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Review

Exploring the Potentials of Halophytes in Addressing Climate Change-Related Issues: A Synthesis of Their Biological, Environmental, and Socioeconomic Aspects

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Abstract: Halophytes are naturally salt-tolerant plants with immense potential to become alternate crops for saline lands. While their economic benefits have gained increasing attention, often, the roles of halophytes in addressing different climate change-related issues are overlooked. Halophytes can be a renewable resource for clean 'carbon-neutral' energy by serving as biofuel or biogas feedstock, help in the sequestration of rising CO_2 as well as the phytoremediation of various pollutants, can be a good source of food and fodder thereby help in achieving food security in arid/saline areas, can help in protection and biodiversity conservation in various ecosystems, and can provide livelihood to poor local communities inhabiting barren lands. This review also attempts to highlight various usages of halophytes in connection with a global change perspective. However, there are still many challenges such as economic viability, customer preferences, environmental impacts, and scale-up challenges, which need further research, innovation, effective policies, and collaboration. In general, this review provides a synthesis of various biological, environmental, and socioeconomic aspects of halophytes to fully exploit the potential of halophytes for human welfare and combating global climate changes.

Keywords: biofuel; carbon sequestration; climate change; food security; halophyte; salinity

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1. Introduction

Halophytes are salt-tolerant plants that thrive in habitats with highly saline (≥200 mM NaCl equivalent; *sensu* [1]) soil or water [2]. They are commonly found in salt marshes, coastal dunes, sabkhat, and inland salt-flats, where they come in contact with saline water through their roots and/or by salt spray [1,3]. These plants differ from glycophytes (i.e., salt-sensitive plants such as most crops) in terms of their anatomy, physiology, biochemistry, and molecular biology [1,4,5]. Common examples of halophytes include mangroves (e.g., *Avicennia marina* and *Rhizophora mangle*), coastal marsh plants (e.g., *Arthrocnemum macrostachyum*, *Salicornia* spp., and *Spartina* spp.) and many fast-emerging crop candidates such as quinoa (*Chenopodium quinoa*).

Halophytes are important for the protection of coastal habitats, where they may act as sand dune binders to prevent sand erosion and also as a barrier to seawater incursion into freshwater habitats [3,6]. Halophytes also provide food and shelter for a large number of aquatic and terrestrial animal species. They can also be used for human welfare in several ways such as crop alternatives, livestock fodder, feedstock for renewable energy purposes, and the phytoremediation of polluted/saline lands, etc. [7,8]. Recently, Garcia-Caparros et al. [9] reported in their review 918 uses of halophytes. In addition, these plants can also help humanity to combat the impacts of global climate changes, which are being intensified with every passing year [10,11]. The aim of this review is to provide a comprehensive overview of the current knowledge and future prospects of halophytes in relation to climate change and its impacts on biodiversity, ecosystem services, food security, and human well-being. We found generally little information about economic viability, customer preferences, environmental impacts, and scale-up challenges about halophyte utilization. Based on this literature search, we highlight various biological, environmental, and socioeconomic aspects of halophytes, in connection with global climate changes-related issues. This review also attempts to identify the knowledge gaps and provide recommendations to promote the use of halophytes in resolving various climate change-related issues.

2. Methodology for Literature Search

We searched the literature with the help of various electronic databases such as Google Scholar, Web of Science, Crossref, and Scopus using keyword filters such as "halophytes", "halophytes and climate change", "halophytes and carbon sequestration", and "halophytes and economic potentials", etc. Document types were restricted to articles and reviews with timespan setting of "all years". Keywords were searched in titles and keywords. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) protocol, as detailed in Koricheva and Gurevitch [12], was followed for literature search and selection. Article titles and abstracts were manually screened to exclude articles not related to the topic. We selected the most relevant articles published in scholarly journals, dealing with mechanisms and different uses of halophytes under various circumstances. A similar approach was also used by Chassagne et al. [13], Raza et al. [14], and Angon et al. [15].

3. Biological Aspects of Halophytes

3.1. Distribution and Classification

Halophytes are found in both coastal as well as inland saline habitats. They are distributed in all continents of the world except Antarctica [16]. Asia has the highest number (15%) of halophyte species [17]. An updated list/database of halophytes can be accessed at eHaloph (https://ehaloph.uc.pt/; accessed on 18 December 2023). They are variously classified and, according to Grigore [5], attempts to classify halophytes date back to 1754, when Hedenberg classified coastal halophytes into marine (continuous contact with seawater) and maritime (occasional contact with seawater) species in his PhD thesis. Among various classification attempts (Figure 1), Chapman [18] coined a practical classification of halophytes into the following categories based on the salinity level of their habitats: (1) Miohalophytes: plants growing in habitats of low salinity (<1% NaCl equivalent), (2) Euhalophytes: plants of highly saline habitats (≥1% NaCl equivalent). Waisel [19] classified halophytes based on their responses to salinity into Euhalophytes (i.e., salt-requiring or -resisting halophytes) and Pseudohalophytes (i.e., salt-avoiding halophytes). Eco-physiological aspects have also been used to categorize halophytes into obligate (salt-requiring), facultative (survive salinity but grow better under non-saline conditions) and habitat-indifferent (found in both non-saline and saline habitats) halophytes [20]. Yensen and Biel [21] classified halophytes based on their ability to absorb or exclude salts into the following categories: (1) excluders (i.e., plants excluding salt at the root level), (2) accumulators (i.e., plants absorbing salt from soil and accumulating it in the tissue), and (3) conductors (i.e., plants absorbing salt from soil and excreting it at the leaf surface). Grigore and Toma [22] classified halophytes based on their morpho-anatomical adaptations into (a) extreme halophytes (i.e., with well-developed irreversible or reversible morpho-anatomical adaptations), (b) mesohalophytes (i.e., with intermediary anatomical adaptations), and (c) glycophytes (i.e., no morpho-anatomical adaptations to survive salinity). Halophytes can also be divided into succulent and non-succulent based on their tissue water content. For chronological details about the various classification attempts for halophytes, see Grigore [5]. In summary, halophytes are classified variously based on a number of criteria.

