AgriSustain-An International Journal

Agriculture

Review

Current scenario and future prospects of Halophytes for facilitating agricultural and environmental sustainability

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Abstract

Salinity is an important abiotic stress influencing plant growth and farming productivity across the globe. Halophytes are a unique group of plants that are salt tolerant and have specific physiological, biochemical, and molecular attributes that promote their growth and development in saline conditions. This review examines the mechanisms by which halophytes achieve salinity tolerance, with an emphasis on osmotic adjustment due to the accumulation of compatible solutes; ion compartmentation, Na^+/H^+ antiporters and selective transporters; and improved antioxidant defense systems to cope with oxidative stress induced by saline stress. Structural features in halophytes are another key form of adaptation; for example, succulence exhibited in leaves or stems and salt glands or bladders. Stress-response genes and transcription factors regulate adaptive responses. Accordingly, this review will explore the ecological context and possible applications for halophytes in saline agriculture, phytoremediation, and bioenergy. Ultimately, the insights provided about the mechanisms of salt tolerance in halophytes will inform knowledge of salt-tolerant crops that can support sustainable climate-resilient ecosystems to enhance management of saline-impacted land and soil.

Keywords: Salinity, abiotic stress, Halophytes and environmental sustainability

Introduction

Soil salinization is one of the most widespread and rapidly evolving environmental issues facing global food security and sustainable agricultural development. Globally, approximately 833 million hectares of land are affected by salinity, including more than 20% of irrigated lands and roughly 2% of dryland agricultural land [1][2]. This, in addition to the human contributions to salt accumulation, including the use of excessive fertilizers, improperly managed irrigation systems, poor drainage systems, saltwater intrusion into coastal irrigated aquifers, as well as climate change through sea level rise and changing precipitation, is an alarming trend. Increased salinity in agricultural soils reduces plant productivity by causing complex physiological and metabolic disruptions. Salinity stress in plants can be considered to consist of two primary components: osmotic stress and ionic toxicity. The osmotic stress is caused by soluble salts (primarily NaCl) occupying the rhizosphere and reducing the water available to the plants. Ionic toxicity occurs when accumulations of sodium (Na^+) and chloride (Cl^-) ions interfere with essential functions within cells and cause the displacement of essential nutrients, such as potassium (K^+) and calcium (Ca^{2+}) [3][4]. Photosynthesis is disrupted either directly or indirectly from competing ions for essential enzymatic or photosynthetic processes. Moreover, the oxidative

OPEN ACCESS

CITATION

Chahal, R.R.S., Bindu Battan and Sunita Dalal Current scenario and future prospects of Halophytes for facilitating ag-ricultural and environmental sustainability . *AgriSustain-an International Journal*, 2025, 03(2), 12-06.

ARTICLE INFORMATION

Received: May 2025
Revised: June 2025
Accepted: July 2025

DOI: **10.5281/zenodo.18222571**

stress caused by salt results in the generation of reactive oxygen species (ROS) that may damage lipids, proteins, and nucleic acids, leading to cellular damage and impaired plant growth. Most common crop plants or glycophytes, in contrast, have a very limited tolerance for salinity and can lose significant portions of their yield from only moderate salt concentrations (>50 mM NaCl). Halophytes (plants able to tolerate saline conditions) are a specific unique diverse group of species that have adapted to be able to develop in saline habitats and can complete their lives in high salt concentrations (often >200 mM NaCl), all other glycophytes may succumb [5][6]. Halophytes are found in numerous saline growing environments, including salt marshes, coastal dunes, mangrove swamps, inland saline lakes, and desert salt flats.

Halophytes use various morphological, physiological, biochemical, and molecular approaches to deal with salty conditions in saline ecosystems. Morphologically, many halophytes will develop succulence (water storage tissue), salt-secreting glands, or epidermal salt bladders that permit them to either exclude or excrete the salt. Physiology of halophytes relies on osmotic balance, so of reliable osmoticum such as `proline`, `glycine betaine`, and sugar alcohols (e.g., `mannitol`, `sorbitol`) serves to stabilize their proteins and organelles, etc., without interfering with metabolism. Halophytes obtain their ion homeostasis through selective uptake of essential ions, active exclusion of toxic ions at the root to soil interface, and cellular compartmentalization into vacuoles (specifically for Na^+ and Cl^- ions), thereby protecting the remainder of the cytosolic material from the ionic stressors. Specific ion transporters and antiporters serve, including the plasma membrane localized Na^+/H^+ antiporter SOS1, the NHX antiporters placed on the tonoplast, a high-affinity potassium transporter, and possibly others [7]. These strategies for ion homeostasis in stress situations are often related to the degree of upregulation in halophytes.

