- and regional-scale ionic dynamics requires understanding, among other things, that the uptake rates of individual pots or small plots of halophytes, which are typically measured from single experimental pots or small fields, will vary greatly: based on spatial heterogeneity (i.e., soil salinity, texture); based on changes in growth rate and biomass allocation over time; based on interspecific competition between different species in multi-specific halophyte communities; based on hydrological inputs and outputs; e.g., salinity of ground water, tidal inundation of plants, rain leaching of salts into plant roots, etc.; and based on lateral transport of ions within the soil due to water movement. (Rengasamy, 2006) [26] Process-based biogeochemical models capable of integrating such multi-scale controls on ionic dynamics are still in their infancy both for developing and ultimately validating saline soil-halophyte systems. (Qadir *et al*., 2007) [40] The potential for developing a remote sensing monitoring approach based on hyperspectral imagery and vegetation indices calibrated for use in saline environments may provide a means for monitoring ecological changes associated with large-scale dynamics of electrical conductivity and halophyte production without the logistical challenges inherent in traditional field sampling methods. (Flowers and Muscolo, 2015) [23]

8.3. Knowledge Gaps in Long-Term Ionic Balance Regulation

The ways in which *S. europaea* regulates ionic homeostasis through multiple reproductive periods when salinity is constantly high are not fully understood, particularly with regard to the regulation of vacuolar expansion and ion loading capabilities at different developmental points. (Munns and Tester, 2008) [9] It is unclear if *S. europaea* has an always-high vacuolar Na$^+$ sequestration capability or if it can alter this capacity in response to external ionic conditions. (Apse and Blumwald, 2007) [35] Understanding this mystery will be important to determine how much phytoremediation *S. europaea* can provide and how genetically engineered crops can become more salt tolerant. (Flowers, 2004) [32] The interaction between the halophyte's ionic regulation system and the soil microbiota—specifically whether the halophyte can recruit bacteria with a halotolerant phenotype that enhance the halophyte's own ionic tolerance—represents an underutilized area of research with many potential uses related to using microorganisms as an additive for the reclamation of saline soils. (Shabala, 2013) [25]

8.4. Future Research: Molecular, Omics, and Integrated Approaches

Multi-omic techniques such as transcriptomics, proteomics, metabolomics, and ionomics, which together facilitate system-level characterization of the actual molecular response of *S. europaea* to salinity stress in conjunction with soil ionic dynamics, will be a major source of future research breakthroughs in this field. (Yang and Guo, 2018) [31] Currently, the sequencing and annotation of the *S. europaea* genome has not yet been completed; this is an important limitation on the application of genomic and reverse-genetic tools for the investigation of the mechanistic biology of *S. europaea* in relation to salinity stress. (Flowers and Muscolo, 2015) [23] Research on the rhizosphere (microbiomes) through the application of shotgun metagenomics and metatranscriptomics will elucidate the functional roles of specific microbial taxa and metabolic pathways that mediate the ionic interactions between plants and soil, including biogeochemical cycling. (Qadir *et al*., 2007) [40] The development of integrated biogeochemical modelling frameworks that integrate plant ecophysiology, soil chemistry, microbial ecology, and hydrology will facilitate projections of long-term sulphate amelioration trajectories under a variety of management regimes and climate projections, and provide a quantitative basis for evidence-based policy support for saline land management. (Rengasamy, 2006) [26] The integration of molecular, microbial and ecosystem-scale approaches represents the frontier of scientific research in relation to *S. europaea* biogeochemistry and its applications. (Shabala, 2013) [25]