3.2. Morphological Features of Halophytes to Cope with Salt Stress?

Halophytes have evolved several morphological features (Figure 2), which enable them to survive harsh environmental conditions of their saline habitats [2,3,23–25]. A number of halophytes such as those belonging to the family Amaranthaceae often have reduced or sometimes no leaves to minimize water loss through transpiration [26]. Examples of halophytes with reduced leaves are the *Salsola* and *Suaeda* species; whereas the *Haloxylon* and *Arthrocnemum* species are good examples of halophytes with no leaves [27]. Similarly, a number of halophytes, especially those from the Poaceae family, possess a large number of glandular or non-glandular trichomes, which are hair-like structures on their leaves and stems to reduce water loss and reflect sunlight [26]. Halophyte grasses such as *Aeluropus lagopoides* and *Urochondra setulosa* are good examples of halophytes with trichomes on their leaves. In addition, many dicot halophytes have salt glands or bladders on their aerial parts, especially the leaves, which help in excreting excess salt from the plant body [28]. Many dicot halophytes including mangrove, *Avicennia marina*, possess salt glands on their leaves to secrete excess salt; whereas quinoa has a large number of epidermal bladder cells to secrete excess salts. A large number of halophytes have succulent leaves and stems that store water and help maintain turgor and dilute salts in the plant cells [1,3]. Halophyte species belonging to *Suaeda*, *Salsola*, *Anabesis*, and *Zygophyllum* have succulent leaves [29], while species from *Arthrocnemum*, *Haloxylon*, and *Halocnemum* have succulent stems [27]. Large variations in the use of succulence for surviving changes in soil/water salinity may exist. For instance, under increasing salinity, halophyte grasses generally reduce above ground biomass more than the below ground biomass with less dependence on the succulence strategy [30], whereas the dicot halophytes show a broad variation in stem and leave succulence depending on the root zone salinity [2,3,23–25].

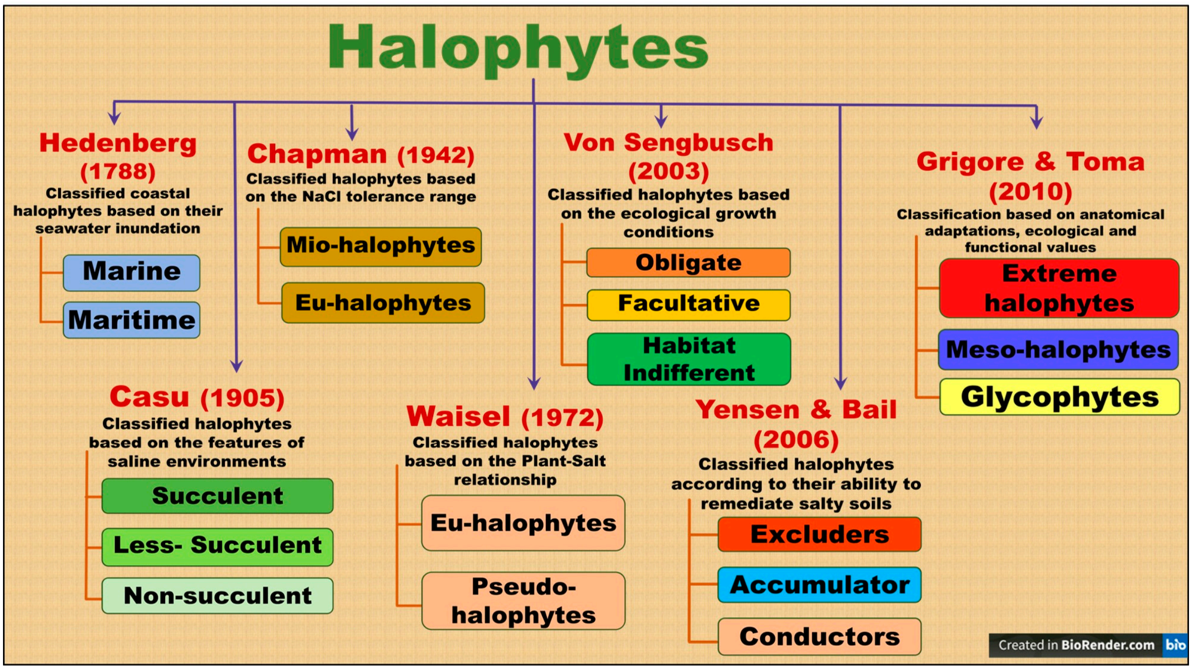

Figure 1. Some common classification schemes of halophytes.

3.3. Physio-Chemical and Molecular Mechanisms of Halophytes to Cope with Salinity

Halophytes utilize many cellular, physiological, biochemical, and molecular processes to cope with high salinity levels [23,31]. Ion homeostasis and transport is considered one of the key aspects of halophyte high-salinity tolerance. Halophytes maintain ion homeostasis by selectively absorbing or excluding certain ions through transporters [1,3,4]. They also compartmentalize toxic Na^+ and Cl^- ions in the apoplast and vacuole of different tissues to prevent toxicity [1,10]. HKT (High-Affinity K^+ Transporter), SOS1 (Salt Overly Sensitive 1), NHX (Na^+/H^+ Exchanger), and HAK (High-Affinity K^+ Transporter) are some widely reported transporters, which help halophytes to prevent a deficiency of essential minerals and get rid of toxic ones [3]. An increase in the membrane-bound transporter genes vacuolar *NHX* and plasma membrane *NXH* or *SOS1* was evident under moderate (373 mM NaCl) but not under high (747 mM NaCl) salinity in halophyte grass *Aeluropus lagopoides* [32]. Similarly, the expression of *HAKs* in a succulent halophyte *Mesembryanthemum crystallinum* was up-regulated under salinity and K^+-starved conditions [33].