Halophytes, at levels of biochemistry and molecules, have surprisingly strong antioxidant defense mechanisms that consist of various enzymatic (superoxide dismutases, catalases, peroxidases, glutathione reductases) and non-enzymatic (ascorbate, glutathione, flavonoids) components to eliminate ROS. Transcriptomic based and/or proteomic based studies of halophytes have also revealed, unique or greater expression of stress-responsive genes, transcription factors (i.e., DREB, NAC, MYB, bZIP), heat shock proteins, and late embryogenesis abundant (LEA) proteins responsible for growth, stress signaling, and cellular repair, needed under saline conditions [8].

Because of their remarkable flexibility, halophytes are increasingly recognized not only as model systems for research into salt tolerance, but also potential candidates for saline agriculture as they can offer chance for food, fodder, and biofuel crop development on marginal lands with brackish water resources, and sustainability of agriculture and rural livelihoods. Halophytes also have the potential to play important roles in phytoremediation by stabilizing and reclaiming salt affected soils and in ecosystem services including carbon sequestering and biodiversity conservation in salt-affected environmental habitats [9].

Although many adaptive traits are displayed by halophytes, the regulatory networks and signaling pathways that control salt tolerance remain understudied; however, new high-throughput omics technologies e.g. genomics, transcriptomics, metabolomics, epigenomics, now allow researchers to begin to delineate these networks and identify key genes controlling salinity tolerance, and subsequently provide a foundation for improving salt tolerance in glycophytic crops using traditional breeding, genetic engineering, and genome editing approaches like CRISPR-Cas9 [10].

Herein, we review and critically assess the mechanisms that are put in place by halophytes to tolerate salinity, assessing physiological responses, biochemical feats and molecular mechanisms of regulation, but also ecological significance and promise for future agriculture, environmental remediation, and saline land use. By better understanding the multi-faceted approaches halophytes utilize to withstand salinity stress, we have the potential to advance our understanding of plant adaptive biology and develop climate resilient agroecosystems that can thrive in the face of increasing soil salinization.

Classification of Halophytes

Halophytes are a polyphyletic group of angiosperms that vary widely in morphological, physiological and biochemical adaptations for living and reproducing in environments with salinity exceeding 200mM NaCl. The understanding of halophyte classification is an important step in our understanding of the diversity of salt tolerance adaptations, as well as the further development of bio-saline agriculture and management practices. Halophytes can be classified into distinct groups based on their ecological niche specialization, demonstrable physiological responses to salinity, and varying degrees of morphological adaptations, each representing particular evolutionary strategies for alleviating saline stress [11].

Ecological Classification of Halophytes: Ecological classification conveys the degree of salt dependency claimed by the halophyte types when they occur in their natural habitats. Notably, ecological classification also categorizes tolerance into obligatory and facultative, a distinction that may determine distribution and community type within saline systems [12].

Obligate halophytes: Taxa that are exclusive to saline conditions (e.g. coastal marshes, inland salt flats, and mangrove swamps). Their ontogeny and life cycle directly connected to elevated salinity, resisting or not growing with no-salinity or freshwater. They utilize highly specialized ion compartmentalization systems, salt extrusion systems, or osmoprotectants. Common examples include *Salicornia europaea*, *Suaeda salsa* and *Avicennia marina.*

Facultative halophytes: Species that tolerate, allow growing, and can produce certain life cycle functions under moderate to high salinity conditions, not locked to saline habitats. A faculty halophyte demonstrates that saline and no-saline soil may be tolerated or occupied, reflecting phenotypic plasticity and inducible pathways for salt tolerance (e.g., upregulation of SOS (Salt Overly Sensitive) signaling pathway, and/or enhanced production of compatible solutes, i.e., proline and *glycine betaine*. Noteworthy examples include *Atriplex halimus, Sporobolus virginicus,* and *Phragmites australis.*

Salt-tolerant glycophytes: Some glycophytic species, while not true halophytes, display a range of levels of halotolerance, likely due to acclimatory responses that are capable of ROS detoxification, existing membrane stabilization, and partially excluding ions. Currently, these species are gaining more traction as the focus of transgenic research and breeding programs for salt tolerance such as *Oryza sativa* and *Zea mays.*

Physiological Classification of Halophytes: Physiological classification is based on the internal mechanisms that plants use to mitigate salt stress at both the cellular level and the whole plant level that encompass strategies for selective ion uptake, long-distance transport, vacuolar sequestration, and active salt extrusion [13].

Salt excluders: These halophytes utilize root-level barrier systems to restrict the entry of Na^+ and Cl^- ions into the xylem. Casparian strips, suberized endodermal cells, and selective ion transporters (e.g. HKT1-type symporters) allow the preferential uptake of K^+ over Na^+ for these plants, so that NaCl concentrations remain very low in above-ground tissues. An example includes *Rhizophora mucronata* and *Avicennia officinalis*.