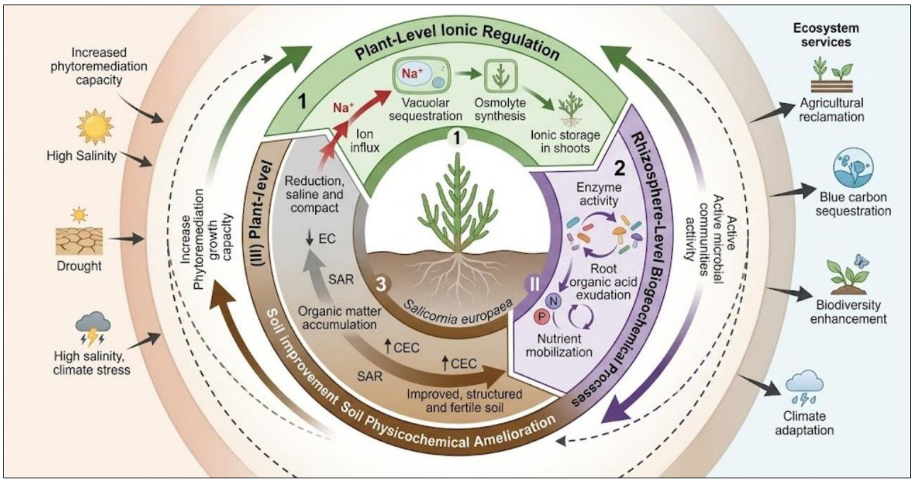

Fig 4: Salinity Stress Amelioration Pathways in Plant–Soil Systems

9. Conclusions

This literature review combines and critically evaluates the available evidence to support the conclusion that *Salicornia europaea* is a halophyte of biogeochemical significance, which improves the chemistry, biology and physics of salinised, soil-derived ecosystems through multiple mechanisms at the plant physiological level, the soil chemical level and the ecosystem ecological level. The ionic tolerance of *S. europaea* has proven to be among the highest of any known halophyte due to synergistic activities of various NHX antiporter proteins located within the tonoplast, various HKT transporters, numerous osmolyte biosynthetic pathways, and various anatomical adaptations within its succulent tissues. As a result of its unique ionic tolerance *S. europaea* thrives on saline soils that are not conducive to agricultural productivity.

Furthermore, the measurable changes in salinity indicators (electrical conductivity [EC], sodium adsorption ratio [SAR], exchangeable sodium cation [Na+], and pH) that occur within soils cultivated with *S. europaea* indicate that in addition to contributing to improved chemical properties of soils, *S. europaea* has also had substantial effects upon biological processes associated with soil biology. These biological benefits include increased rhizosphere-associated microbial activities and increases in enzyme functions pertaining to nutrient cycling (e.g., N-mineralisation, P-solubilisation and C-accumulation) occurring within the reclaimed soil. The collectively improved physical, chemical and biological characteristics of reclaimed soils will lead to increasing soil conditions favourable for the establishment of crops in subsequent years and the sustainable production of crops from reclaimed soils.

S. europaea is a keystone species and provides critical functions of ecological engineering at the level of ecosystems, including pioneer vegetation, sediment stabilization, blue carbon sequestration, and promoting biodiversity in coastal salt marshes. Furthermore, due to its response or lack of response to future environmental stressors that will increase with climate change scenarios (i.e. sea-level rise, drought, and salt establishment in soil), it is an ecologically important species; its conservation/managed cultivation should be included in both national and international land management and climate adaptation strategies.

Therefore, *S. europaea* can provide solutions to develop a biosaline farming system that provides both environmental and economic benefits by integrating phytoremediation (remediation of contaminated land through biological processes) with the ability to generate income from the biomass produced. This will foster the goals of restoring saline soil and producing food on salt-affected soils where there is a crisis and the underutilisation of agricultural land. Recommended future research priorities include genome sequencing, long-term field monitoring of soil ionic dynamics in the cultivation of *S. europaea*, functional characterisation of the rhizosphere and microbiome, and development of biogeochemical models that predict reclamation patterns based on different soil, climate, and management regimes. Ultimately, the biogeochemical legacy of *S. europaea* is a model of evolutionary optimisation and a guide for land stewardship in an increasingly saline world.