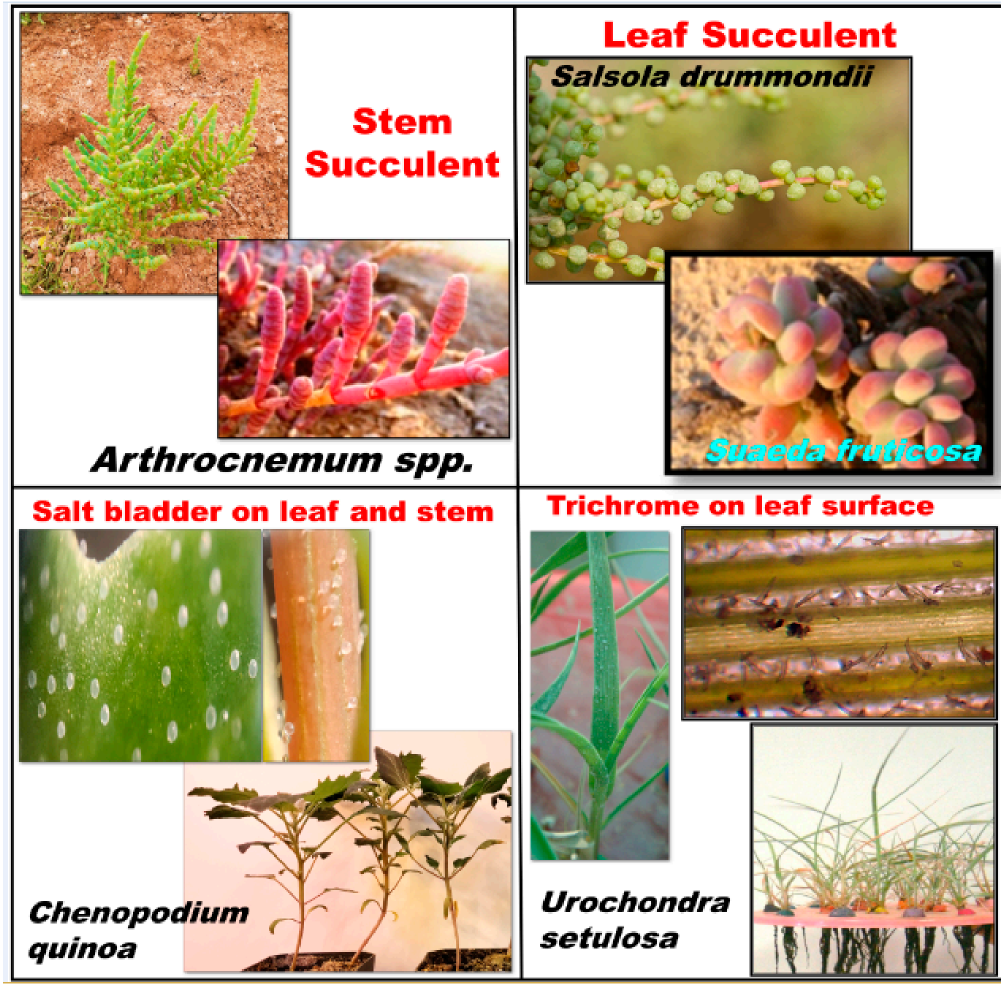

Figure 2. Some common morphological adaptations of halophytes.

Halophytes synthesize compatible solutes or osmolytes such as proline, glycine betaine, and sugars to maintain an osmotic balance, which is essential to cope with hyperosmotic conditions under high salinity [1,34]. The accumulation of these compatible solutes in cytosol, alongside the compartmentalization of salts in the vacuole and apoplast, help achieve osmotic adjustment [1]. An increase in proline, glycine betaine, and/or sugars has been observed in many halophytes such as *Suaeda fruticosa* [35], *Prosopis strombulifera* [36], and *Atriplex halimus* [37].

Stomatal regulation is another important aspect of the high-salinity tolerance of halophytes. Halophytes have efficient control over stomatal opening and closing to minimize water loss through transpiration, thereby increasing water use efficiency [38,39]. They may substitute K^+ for Na^+ for stomatal regulation [30]. Many halophytes can also show decreased stomatal density to improve their water use efficiency under saline conditions [38].

Environmental stresses including salinity cause the excessive production of reactive oxygen species (ROS), which are partially reduced or excited forms of molecular oxygen with a high potential to oxidatively damage different cellular components if not regulated to low levels [35]. Halophytes possess efficient antioxidant defense systems to minimize oxidative damages caused by excessive ROS under high salinity [3,40,41]. Superoxide dismutases (SODs), catalases (CATs), and different peroxidases (PODs) are important antioxidant enzymes, while ascorabte (AsA), glutathione (GSH), tocopherols

(Toc), polyphenols, and carotenoids are key non-enzymatic antioxidants of the plant cells including those of halophytes [3,35]. An increase in various antioxidant enzymes as well as non-enzymatic antioxidants is often reported in halophytes such as *Limonium stocksii* [42] and *Atriplex portulacoides* [43] under saline conditions.

Specific genes implicated in stress responses, such as those encoding ion transporters, osmolyte production, and antioxidant enzymes, are up-regulated in halophytes [1,44]. For instance, Diray-Arce et al. [45] reported 44 up-regulated genes in *Suaeda fruticosa* under salinity, a number of which were related to ion transport, transcription, antioxidant defense, and photo-protection. Furthermore, halophytes display complex signal transduction pathways, which regulate gene expression and protein synthesis under salinity stress [46,47]. ROS, Ca^{++}, K^{+}, polyamines, and various hormones have emerged as important signals for the regulation of the salt tolerance responses of halophytes [48–51].

The aforementioned processes work together in halophytes to maintain 'normal' physiological functions under salinity stress. However, above the threshold level of salinity, which varies among species, malfunctioning in the above processes may result and thereby, growth reductions and/or tissue injuries occur [3]. The following are some halophytes which have been extensively studied as model systems for understanding salt tolerance mechanisms:

Arabidopsis thaliana: Despite not being a halophyte, *Arabidopsis thaliana* has been utilized as a model plant in a large number of studies on salt tolerance [52]. It has enabled comparative analyses with salt-tolerant plants to decipher the genetic modifications that permit a halophytic lifestyle [53–55]. *Eutrema salsugineum* (previously known as *Thellungiella salsuginea*): It is a close relative of *Arabidopsis thaliana* that has been proven to be a transformation-competent model with a variety of genetic resources, including high-quality genome assemblies [56]. It has facilitated the deciphering of the genetic modifications leading to halophytism in plants by powerful comparative comparisons with the salt-sensitive *Arabidopsis thaliana* [55,57].

Schrenkiella parvula: It is another close relative of *Arabidopsis thaliana* and has many similarities with *Eutrema salsugineum* and has also been established as a halophyte model [56,58]. It has facilitated powerful comparative analyses with the salt-sensitive Arabidopsis to unravel the genetic adaptations that enable a halophytic lifestyle [59,60].

Salicornia spp.: Salicornia is a genus of succulent halophytes that are widely distributed in coastal areas around the world [61–63]. *Salicornia* spp. have been studied for their exceptional morphological and physiological adaptations to high salinity including succulence as well as for their economic potentials [61,64].

Chenopodium quinoa: It is an Andean halophyte that has gained attention as a nutritious crop with a high protein content [65,66]. It has been studied for its peculiar osmotic adjustment mechanisms under salinity through the synthesis of compatible solutes such as proline and glycine betaine [67]. An increasing number of research studies also exist about its breeding and genomics [68,69].

Suaeda salsa: It is an annual succulent halophyte found commonly in the coastal areas of China and adjoining countries. It has been widely studied for its morphological and physiological adaptations to high salinity, including succulence, ion regulation, ROS homeostasis, and molecular studies [59,70,71].