Salt excreters: This group of halophytes utilizes specialized salt glands, hydathodes, or epidermal bladders to excrete excess ions actively from the leaf surface to replace lost ions and provide cytosolic ionic homeostasis. The secretion process is energetically dependent and typically occurs when transpiration rates are high. Examples include *Atriplex nummularia, Tamarix aphylla,* and *Limonium vulgare.*

Salt accumulators: These halophytes deal with high internal salt concentrations by a process of efficient vacuolar sequestration made possible by the vacuolar NHX1-type Na+/H+ antiporters, along with vacuolar H+-ATPases. This process allows salty cells to maintain an osmotic adjustment and avoid ionic toxicity in the cytoplasm. These halophytes tend to be exceptionally succulent and have high concentrations of ions in their tissues. Examples of salt accumulators include *Salicornia bigelovii, Halostachys caspica,* and *Suaeda fruticosa*.

All of these physiological strategies can interact with putative osmoregulatory strategies, either independently or together in the same plant where physiological strategies can differ by organ, developmental stage, or environmental gradients.

Morphological Classification of Halophytes: Morphological classification considers morphological characteristics which primarily aid in plant fitness under salt stress through modifying plant-water relations, ion transportation and desiccation avoidance. These characteristics are frequently viewed as those which reflect long-term evolutionary adaptations to chronic salinity [14].

Succulent halophytes: Exhibits hypertrophied tissues, characterized by water-rich contents which help to dilute cytosolic salt concentrations and to reduce potential water concentration. Succulence is often considered indicative of Crassulacean Acid Metabolism (CAM) and is usually associated with plants exhibiting lower surface area to volume ratios that minimize transpiration rates. Examples of succulent halophytes include taxa such as *Salicornia spp., Zygophyllum spp., and Mesembryanthemum crystallinum*.

Non-succulent halophytes: This group does not have succulent tissues and uses different adaptations such as deep rooting, xeromorphic leaf anatomy, and salt excretion to facilitate salt tolerance. With respect to adaptations to salt stress, non-succulent halophytes include trees and woody shrubs such as *Tamarix spp., Artemisia monosperma, Calligonum spp*

Recretohalophytes: Characterized by their morphological specialization for excretion of salt, these species have salt glands or bladder cells on the leaf surface since they are morphologically specialized, those structures lie in between seawater and freshwater salt concentration, for this reason those characteristics are well differentiated, they can do active ions transport hence impact ionic toxicity, species include *Atriplex vesicaria, Limonium perezii, Tamarix nilotica* etc.

Euhalophytes: Used as a term for halophytes that show all the possible strategies and adaptations (succulence, excretion and exclusion) during

Halophyte development, they provide examples to show something about convergent evolution for saline adaptations, species include *Suaeda salsa, Halocnemum strobilaceum*.

- **Phylogenetic and Taxonomic Considerations**
  The taxonomic breadth of halophytes is large, spanning over 100 families within monocots and dicots. Halophytes are dominantly represented in the *Amaranthaceae, Chenopodiaceae, Plumbaginaceae, Poaceae* and *Tamaricaceae* families. Phylogenomic analyses reveal that salt tolerance has evolved independently in different lineages, mostly through genome duplication and neofunctionalization of stress-responsive genes including transcription factors (DREB, MYB), ion transporters (SOS1, HKT1, NHX) and reactive oxygen species scavenging antioxidant enzymes.
  While glyophytes and halophytes under saline conditions realize differences at the transcriptome level, the species level differences could be correlated to the activity of ABA signaling, osmolyte biosynthesis, and membrane transport- related genes that were upregulated during saline conditions. The molecular strategies that promote halophytism, and how that knowledge can be translated for crop genetic engineering into non-halophyte species, is changing rapidly.

Table:1 Predominant family of Halophytes and their representative species

Family	Species
Amaranthaceae	*Allenrolfea occidentalis, Arthrocnemum machrostachyum, Atriplex sp., Suaeda sp., Salsola sp., Haloxylon sp.*
Tamaricaceae	*Tamarix sp.*
Poaceae	*Urochondra sp., Sporobolus sp., Aleuropus sp., Spartina alterniflora*
Leguminosae	*Trifolium sp., Prosopis sp., Desmodium sp.*
Solanaceae	*Solanum chilense*

- **Implications of Classification for Applied Research:** The classification of halophytes is not just of taxonomic consideration, but is of applied concern for saline land reclamation, sustainable agriculture, and climate change. Exploring the adaptive diversity of halophytes allows for their optimization for use in:
  - Phytoremediation of salt-affected soils
  - Domestication and breeding of salt-extracting food, fodder, and biofuel crops
  - Protecting coastal and arid ecosystems from increasing salinization

  Using halophyte biology in land-use planning and agroecological modelling provides a significant opportunity to achieve productive agriculture in saline-prone amounts [15].