References

1. Flowers TJ, Colmer TD. Salinity tolerance in halophytes. New Phytologist. 2008;179(4):945–963.
2. Koyro HW. Effect of high NaCl salinity on plant growth, leaf morphology and ion composition in the halophyte *Beta vulgaris* ssp. *maritima*. Journal of Experimental Botany. 2006;57(6):1413–1423.
3. Redondo-Gómez S, Mateos-Naranjo E, Figueroa ME, Davy AJ. Salt stimulation of growth and photosynthesis in an extreme halophyte *Arthrocnemum macrostachyum*. Plant Biology. 2010;12(1):79–87.
4. Lv S, Jiang P, Chen X, Fan P, Wang X, Li Y. Multiple compartmentalization of sodium conferred salt tolerance in *Salicornia europaea*. Plant Physiology and Biochemistry. 2012;51:47–52.
5. Aghaleh M, Niknam V, Ebrahimzadeh H, Razavi K. Salt stress effects on growth, pigments, proteins and lipid peroxidation in *Salicornia europaea* and *Salicornia persica*. Biologia Plantarum. 2009;53(2):243–248.
6. Pujol JA, Calvo JF, Ramírez-Díaz L. Recovery of germination from different osmotic conditions by four halophytes from southeastern Spain. Annals of Botany. 2000;85(2):279–286.
7. Davy AJ, Bishop GF, Costa CSB. *Salicornia* L. (*Salicornia pusilla*, *S. ramosissima*, *S. europaea*, *S. obscura*, *S. nitens*, *S. fragilis* and *S. dolichostachya*). Journal of Ecology. 2001;89(4):681–707.
8. Parida AK, Das AB. Salt tolerance and salinity effects on plants: a review. Ecotoxicology and Environmental Safety. 2005;60(3):324–349.
9. Munns R, Tester M. Mechanisms of salinity tolerance. Annual Review of Plant Biology. 2008;59:651–681.
10. Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ. Plant cellular and molecular responses to high salinity. Annual Review of Plant Physiology and Plant Molecular Biology. 2000;51:463–499.
11. Cheeseman JM. The integration of activity in saline environments: problems and perspectives. Functional Plant Biology. 2013;40(9):759–774.
12. Shabala S, Cuin TA. Potassium transport and plant salt tolerance. Physiologia Plantarum. 2008;133(4):651–669.
13. Ashraf M, Foolad MR. Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environmental and Experimental Botany. 2007;59(2):206–216.
14. Rozema J, Schat H. Salt tolerance of halophytes: research questions reviewed in the perspective of saline agriculture. Environmental and Experimental Botany. 2013;92:83–95.
15. Khan MA, Duke NC. Halophytes – a resource for the future. Wetlands Ecology and Management. 2001;9(6):455–456.
16. Grigore MN, Toma C. Botanical Illustrations of Chenopodiaceae/Amaranthaceae Halophytes. Cham: Springer; 2017.
17. Barbieri G, Vallone S, Orsini F, Paradiso R, De Pascale S, Negre-Zakharov F, Maggio A. Stomatal density and metabolic determinants mediate salt stress adaptation and water use efficiency in basil. Journal of Plant Physiology. 2012;169(17):1737–1746.
18. Song J, Feng G, Tian CY, Zhang FS. Strategies for adaptation of *Suaeda physophora*, *Haloxylon ammodendron* and *Haloxylon persicum* to a saline environment during seed germination stage. Annals of Botany. 2005;96(3):399–405.
19. Tavakkoli E, Rengasamy P, McDonald GK. High concentrations of Na^+ and Cl^- ions in soil solution have simultaneous detrimental effects on growth of faba bean under salinity stress. Journal of Experimental Botany. 2010;61(15):4449–4459.
20. Ismail A, Takeda S, Nick P. Life and death under salt stress: same players, different timing? Journal of Experimental Botany. 2014;65(12):2963–2979.
21. Guo J, Suo S, Wang BS. Sodium chloride improves seed vigour of the euhalophyte *Suaeda salsa*. Seed Science