3.4. Biological Diversity of Halophytes

Halophytes are a small but diverse group of plants that have adapted to high-salinity environments [1]. They exhibit a remarkable diversity of form and functions [72]. For instance, halophytes are found in diverse plant families such as Amaranthaceae, Poaceae, Plumbaginaceae, Plantaginaceae, Aizoaceae, and Brassicaceae [72]. Each family has its own distinct traits and adaptations to survive in environments with high salt. Halophytes also exhibit a wide range of morphological and anatomical adaptations, as detailed above, that help them survive in saline environments [72]. For example, halophytes may or may not be succulent, some possess salt glands and some do not, and lifecycle may also range from annual to perennial [27,72]. Likewise, halophytes also show a wide range of photosynthetic pathways ranging from C_3, through C_4 to CAM [36]. Halophytes also exhibit genetic diversity within and between species [73–75]. Furthermore, genetic studies have revealed variations in genes associated with salt tolerance mechanisms, such as ion transporters and osmolyte synthesis enzymes [32,34,76]. Halophytes occupy diverse habitats, including coastal areas, salt marshes, mangroves, and saline deserts [56,77]. Each habitat presents unique challenges and opportunities for halophyte survival [56].

The high biological diversity of halophytes is important for their utilization in mitigating many global climate change-related problems. Ecosystems that are more biologically diverse have greater resilience to climate change-related weather anomalies. Furthermore, higher amounts of carbon dioxide can be absorbed and stored by ecosystems with high biodiversity than by those with low biodiversity [78]. Since halophytes can grow in arid/saline environments and thus offer alternate sources of income and nutrition to poor communities, they may also contribute to food security in the future [79,80].

4. Environmental Aspects of Halophytes

4.1. Ecological Roles and Functions of Halophytes in Different Saline Habitats

Halophytes play important roles and functions in a variety of saline habitats. For instance, they contribute to the primary productivity and biodiversity of saline habitats [41,81]. Furthermore, halophytes also provide various ecosystem services including carbon sequestration, soil stabilization, water purification, nutrient cycling, and act as habitats for wildlife or fisheries [6,82,83]. Table 1 contains examples of some commonly found halophytes in various types of habitats, whereas the ecological roles of halophytes in the habitat-specific perspective are given below:

- *Mangrove mangles*: Mangroves are woody halophytes found in intertidal zones of tropical and subtropical regions [84,85]. They have pneumatophores (aerial roots), which help them to cope with anoxic waterlogging conditions and also have salt glands to excrete excess salt through their leaves [86]. Mangroves are highly productive ecosystems capable of sequestering large amounts of carbon in their biomass and sediments [87], which is termed blue carbon. Mangroves can store approximately 694 Mg C ha^{-1} blue carbon [88]. They also guard the coastline from erosion, storm surges, and tsunamis. Furthermore, they also provide a habitat for a variety of fishes, crabs, and birds [87].
- *Salt marshes*: Salt marsh halophytes possess succulent leaves, which store water to dilute salts. Salt marshes are also among the highly productive ecosystems with large quantities of blue carbon sequestered in their below-ground biomass and sediments [89]. For instance, salt marshes along Tampa bay, Florida, USA contained as much as 66.4 Mg C ha^{-1} blue carbon [90]. They also buffer the effects of tides, waves, or floods. They are home to a variety of insects, mollusks, and birds [91].
- *Coastal Sand dunes:* Plants growing on the coastal sand dunes are adapted to harsh environments, characterized by frequent sand and wind blasting, low nutrient and water availability, high temperature, lack of shade, salt spray, and high soil salinity [92]. Their adaptations include deep root systems, vegetative growth, high nutrient use efficiency, thick outer layers, trichomes over leaves, and succulent leaves that protect them from sand scour, water loss, and nutrient limitation [92]. Dune halophytes help in increasing the diversity of organisms at both above and below the soil surface due to their roles as sources of carbon and role as hosts for insects, bacteria, fungi, birds, and mammals of various kinds [92]. Halophyte vegetation also covers the sand dunes to reduce the sand erosion/dunes movement to support recreational activities [27,92].
- *Sabkhat or salt flats*: Sabkhat (Singular: Sabkha) are characterized by sparse halophytic vegetation with specialized adaptations [93]. Salt flats are generally low-productivity ecosystems, where halophytes fix soil and provide habitats for some species of insects, reptiles, or birds [93]. Loughland and Cunnigham [94] reported 10 mammal and 21 reptile species from the sabkhat of Arabian Peninsula and 17 mammals and 9 reptiles

from Central Asia. Similarly, Hogarth and Tigar [95] reported the occurrence of insects belonging to Hemiptera, Homoptera, Lepidoptera, and Coleoptera from the sabkhat.

- *Playa:* The playas are often considered synonymous to sabkhat, but differ mainly in geographical and hydrological characteristics [93,96]. Playas are often defined as inland permanent or occasionally inundated saline flats in proximity of a water body such as mountainous lakes [93]. Playa vegetation is halophytic in nature and has adaptations to cope with wet–dry cycles, and thereby, the rapid fluctuations of the environmental variables in these habitats [97]. A large number of playa halophytes are annuals, which endure periods of harsh conditions in the form of seed banks and actively grow when the conditions of the playa are conducive for plant growth such as after sufficient rainfall. Playa halophytes help in the formation of substrates by increasing the soil thickness and enhance the organic content of soil to support the next stage of vegetation succession [97].

Table 1. List of common halophyte species found in different types of saline habitats.

Habitat	Species (Examples)	Reference
Mangroves/mangles	*Avicennia marina*	[98]
	Rhizophora mucronata	
	Ceriops tagal	
	Aegiceras corniculatum	
	Avicennia macrostachyum	[99]
	Avicennia germinans	
	Laguncularia racemosa	
Salt marshes	*Arthrocnemum macrostachyum*	[27]
	Arthrocnemum indicum	
	Aeluropus lagopoides	
	Sprolobolus tremulus	
	Cressa cretica	
	Spartina alterniflora	[100]
	Zostera japonica	
	Sarcocornia quinqueflora	[101]
	Salicornia spp.	[102]
Coastal dunes	*Cyperus conglomeratus*	[27]
	Heliotropium bacciferum	[103]
	Halopyrum mucronatum,	
	Ipomoea pes-caprae	
	Salsola imbricata	
	Suaeda fruticosa	[104]
	Limonium stocksii	
	Aeluropus lagooides	
	Urochondra setulosa	
	Arthrocnemum macrostachyum	
	Cyperus aucheri	
	Halocnemum strobilaceum	
	Halopeplis perfoliata	
	Limonium spp.	