Mechanisms of Salt Tolerance in Halophytes

Halophytes have developed a complex and integrated suite of mechanisms to withstand and thrive in saline environments where similar non-halophytic species would fail. These mechanisms alleviate the detrimental effects of salt stress imposed by the saline environment for example osmotic imbalance, ion toxicity and oxidative damage, and correspondingly support continuous growth and development and reproduction where high saline environments persist. The processes of halophytes with respect to salinity may be grouped into categories of Ion homeostasis and compartmentalization, osmotic adjustment, antioxidant defense, morphology and molecular regulation [16][17].

- **Ion Homeostasis and Compartmentalization**
  Ion toxicity, especially Na^+ and Cl^- excess in the cytosol, is one of the largest challenges under saline conditions. Halophytes homeostate ions through highly selective uptake, extrusion, and compartmentalization processes. At the root level, they restrict Na^+ entry by selectively employing ion channels and ion transporters that prioritize K^+ over Na^+, such as HKT-type transporters [18]. When Na^+ enters into the plant, the Salt Overly Sensitive (SOS) pathway becomes activated, and in particular, the SOS1 plasma membrane Na^+/H^+ antiporter can extrude Na^+ from root cells or load Na^+ into the xylem for shoot transport in a regulated manner [19].
  To avoid Na^+ harming cytoplasmic processes, halophytes wilt excess ions, such as Na^+, into vacuoles with tonoplast-localized Na^+/H^+ antiporters (e.g. NHX1), which swim on the aquatic potential from vacuolar H^+-ATPases and H^+-pyrophosphatases. While this vacuolar sequestration detoxifies the cytoplasm, it also osmotic regulation. Some halophytes even have specialized salt-secreting structures (e.g. epidermal salt glands and bladder cells) to excrete the salts they have accumulated onto the leaf surface [20].

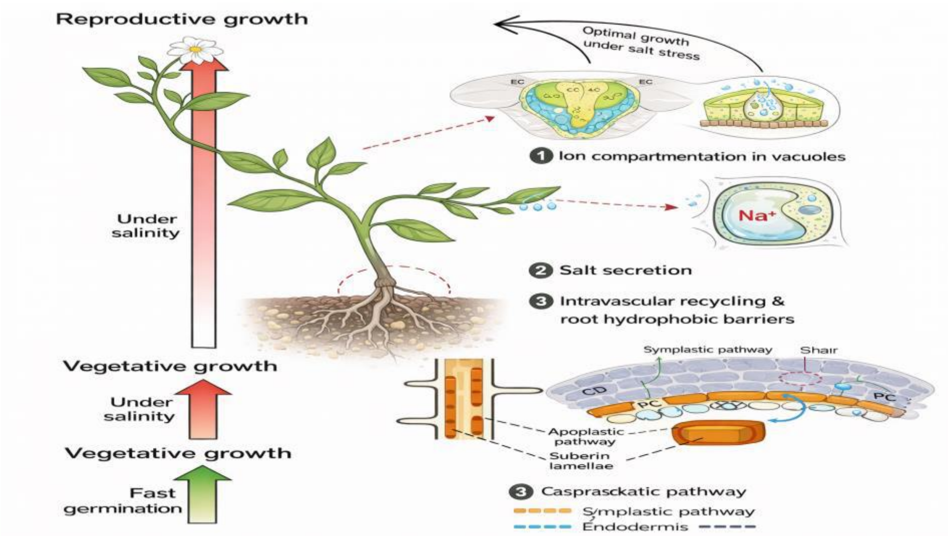

Figure 1. Halophytes exhibit salt tolerance through: (1) Ion compartmentalization—Na^+ accumulates in vacuoles, protecting the protoplast; (2) salt secretion—via multicellular salt glands (SC, AC, IC, OC, EC, MC) and bladders and (3) ion recycling and root apoplastic barrier—Casparian strip and suberin lamellae block apoplastic flow, directing ions through symplastic route via passage cells (PC). Other key structures: XY (xylem), CO (cortex), EN (endodermis).

Osmotic Adjustment

High external solute concentrations as a result of saline soils will cause water to move from plant cells resulting in osmotic stress and loss of cell turgor. To counter osmotic pull of water, halophytes accumulate organic osmolytes, sometimes called compatible solutes, that do not interfere with cellular metabolism when present at high levels [21]. Halophyte osmolytes include sugars (e.g. trehalose and raffinose), polyols (e.g. mannitol and sorbitol), proline and glycine betaine.

The accumulation of these compounds acts to lower the cell's osmotic potential and allows the plant to take up and maintain water when in saline conditions. Compatible solutes do not only stabilize osmotic pressure, they protect macromolecules and the integrity of cellular membranes, they also aid Osmo protection through their role as molecular chaperones and ROS scavengers [22]. Synthesis of compatible solutes is tightly regulated (and often stress-inducible), which means that synthesis of compatible solutes will usually involve the induction of a regulated set of biosynthetic enzymes associated with compatible solute production after exposure to salt environments. The cellular trafficking and diffusion of osmolytes is mediated by solute transporters, therefore allowing for maximal Osmo protection [23].