Research. 2015;25(1):69–77.
22. Bria PN, Pedersen O, Shabala S. Casparian strip and the role of roots in ion exclusion and compartmentalization. Frontiers in Plant Science. 2021;12:659–671.
23. Flowers TJ, Muscolo A. Introduction to the special issue: halophytes in a changing world. AoB Plants. 2015;7:plv020.
24. Kronzucker HJ, Britto DT. Sodium transport in plants: a critical review. New Phytologist. 2011;189(1):54–81.
25. Shabala S. Learning from halophytes: physiological basis and strategies to improve abiotic stress tolerance in crops. Annals of Botany. 2013;112(7):1209–1221.
26. Rengasamy P. World salinization with emphasis on Australia. Journal of Experimental Botany. 2006;57(5):1017–1023.
27. Zhao KF, Fan H, Jiang XY, Song J. Critical day length and photoperiodic control in the halophyte *Suaeda salsa*. Plant, Cell & Environment. 2003;26(12):1929–1937.
28. Horie T, Hauser F, Schroeder JI. HKT transporter-mediated salinity resistance mechanisms in *Arabidopsis* and monocot crop plants. Trends in Plant Science. 2009;14(12):660–671.
29. Zhu JK. Plant salt tolerance. Trends in Plant Science. 2001;6(2):66–71.
30. Mahajan S, Tuteja N. Cold, salinity and drought stresses: an overview. Archives of Biochemistry and Biophysics. 2005;444(2):139–158.
31. Yang Y, Guo Y. Unraveling salt stress signaling in plants. Journal of Integrative Plant Biology. 2018;60(9):796–804.
32. Flowers TJ. Improving crop salt tolerance. Journal of Experimental Botany. 2004;55(396):307–319.
33. Loeppert RH, Inskeep WP. Iron. In: Sparks DL, editor. Methods of Soil Analysis, Part 3: Chemical Methods. Madison (WI): Soil Science Society of America; 1996. p. 639–664.
34. Mäser P, Hosoo Y, Goshima S, Horie T, Eckelman B, Yamada K, *et al*. Glycine residues in potassium channel-like selectivity filters determine potassium selectivity in four-loop-per-subunit HKT transporters from plants. Proceedings of the National Academy of Sciences of the United States of America. 2002;99(9):6428–6433.
35. Apse MP, Blumwald E. Na^+ transport in plants. FEBS Letters. 2007;581(12):2247–2254.
36. Rajendran K, Tester M, Roy SJ. Quantifying the three main components of salinity tolerance in cereals. Plant, Cell & Environment. 2009;32(3):237–249.
37. Läuchli A, Grattan SR. Plant growth and development under salinity stress. In: Jenks MA, Hasegawa PM, editors. Advances in Molecular Breeding Toward Drought and Salt Tolerant Crops. Dordrecht: Springer; 2007. p. 1–32.
38. Song J, Shi G, Gao B, Fan H, Wang BS. Waterlogging and salinity effects on two *Suaeda salsa* populations. Physiologia Plantarum. 2011;141(3):344–355.
39. Misra AN, Misra M, Singh R. Nitric oxide alleviates salt stress in plants. HAYATI Journal of Biosciences. 2011;18(2):95–101.
40. Qadir M, Oster JD, Schubert S, Noble AD, Sahrawat KL. Phytoremediation of sodic and saline-sodic soils. Advances in Agronomy. 2007;96:197–247.
41. Grieve CM, Grattan SR. Mineral nutrient acquisition and response by plants grown in saline environments. In: Pessarakli M, editor. Handbook of Plant and Crop Stress. New York: Marcel Dekker; 1999. p. 203–229.
42. Pessarakli M, Huber JT, Tucker TC. Protein synthesis in green beans under salt-stress conditions. Journal of Plant Nutrition. 1989;12(10):1105–1121.
43. Ghassemi F, Jakeman AJ, Nix HA. Salinisation of Land and Water Resources. Wallingford (UK): CAB International; 1995.
44. Läuchli A, Lüttge U, editors. Salinity: Environment–Plants–Molecules. Dordrecht: Kluwer Academic Publishers; 2002.

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