Table 1. *Cont.*

Habitat	Species (Examples)	Reference
Sabkha/salt flats	*Salicornia perennans*	[105]
	Seidlitzia rosmarinus	
	Tetraena spp.	
	Juncus rigidus,	
	Odyssea mucronata	
	Sporobolus spicatus	
	S. consimilis	
	Salsola drummondii	
	Suaeda vermiculata	
	Suaeda aegyptiaca	
	Anabasis setifera	
	Tetraena qatarense	
Playa	*Halogeton glomeratus*	[106]
	Lepidium latifolium	
	Peganum harmala	
	Suaeda heterophylla	[107]
	Salicornia rubra	[108]
	S. utahensis	
	Distichlis spicata	
	Allenrolfea occidentalis	

4.2. Effects of Climate Change Factors on Distribution, Diversity, and Productivity of Halophytes

Despite their high tolerance for salinity, halophytes are vulnerable to the effects of climate change, which can affect their distribution, diversity, and production in complicated and unanticipated ways [109–111]. Rising temperatures are considered one of the key climate change factors affecting halophytes. Temperature rise can directly influence many physiological processes of halophytes, such as photosynthesis, respiration, transpiration, and water use efficiency [112,113]. Temperature can also affect halophytes indirectly by altering their interactions with other biotic and abiotic factors, such as pathogens, herbivores, competitors, soil moisture, and salinity [113,114]. Halophytes' responses to temperature fluctuations may, however, differ depending on the species, population, and ecosystem level. Warmer temperatures may help some halophytes flourish or expand their niche while harming others. For example, Mahdavi and Bergmeier [115] reported the dominance of C_4 species under warmer conditions in central Iran, whereas Borges et al. [116] reported that the *Spartina* species can benefit from the global climate change and show expansion in their distribution. Increasing temperature can also impact the germinability of the seeds of halophytes, as most halophyte seeds prefer to germinate under moderate temperature regimes and higher temperatures are inhibitory to germination [113]. However, the seed germination of some halophytes such as *Desmostachya bipinnata* was insensitive to changes in temperature including higher (25/35 °C) temperatures.

Variability in precipitation is another important climate change factor that affects halophytes [117,118]. Changes in precipitation patterns can alter the availability/quality of water resources and the magnitude of salinity for halophytes, which can in turn affect their growth, survival, and reproduction. Halophytes adapt to different soil moisture levels by adjusting their morphology, physiology, or phenology. For example, a study by Martìnez et al. [119] showed that the two populations of *Atriplex halimus* from Kairouan

(Tunisia) and Tensift (Morocco) increased their water use efficiency by reducing their stomatal conductance.

Sea level rise is another major climate change factor that affects halophytes [120,121]. Sea level rise can increase the frequency/intensity of coastal flooding, enhance erosion and increase salinity, which can threaten the habitats and populations of halophytes. Halophytes' responses to sea level rise may differ based on the species, population, and ecosystem level. Some halophytes may be more resilient to sea level rise than others. For example, Xue et al. [121] reported that the invasive species *Spartina alterniflora* was better adapted to seawater rise than the native species *Phragmites australis* and *Scirpus mariqueter* in the Yangtze River Estuary, China.

In short, the responses of halophytes to global climate changes may differ depending on the species, population, and ecosystem level. Understanding how different climate change factors affect halophytes therefore appears crucial for halophyte conservation as well as their utilization.

4.3. Influence of Halophytes on the Soil Quality, Water Balance, Carbon Sequestration, Nutrient Cycling, and Biodiversity Conservation of Saline Ecosystems

Halophytes can influence the characteristics of their habitats in multiple ways, which can help in the restoration and improvement of saline habitats. For instance, halophytes can improve soil quality by increasing soil organic matter, reducing soil salinity, enhancing soil aggregation and porosity, and stimulating soil microbial activity and enzyme activity [51,122–124]. Halophytes can also affect habitats' water balance by modifying evapotranspiration, runoff, permeation, and groundwater recharge [125–127]. Halophytes can enhance carbon sequestration by increasing carbon inputs to biomass or soils, decreasing carbon outputs from respiration or decomposition, or altering carbon allocation patterns among different plant organs or fractions [128–131]. Halophytes can also influence the nutrient cycling of the habitat by modifying nutrient inputs, outputs, transformations, and interactions [132–134]. Furthermore, halophytes can promote biodiversity conservation by increasing species richness, evenness, diversity, and composition at different trophic levels in saline habitats [5]. Likewise, when grown in coastal regions such as marshes and estuaries, halophytes can be beneficial for the marine environment as well as the fishing/shipping industry by improving water quality and protecting the shoreline from storm surges and wave action (https://en.wikipedia.org/wiki/Halophyte; Accessed on 27 November 2023 [135]). Besides absorbing greenhouse gases, halophytes also reduce the drag and noise of ships depending on their vegetation density and thickness [136]. In contrast, the excess growth of halophytes such as mangroves and sea-grasses very close to ports or docking areas may result in the blockage of the harbors or channels that are used by ships for docking, which can easily be managed by periodic trimming/cleaning by the port authorities. Halophytes therefore seem to be beneficial plants that can enhance soil quality, habitat water balance, carbon sequestration, nutrient cycling, and biodiversity preservation in saline habitats.

4.4. Potential Threats and Challenges for Halophyte Conservation and Management

As discussed above, halophytes can provide multiple ecosystem services. However, they are also facing many threats and challenges, which impede their conservation and management. One of the major threats for halophytes is habitat loss and/or degradation, caused by numerous factors such as urbanization, industrialization, agriculture, mining, tourism, climate change, and invasive species [137–139]. Another major challenge for halophyte conservation is the lack of knowledge and awareness about their ecological importance, economic value, and cultural significance [80,140–142]. In addition, there is a dearth of knowledge about the mechanisms enabling halophytes to tolerate high salinity and information on the optimal conditions for growing halophytes [2]. Some potential ways to address these threats and challenges include the following [143–146]: (a) more research on diverse halophyte biology and utilization issues; (b) raising awareness about halophytes among various societal segments through research, education, involvement, and communication; (c) improved conservation policies, plans, and actions for halophytes through legislation, regulation, incentives, and enforcement; (d) intensified conservation practices for halophytes through restoration, rehabilitation, cultivation, and utilization.

5. Socioeconomic Aspects of Halophytes

5.1. Potential Uses and Importance of Halophytes for Human Welfare

Halophytes are highly valuable for human welfare (Figure 3) and can be utilized for the following purposes:

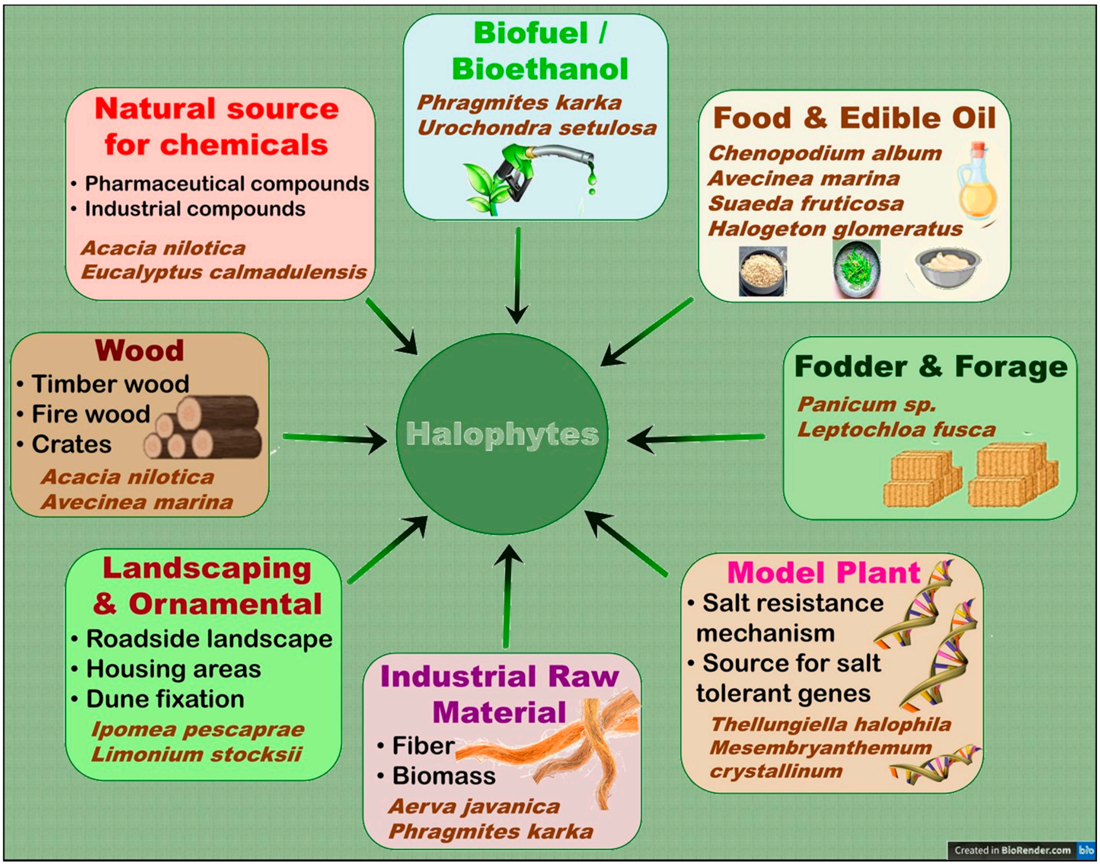

Figure 3. Potential uses and crop candidate species of the halophytes as detailed in Section 4.1.

a. *Food security in arid/saline regions*: Many halophytes can be a source of food for humans and livestock in arid and semi-arid regions, where soil salinity and fresh water scarcity are major constraints to crop production [3,7,128]. Khan et al. [79] reported that the halophyte grass *Panicum turgidum* can produce up to 60,000 kg year^{-1} ha^{-1} fresh biomass on saline lands and is comparable to maize in its fodder properties. Besides their use as fodder [79], halophytes can also be used to produce a variety of food products, including vegetables and grains [7]. Many halophytes such as quinoa, Purslane, and Salicornia have already gained popularity as alternative food crops [7,63,147,148]. In fact, quinoa grains are now widely sold and considered a super-food with multiple benefits [149,150]. In addition, Barreira et al. [148] evaluated the nutritional characteristics of the halophytes *Sarcocornia perennis* subsp. *perennis*, *Sarcocornia perennis* subsp. *alpini* and *Salicornia ramosissima* and *Arthrocnemum macrostachyum* and found them suitable for human consumption.

b. *Phytoremediation of saline/polluted soils*: Halophytes have the remarkable ability to remove excess salts from soil and water, thereby improving the soil [122,151]. Farzi et al. [152] found that the halophytes *Salicornia europaea*, *Salsola crassa*, and *Bienertia cycloptera* had very good ability to reduce the water salinity of the constructed wetlands. Halophytes can also be used to treat wastewater from industries such as oil and gas [153,154]. In addition, many halophytes are hyper-accumulators of heavy metals and therefore can be used for the phytoremediation of heavy-metal-polluted soils [155]. In this context, *Arthrocnemum macrostachyum* [156], *Halogeton glomeratus* [157], *Suaeda fruticosa*, *Atriplex lentiformis* [158], *Salicornia fruticosa* [159], *Tamarix africana* [160], *Sesuvium portulacastrum* [161], *Spartina alterniflora* [162], *Suaeda glauca*, and *Kochia scoparia* [163] are some examples of halophytes with the ability to phytoremediate heavy-metal-polluted soils.

c. *Medicinal compounds and essential oil production*: Halophytes have been used in traditional medicine to treat various ailments such as inflammation, pain, and infections [164,165]. For instance, Qasim et al. [164] reported that 45 halophytes of the coastal and near-coastal areas of Pakistan are being used to treat seven different disease conditions by locals, whereas Garcia-Caparros et al. [9] recently reported a total of 258 halophytes from different parts of the world with medicinal properties. Halophytes contain bioactive compounds that have antimicrobial, antioxidant, and anti-inflammatory properties [166,167]. For instance, the halophytes *Sonchus brachyotus* and *Limonium tetragonum* had high phenolic content, antioxidant and anti-inflammatory activities [168]. Similarly, another halophyte, *Suaeda fruticosa*, also had high anticancer, antioxidant, antidiabetic, and antimicrobial potential [169–171]. Halophytes are also source essential oils [124,125]. Two edible halophytes *Crithmum maritimum* and *Inula crithmoïdes* reportedly contain essential oil with good antimicrobial activity [172], whereas essential oil from a Tunisian halophyte *Lobularia maritima* has good potential to be used as a preservative in the meat industry.

d. *Biofuel and renewable energy production*: Halophytes may also be used as a renewable source of bioenergy, such as biofuel, thus helping to reduce reliance on fossil fuels and fight climate change [173–175]. They can be grown on marginal lands, which are not suitable for conventional crops, thereby would reduce the food versus fuel dilemma [176]. Interestingly, many halophytes have a similar or even better ligno-cellulose composition compared to conventional biofuel feedstock, which makes the halophytic biomass highly suitable for the production of bio-ethanol, a common type of biofuel [175]. Similarly, the seeds of a number of halophytes are rich in oil, which can be converted into bio-diesel, another form of biofuel [176]. Many halophytes such as *Alhagi maurorum*, *Atriplex rosea*, *Arthrocnemum macrostachyum*, *Cressa cretica*, *Halogeton glomeratus*, *Salicornia fruticosa*, and *Kosteletzkya virginica* are reportedly promising candidates for the bio-diesel production [177]. In addition, many halophytes such as *Salicornia* spp. can also be a source of biogas/bio-methane production [178].

e. *Environmental conservation and eco-tourism*: Halophytes play an important role in environmental conservation through various ecosystem services such as coast protection, soil stabilization, and land reclamation and carbon sequestration [124,127]. Halophytes such as mangrove mangles can also be utilized for eco-tourism sites [6,179,180] and fish/shrimp farming [181–183]. In this context, Özcan et al. [184] reported that owing to its diverse topography and rich halophyte diversity, Kavak Delta of North-west Turkey has high potential for eco-tourism. Likewise, artificial floating-mangrove jetties can help not only in coastal protection but also in game-fishing and carbon sequestration purposes [185]. Mangrove forests are also a popular tourist destination in Bali, Indonesia, for scientists and environmentalists, where they can experience natural scenic view, explore diverse plants and animals, and understand the ecological and cultural significance of mangroves [186]. Sundarban mangrove forest, which is recognized as a UNESCO World Heritage Site, is another example of a popular tourist attraction site [187].