Antioxidant Defense and Reactive Oxygen Species (ROS) Scavenging: Salt stress induces excessive reactive oxygen species (ROS), such as superoxide anions (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (·OH), that cause oxidation damage to lipids, proteins, and nucleic acids [24][25][26]. Halophytes have the acquired attention of biologists, because of their exceptional and organized oxidative stress resistance processes (antioxidant defense systems). Antioxidant defenses have been shown to contain both enzymatic antioxidants, including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and also non-enzymatic antioxidants that comprise of ascorbate, glutathione, tocopherols, and flavonoids [27][28]. The combined action of both antioxidant processes governs the process of inhibition of superoxide, hydrogen peroxide, and hydroxyl free radical production as well as help prolong redox homeostasis. In addition, halophytes often display higher rates of expression of genes that encode antioxidant enzymes during salt stress, reiterating their transcriptional regulation mechanism of action towards ROS detoxification [29].

Morphological and Anatomical Adaptations: Partially evergreen halophytes have unique morphological and anatomical characteristics that help them live in ecosystems with high salinity. Succulence—thick fleshy leaves or stems that store water and dilute intracellular concentrations of salts—is perhaps the most common morphological adaptation. Succulence reduces cellular toxicity to salts and enhances water use efficiency [30].

Other structural adaptations, such as reduced leaf surface area, thick cuticles, sunken stomata, and trichomes, have also reduced transpiration and therefore, water loss. Some halophytes have a much larger, bulky root system or root systems that are deep enough to access fresh water bodies or allow for salt exclusion. Additional mechanisms of morphological adaptations include salt bladders or salt glands on leaf surfaces that excrete excess salts, which reflects how poorly or poorly salt tolerant a halophyte is based on the habitat [31].

Molecular and Genetic Regulation of Salt Tolerance: Halophyte salt tolerance is strongly established in part by a complex repository of salt-reflective genes and transcriptional regulators. Ion transport genes (i.e. SOS1, HKT1, NHX1), osmolyte biosynthesis (i.e. P5CS for proline, BADH for betaine), antioxidant genes, and hormones are normally regulated upward in response to saline environments. It is the transcription factors such as DREB, bZIP, NAC, MYB, and WRKY families that facilitate the transcriptional reprogramming needed for stress acclimation [32].

Among halophyte transcriptomic and proteomic studies, many stress-responsive genes are constitutively expressed or can be induced, typically at baseline rates greater than glycophytes [33]. The epigenetic modifications of DNA methylation and histone acetylation may supply the stress memory and long-term acclimation. Finally, those small RNAs & microRNAs (miRNAs) may also be implicated as important post-transcriptional regulators for halophyte salt stress [34].

Molecular Basis of Salt Tolerance in Halophytes

High salinity environments do not only elicit physiological and biochemical adaptations in halophytes. The ability to co-exist with salinity, in halophytes, is likely influenced by complex molecular networks composed of salt-responsive genes, transcriptional and post-transcriptional regulatory networks, signal transduction pathways, and hormonal interactions. Establishing the molecular basis for salt tolerance in halophytes is an important step to characterize the genetic determinants that could be applied to develop salt tolerant crops using biotechnological strategies [35].

Salt-Responsive Gene Families: Halophytes, which often possess unique adaptive traits, show differential expression of a wide range of genes under salt stress. Many of these genes are not found or only weakly expressed in glycophytes, including genes involved in ion transport, osmolyte biosynthesis, antioxidative defense, and membrane stabilization [36]. For example, the SOS1 (Salt Overly Sensitive 1), HKT1 (High-Affinity K^+ Transporter 1), and NHX1 (Na^+/H^+ exchanger 1) genes are important genes involved in ion homeostasis [37], whereas proline and glycine betaine biosynthesis utilize P5CS (Δ^1-pyrroline-5-carboxylate synthetase) and BADH (Betaine aldehyde dehydrogenase), respectively [38].

For these above-mentioned genes in halophytes, there can be a constitutive expression or onset of rapid transcription time points after the onset of salt exposure, implying a working system for early stress response and efficiency when compared to glycophytes. Comparative transcriptomic studies in halophytes versus glycophytes have shown that halophytes often have more than one isoform or undergo increased promoter activity of the same particular stress-related gene or function [39].

Transcription Factors and Regulatory Networks: Salt tolerance is regulated at the transcriptional level by a number of different families of transcription factors (TFs) that activate or repress downstream target genes [40]. The primary classes of TFs in halophytes include members of the DREB (Dehydration-Responsive Element-Binding) protein family, NAC, MYB, bZIP, and WRKY families [41]. These TFs bind to specific cis-regulatory elements in their promoter regions of salt-responsive genes and either induce or repress gene expression in the face of salinity stress. For example, DREB2A can activate stress-inducible genes through an ABA-independent cascade while the AREB/ABF TFs function in ABA-dependent signalling pathways [42]. The coordinated action of these transcription factors forms a regulatory cascade that modulates complex physiological responses to salinity.

Signal Transduction Pathways: Salinity perception starts at the plasma membrane, where salt sensors trigger signal transduction cascades comprised of calcium signaling, kinase activation, and secondary messengers [43]. One of the best studied signaling modules in halophytes is the Salt Overly Sensitive (SOS) pathway [44]. It consists of SOS3 (calcium binding sensor protein), SOS2 (serine/threonine kinase), and SOS1 (Na^+/H^+

antiporter). Under salt stress, elevated cytosolic Ca^{2+} levels activate SOS3 which subsequently activates SOS2. The SOS3-SOS2 complex phosphorylates and activates SOS1, which leads to Na^+ extrusion from the cytosol.

Besides SOS, halophyte responses to salt stress also involve Mitogen-Activated Protein Kinase (MAPK) cascades, calcium-dependent protein kinases (CDPKs), and cGMP signaling [45]. These signaling networks transmit and integrate obvious environmental signals and then mediate appropriate downstream responses.

Role of Hormonal Regulation: Phytohormones act as vital components of the stress signalling pathways and the resulting adaptive responses of plants. In halophytes, the hormonal crosstalk upon salinity conditions means that hormones can impact gene expression, growth, and associated metabolic pathways. Abscisic acid (ABA) is one of the major phytohormones that accumulates rapidly during salt stress, resulting in stomatal closure and the expression of ABA responsive gene products. Regardless of the specific pathways for each hormone, crosstalk occurs in a manner that connects ABA signalling with other hormones like ethylene, salicylic acid (SA), jasmonic acid (JA), cytokinins and auxins, all of which are important for the modulating roles as well [46][47].

It is interesting that there are often different hormone history/status profiles when comparing halophytes to glycophytes, such as the initial basal amount of ABA displaying higher values, or perhaps glycophytes have a better hormonal balance or cope with the same salinity more effectively than halophytes. It is important to remember that hormonal signalling is often coupled with TF networks and second messengers and works in a nice interplay.

Epigenetic and Post-Transcriptional Regulation: Emerging evidence reveals the involvement of epigenetic modifications- such as DNA methylation, histone acetylation, and chromatin remodelling- in halophyte salt tolerance. Epigenetic modifications dynamically modify the accessibility and transcriptional activity of genes in response to salt stress through gene regulatory reprogramming [48].

Furthermore, microRNAs (miRNAs) and long non-coding RNAs (lncRNAs) post-transcriptionally regulate salt-responsive genes. MicroRNAs, such as miR398 and miR393, target transcripts that are involved in ROS detoxification and hormone signalling, respectively. The potential regulatory role of non-coding RNAs further contributes complexity to the halophyte stress response.

Application of Halophytes in Agriculture and Biotechnology

Halophytes are naturally salt-tolerant plants. They exhibit unique physiological, morphological, biochemical, and genetic characteristics which make them ideal candidates for a variety of uses in agriculture, environmental remediation, and industrial biotechnology. With salinization globally affecting roughly 20% of all irrigated land area and that proportion expected to increase with climate change, rising sea levels, and poor irrigation practices, we must find novel methods to utilize saline land areas. Halophytes offer one viable sustainable solution, as they can grow naturally without competition from traditional crops on saline and arid lands, which may greatly expand food production, soil reclamation, biofuels, and sources of genetic traits [49][50].

Halophytes as Genetic Resources for Salt-Tolerant Crop Development: Euryhaline organisms like many crops (glycophytes) are intolerant of salt, exhibiting great sensitivity to osmotic and ionic salinity stress. Halophytes are salt-tolerant because they have developed salt tolerance mechanisms, which are expressed/regulated by genes and regulatory pathways. Advances in molecular studies and transcriptomics have revealed a considerable number of salt-responsive genes from halophytes that are either absent or at least less active in traditional glycophytes. These genes include ion transporters (e.g., SOS1, NHX1, HKT1;1), osmotic protective biosynthetic enzymes (e.g., P5CS, BADH), antioxidative enzymes (e.g., SOD, CAT) or stress- responsive transcription factors (DREB, MYB, NAC) [51][52]. Modern biotechnological approaches, including transgenic technologies and genome-editing technologies (e.g., CRISPR-Cas systems) are being adopted to insert these genes into major crops (rice, wheat, maize, tomato, etc.) that can enhance their salt tolerance. For example, AtNHX1 has been over expressed in rice, which improved salt exclusion and yield in salinity. Furthermore, halophyte transcriptional regulators when expressed in glycophytes have been able to regulate a broader range of downstream stress-response pathways. These halophyte genetic tools are critical for breeding salt-resilient crops to combat global salinization.