5.2. Challenges for Large Scale Cultivation of Halophytes

To be economically feasible and competitive with other crop options for farmers, halophytes must be grown on a large scale [80,129]. For this purpose, significant infrastructure and technical investments would be necessary for large-scale halophyte cultivation [144,146]. Halophyte cultivation on a large scale could have both beneficial and harmful impacts on the environment. Therefore, it is crucial to carefully study the feasibility of large-scale halophyte production in any area [80,129].

There may be a number of technical difficulties associated with large-scale halophyte cultivation, including agronomic techniques, farmer training, machinery modifications, etc. [61,145]. Saline water is needed for halophyte cultivation, which can lead to corrosion, clogging, and salt buildup in the irrigation system. It is therefore important to determine the best way to use water, the rate at which soil salinity is increasing, and any potential effects on the surrounding ecosystems [188]. Halophytes are wild plants that have not been domesticated for cultivation; thus, specialized breeding programs are also required to develop improved varieties of halophytes with desirable traits to achieve uniform yield, high productivity, and simultaneous harvest under different types of habitats. In this connection, special attention will be required towards habitat conditions, where halophyte cultivation is intended. For instance, to cultivate halophytes in arid/desert regions, plants with higher water use efficiency, succulence, small leaves, and C_4 or CAM types of photosynthesis will be required [129]. For salt/coastal marsh environments, halophyte crop candidates with a higher ability to withstand anoxia/inundation in the form of pneumatophores, aerenchyma, and salt glands will be suitable, whereas for inland saline barren lands, halophytes with the ability to grow under high inland salinity, low fertility, and in some cases, with higher/alkaline soil pH, will be useful [129,144,145].

Similarly, not much is known about consumer preferences for halophyte products, and hence there is a need for in-depth research on consumer preferences [145,189]. In fact, many consumers may not be aware of the uses of halophytes as alternate crops or even may have negative perceptions about the quality, composition, and taste of halophyte products [144,145]. Hence, there is an urgent need for the evaluation of consumer preferences, which can in turn help in creating awareness among consumers about the uses of halophytes and ultimately their commercialization.

To overcome the aforementioned challenges towards large-scale halophyte cultivation, there is a need for more research and commitment from researchers, farmers, and policymakers. By addressing these issues, we can possibly unlock the full potential of halophytes for sustainable agriculture and other economic and ecological applications.

6. Discussion

As described above, halophytes can be used for the mitigation of a number of climate change-related issues including food security and carbon emissions. Many halophytes such as *Chenopodium quinoa* (many South American countries such as Peru and Bolivia), *Sesuvium portulacastrum* (many South Asian countries), *Portulaca oleracea* (a number of countries), *Batis maritima* (Southwestern USA), *Salicornia*, and *Sarcocornia* species (Europe and USA) are already being used as food/vegetables [7]. Similarly, the cultivation of many other halophytes such as *Panicum turgidum* (Pakistan; [79]), *Salicornia bigelovii* (Arab region; [190]) and *Leptochloa fusca* (Egypt; [191]) on saline lands have also led to good results in various countries/regions. In addition, aqueous extracts of many halophytes such as *Salicornia bigelovii* [192], *Salicornia europaea* [193], and *Sesuvium portulacastrum* [194] can be used to prevent harmful algal blooms in fresh/brackish water ecosystems, which are likely to be intensified with global climate changes [195]. However, there can be some drawbacks with the large-scale cultivation of halophytes, if not properly planned/managed. For instance, some halophytes may possess allelopathic or invasive characteristics that could be detrimental to the ecosystem's natural fauna and flora. Bibi et al. [196] recently reported that the allelopathy of the invasive *Prosopis juliflora* has negative effects on many native plants of Qatar. Similarly, Tahar et al. [197] also reported allelopathic effects of *Atriplex canescens* on a native forage species *Artemisia herba-alba* in the Algerian rangelands. Some species of halophytes such as *Spartina patens* [198] and *Phragmites australis* [199] have invasive properties and can be harmful for the native plants. Furthermore, without proper management (e.g., salt removal or leaching) the cultivation of halophytes with saline/brackish water irrigation can steadily increase the soil salinity beyond the tolerance limit of most halophyte crop candidates. In this aspect, Khan et al. [79] developed a drip-irrigation-based cropping system for the production of fodder on arid–saline lands by combining the cultivation of a fodder grass, *Panicum turgidum*, with the salt-accumulating shrub *Suaeda fruticosa* that can minimize salt buildup with time. Hence, the selection of appropriate halophyte species, proper cultivation practices, and the management of the cultivation site are key to the success of sustainable halophyte utilization to combat climate change-related issues on a long-term basis. Ripple et al. [200], in their analysis, suggested six critical and interrelated steps to lessen the worst effects of climate change, which include the following: (i) replacing fossil fuels with low-carbon renewables and other cleaner energy sources, (ii) reducing the emissions of short-lived climate pollutants, (iii) protecting and restoring Earth's ecosystems, (iv) preferring mostly plant-based foods with reduced consumption of animal products, (v) prioritizing preserving ecosystems and enhancing human well-being over GDP development and the chase of wealth, and (vi) stabilizing the world population. As described above in different instances such as Section 5.1, halophytes can be helpful in most of the aforementioned suggestions except the last point, as they can be a renewable resource for clean energy in the form of biofuel or biogas feedstock, can help in the sequestration of rising CO_2 as well as the phytoremediation of various pollutants, can be a good source of food and fodder in arid/saline areas, help protect various ecosystems alongside providing livelihood to poor local communities inhabiting barren saline/arid lands. However, there are also some research biases concerning the use of halophytes, which require research attention in the near future. For example, disregarding the erratic and unpredictable nature of climate change and its effects on halophyte performance is often neglected. Recently, Feizizadeh et al. [201] performed a scenario-based analysis of the suitability of European *Salicornia* as an alternate crop for a dying lake in Iran and found that it was suitable for only 4.6% of the studied area (2372 km^2). Studies on such topics are scarce and warrant attention in future research. Although a number of studies such as Qasim et al. [202], Renna and Gonnella. [203], and Ozturk et al. [204] have explored the traditional knowledge and uses of halophytes by local communities, but the ethical and cultural implications of halophyte utilization, including local populations' rights, choices, and customs are often overlooked and constitute another important research bias related to the mass-scale cultivation of halophytes. Hence, effective policies and institutional support are important in realizing halophytes' full potential as a sustainable and climate-resilient resource, addressing multiple challenges related to climate change, land degradation, and food security [189]. In this context, we recommend the following points, which can be useful in promoting halophytes' utilization and commercialization:

a. Collaborative research projects involving academic institutions, research centers, governmental agencies, and the corporate sector to hasten the development of halophyte-based solutions and close the gap between knowledge and application.
b. Develop extension services and training programs to educate farmers and agricultural communities about halophyte cultivation techniques.
c. The development of markets and marketing campaigns for halophyte products.
d. Ensuring and safeguarding the intellectual property rights for halophyte varieties developed through local breeding initiatives, which can also promote private sector investment.
e. Establishing regulatory frameworks or organizations for land rights, water use, harvesting, farming, and environmental impact. However, rules and regulations should be flexible enough to accommodate the developing halophyte utilization field.
f. Governmental and international organizations' research funding and programs might encourage academic institutions and research organizations to investigate the potentials of halophytes.
g. Offering subsidies, tax exemptions, or preferential access to resources like saline water or land for halophyte production to farmers as incentives to adopt halophyte cultivation.

h. International collaboration, conferences, and seminars to exchange information on halophyte research and development.
i. Public education and awareness initiatives on halophytes' benefits and their involvement in tackling issues like food security and climate change.

7. Conclusions

Halophytes are salt-tolerant plants that can thrive in saline environments (200 mM NaCl equivalent or greater), which would otherwise kill most crop plants. They have the potential to be used as a sustainable source of food, fuel, fodder, fiber, essential oils, and pharmaceuticals, among many other uses. Owing to their abilities to withstand high salinity and drought, accumulate large quantities of salts and toxic metal ions, and low maintenance during the growth stage, halophytes have enormous potential for land reclamation, improving soil fertility, increasing carbon sequestration, and producing 'carbon-neutral' feedstock for biofuel, which can help mitigate the negative effects of global climate changes (Figure 4).

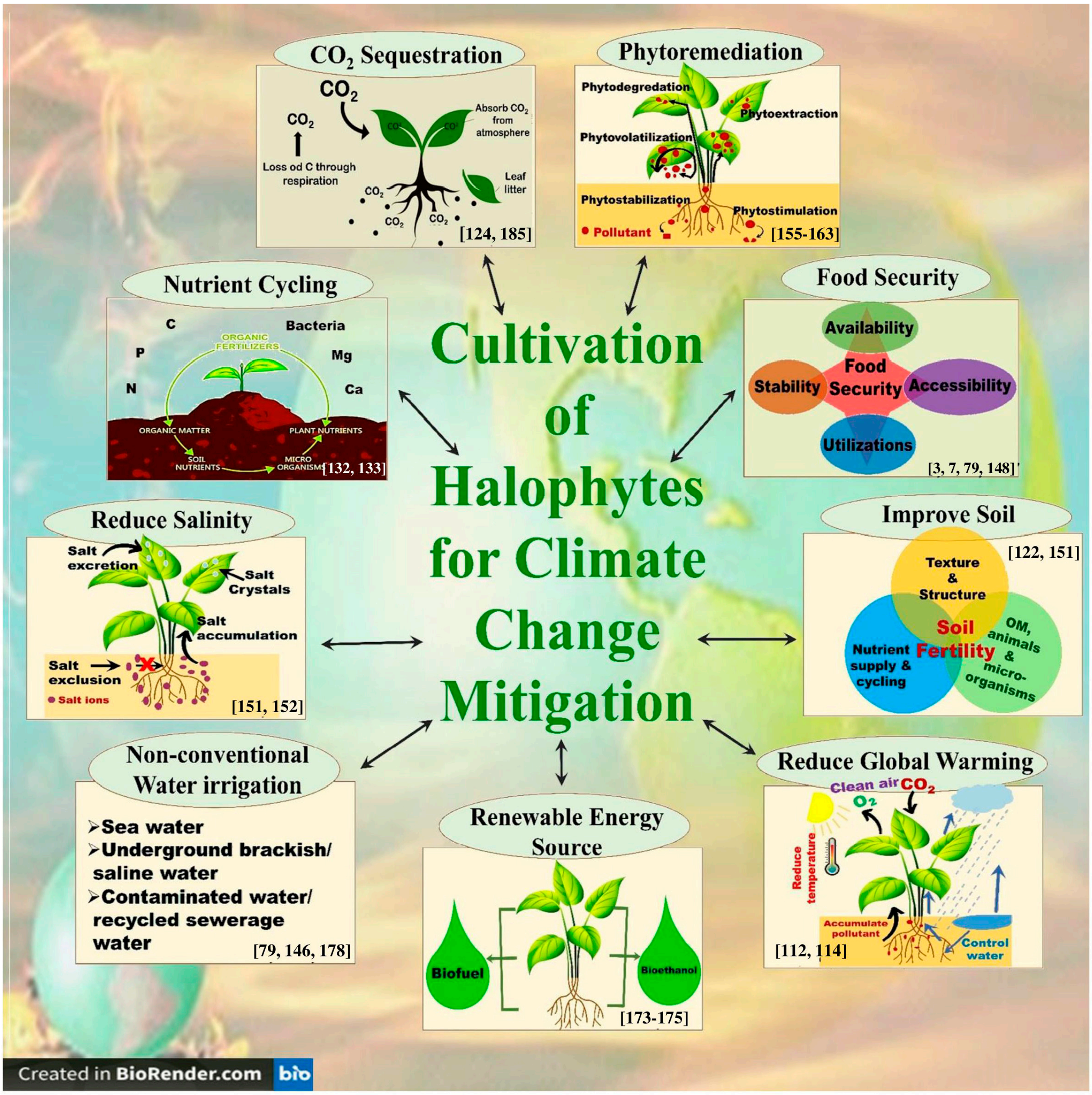

Figure 4. Roles of halophytes in combating global climate changes.

It is important to note that while halophytes have potential benefits, there are also some limitations in their use, which necessitate further research on issues such as economic viability, customer preferences, environmental impacts, and scale-up challenges. It should also be kept in mind that the halophytes are only one component of a broader set of strategies for mitigating and adapting to climate change. More field experiments, modeling studies, agronomic innovations, and meta-analyses that examine diverse climate change scenarios are consequently needed to fill these gaps. For integrating halophytes into climate change mitigation/adaptation programs, it is also important to take into account local conditions and potential trade-offs with other land uses and conservation activities. Hence, research-based appropriate strategies and policies are also required to achieve the full potential of halophytes as a sustainable resource to address climate change-related issues.

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