Halophytes as Alternative Crops for Saline and Marginal Lands: One of the most practical ways to utilize halophytes is to cultivate them as crops straight out as alternative crops in the salt-affected regions where traditional agriculture fails. Several halophyte species have economic value and are already being cultivated for food, fodder, fiber, oilseed, and even medicinal products. Examples of halophytes that are evaluated and investigating in saline and dryland areas include *Salicornia bigelovii, Atriplex hortensis, Suaeda fruticosa, the quinoa plant (Chenopodium quinoa)*, and *Mesembryanthemum crystallinum* [53].

Salicornia bigelovii provides high-value food-grade edible oil and protein-rich meal from its seeds and can be grown using seawater, which makes it a candidate for sustainable coastal agriculture. *Atriplex* spp. are also protein-rich, providing forage for livestock in dry degraded rangelands. *Quinoa* is a facultative halophyte and is already consumed globally as a pseudocereal known for its highly nutritious qualities, and although it is not only approximated salt-tolerant. They can also be cultivated in intercropping systems or as rotation crops.

Phytoremediation and Ecological Restoration of Saline and Polluted Lands: Halophytes provide a low-cost and natural solution to phytoremediation—the employment of plants in the removal, stabilization, or degradation of contaminants from water and soil. As biological desalinators and detoxifiers, they can accumulate and store in vacuoles or certain tissues excessive salts and poisonous ions like Na^+, Cl^-, Cd^{2+}, and Pb^{2+} [54][55]. Species such as *Sesuvium portulacastrum, Tamarix spp.*, and *Suaeda maritima* can be demonstrated to extract and tolerate salt and metal ions in high concentrations and are therefore good options for remediating saline, sodic, and heavy-metal-polluted soils.

In addition, halophytes are also important for ecological rehabilitation as they stabilize sand dunes, discourage coastal erosion, and enhance soil fertility by depositing organic matter and influencing the rhizosphere. They also improve soil structure and microbial activity due to their deep roots, allowing them to restore degraded environments progressively. In dry areas and coastlines, halophytes combined with mycorrhizal inoculants can increase survival rates and speed up land reclamation.

Halophytes in Bioenergy and Green Industrial Applications: Halophytes are emerging as a sustainable biofuel and bioenergy feedstock because of their high growth rates, high biomass production, and capacity to cultivate on salt-affected or non-arable lands with the use of brackish water or saline water. The lignocellulosic biomass of *Spartina alterniflora*, *Kosteletzkya virginica*, and *Distichlis spicata* can be upgraded to generate bioethanol, biogas, or biochar [49]. Halophytes with high oil content such as *Salicornia bigelovii* and *Crithmum maritimum* also yield seeds containing 25–30% oil with biodiesel potential [56].

Besides energy, halophytes are also important in the green chemical sector as sources of secondary metabolites, biopolymers, and natural dyes. Halophytes-based compounds like flavonoids, saponins, alkaloids, and terpenoids possess antimicrobial, antioxidant, anti-inflammatory, and anticancer activities. These bioactives are found useful in pharmaceutical formulations, cosmetics, and functional foods. The cellulose and hemicellulose from halophytes are also being investigated as bioplastics, hydrogels, and biodegradable packaging films [57].

Contribution to Climate Change Mitigation and Carbon Sequestration: Halophytes make important contributions to global climate change mitigation by sequestering carbon, particularly in salt marshes, mangroves, and coastal wetlands. These environments are "blue carbon sinks," sequestering CO_2 from the atmosphere and storing it as biomass and sedimentary layers for extended periods. *Spartina alterniflora, Avicennia marina*, and *Juncus spp.* are some of the high-primary-producing species that have strong below-ground biomass, allowing for long-term carbon storage [58].

In addition, halophytes mitigate greenhouse gas emissions by stopping soil degradation, reducing fertilizer leaching, and enhancing nutrient cycling. By their contribution to coastal buffer zones, the effects of storm surges, sea-level rise, and salinity intrusion are curbed, thus enhancing ecosystem resilience and biodiversity conservation. All these make halophytes important partners in the achievement of global climate action and sustainability goals.

Prospects for the Future and Challenges

Being able to tolerate extreme environmental conditions, halophytes provide a solution to ensure the sustainable production of food and environmental management in view of the upcoming global challenges like climate change, soil salinization, water shortage and growing population. Their capability to survive under salt-affected soils and harsh conditions makes them the keystone species for the agriculture of the future, environmental biotechnology and ecosystem restoration. Despite this potential, the industrial use of halophytes in the broadest context (i.e., replacing otherwise-used crops) is confronted with a series of scientific-technical, socio-economic, and policy-related barriers.

Increasing genetic/genomic tools: Despite salt tolerance mechanisms in numerous species of halophytes are analyzed, the genetic and genomic resources are relatively less compared to the model and crop plants. The whole-genome sequencing, transcriptomics, proteomics and metabolomics of different halophyte species should be employed more broadly to elaborate the regulatory networks and adaptive pathways underpinning salt tolerance [59].

Bloodgate further said that the next step in research would be the construction of high-quality reference genomes, the detection of salt-tolerant QTL (quantitative trait loci), and the production of molecular markers for breeding programs [60]. Similarly, gene-editing tools like the CRISPR-Cas systems should be used to demonstrate and validate critical salt tolerance genes and their regulatory elements, and facilitate specific improvement of trait(s) in halophytes and glycophytes.

Incorporating Halophytes into Agroecosystems: Despite their hardiness, introducing halophytes into broad-acre agriculture is in its early stages. Limitations are low germination of seed in hypersaline conditions, low biomass in certain species, non-existence of mechanized farming practices, and low price of halophyte products on the market. Also, the majority of halophytes remain largely undomesticated, and there are limited guidelines for their culturing, harvesting and post-harvest processing [61].

Future work should focus on the domestication of wild halophytes by selecting and optimizing breeding and agronomy. Integrated farming systems associating halophytes with aquaculture (e.g., halophyte–aquaculture systems) or agroforestry may increase productivity and sustainability in coastal saline-affected areas.

Environmental and ecological issues: Although halophytes have advantages on ecology such as soil rehabilitation and erosion prevention, the utilization of halophyte is still debated when they are introduced into a new environment. Some halophyte species are invasive when introduced outside of their native habitats, threatening the native flora and fauna and ecosystems. Additionally, if not well controlled, the regular use of salty water for irrigation might cause additional secondary salinization or soil quality degradation [62].

The ecological impact assessments, species-specific risk assessments and sustainable water management practices are necessary to make sure that the halophyte-based systems will not result in unintended harmful consequences [63].

Improving Biotechnological Use: So far, the bio-technological potential of halophytes is huge but still underutilized (as bioenergy application, phytoremediation, pharmaceuticals and as functional food). Limitations include low extraction efficiency, poor scalability and variability of the resulting bioactive compound yields which prevent widespread commercialization. Additionally, relatively less attention is given for biofuel conversion technologies of halophyte biomass as compared to that of the traditional bioenergy crops [64][65].

To address these issues, interdisciplinary studies are required to improve the extraction procedure, upscale cultivation systems, and modify metabolic pathways in halophytes for increased secondary metabolite yield. These salt-adapted biosynthetic modules, including all members of the adenosine nucleotide and aromatic amino acid pathways, are candidates for heterologous reprogramming into microbial or plant chassis by synthetic biology.

Policy, economic incentives, and public awareness: The mainstreaming of halophyte is a success that need the enabling policies, incentives and public private participation. Halophytes need to be recognized by the Governments and agricultural organizations as a strategic resource for national food and environmental security. Investment in halophyte research, infrastructure development and farmer education processes are critical to promote interest and lower the adoption barrier. Awareness of the nutritional, ecological and economic benefits of halophyte products must be raised through outreach and cooperation with industry, NGOs, and academia.

Conclusion

Salt-tolerant plants, such as halophytes, have a great potential to help solving some of the most urgent global problems in the 21st century, including soil salinization, climate change, food insecurity and deterioration of marginal lands. Through their specific physiology, biochemistry and molecular biology where ion's homeostasis, osmotic adjustments, antioxidative systems of defense and some valuable way of salt compartmentalization, halophytes manage to not simply survive, but to thrive, where the majority of crops cannot succeed.

Their differentiation into obligate, facultative and habitat-indifferent halophytes demonstrates the wide range of adaptive mechanisms among species, harboring divergent genetic and agronomic potential. As bioresources, halophytes have broad potentials, from genetic pools for breeding salt-tolerant crops and goods for cultivation in saline soils, and for phytoremediation and biofuel, nutraceutical, and pharmaceutical use and for blue carbon accumulation and climate change mitigation.

However, the translational pipeline of halophyte research and its commercialization are mostly challenged by several bottlenecks. However, poor genomic resources, lack of efforts in developing agronomical practices, inefficient economic yield and lack of supports limit their universal application. Furthermore, the potential impact on introduced alien ecosystems and sustainability of soil quality also requires careful consideration.

All the above studies clearly indicate that multiple interdisciplinary science should be combined such as plant physiology, molecular biology, genetic engineering, soil science, environmental policy, and socioeconomics to unlock the potential of halophytes. Investment will be required on omics sciences technologies, technological interventions in biotechnology, field-level trials, as well as farmer's training. Furthermore, inclusion of halophytes in sustainable agrosystems especially in the coastal and saline zones can significantly add to food supply, ecological stability and livelihood security.

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