Salt tolerant horticultural plants to save freshwater usage

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Abstract

As freshwater becomes scarce worldwide due to climate change and population increases, there is an urgent need to develop innovative approaches to address the issue of reducing freshwater consumption. Selecting species with high ornamental value and salt tolerance for use as green hedges or bonsai in urban or coastal areas could be a strategic approach for promoting greening and maintaining water resource sustainability. Therefore, this review's first part focuses on identifying suitable species for seawater irrigation by understanding the adaptation mechanisms of halophytes, such as salt exclusion, salt secretion, osmotic adjustment, ionic homeostasis, and salt-tolerance-responsive genes. The second part involves the classification of different salt tolerance levels of species to select horticultural plants as potential candidates for use in saline, arid, and semi-arid regions, or seawater irrigation. Following that, the review examines successful cases to analyze the possibility of application, and subsequently, it concludes with an exploration of limitations, challenges, and opportunities.

Keywords: Climate change, freshwater scarcity, halophyte, salt tolerance, bonsai

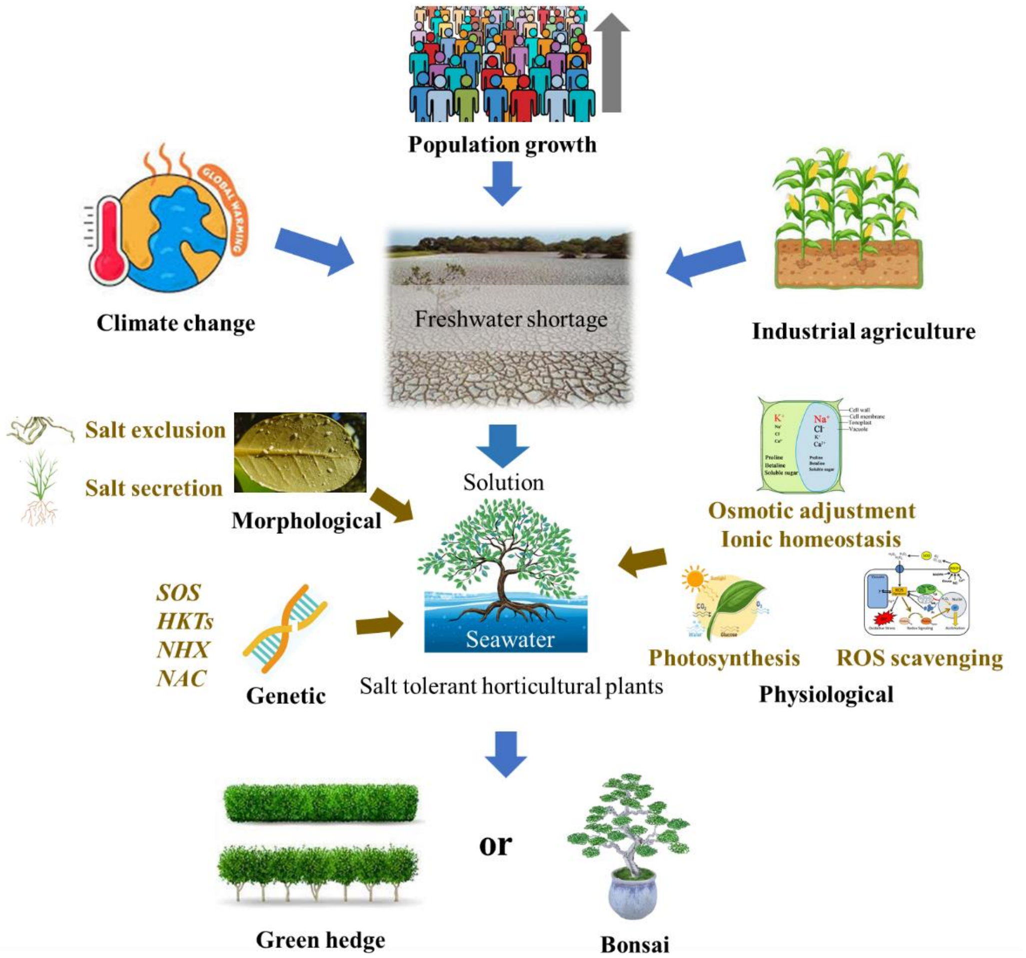

Figure 1. Graphical summary of the abstract.
(Picture sources: Aslam *et al*., 2022；Drennan and Pammenter, 1982；Guo *et al*., 2022；https://en.wikipedia.org/wiki/Photosynthesis)

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1. Introduction

Freshwater is a crucial resource on Earth, constituting approximately 2.5% of the total water. Nearly two-thirds of this freshwater is frozen in glaciers (Mikosch *et al.*, 2020). Presently, numerous regions around the world grapple with water scarcity. Projections indicate an imminent rise in the global population growth rate, implying heightened future demands for food, directly impacting agricultural water usage. Moreover, the exacerbation of water scarcity and drought due to climate change is expected to prompt widespread water usage for irrigation. This trend is anticipated within the framework of intensifying competition between agriculture and other sectors of the economy (Mancosu *et al.*, 2015). Hence, utilizations of marginal saline lands or seawater are important to address the issue of reducing freshwater consumption (Khan & Qaiser, 2006).

Salinity stands out as a significant limiting factor in agricultural productivity. The cultivation of salt-tolerant plants, such as ornamental plants, food crops or animal feeds, emerges as a promising strategy for making effective use of saline irrigation or substrates (Guo *et al.*, 2022；Munir *et al.*, 2021). Halophytes, including mangroves and other shrubs, exhibit remarkable morphological, physiological, and genetic adaptations that enable them to thrive in saline environments (Tipirdamaz *et al.*, 2021). These plants contribute to the amelioration of salt-affected soil through various physiological processes, such as ion compartmentalization, salt inclusion, salt excretion, ion transportation, as well as antioxidant and osmotic regulation (Balasubramaniam *et al.*, 2023; Guo *et al.*, 2022). Consequently, their role in saline horticulture is pivotal, as they possess the ability to flourish on land and utilize water resources unsuitable for conventional crops. Simultaneously, they serve dual purposes by contributing to landscape reintegration and facilitating soil rehabilitation (Munir *et al.*, 2022).

This literature review will concentrate on identifying plants capable of thriving in high-salt environments and possessing ornamental value. It will also encompass crucial topics related to the biological attributes of saline horticultural conditions and explore successful cases utilized for greening purposes. We hypothesize that salt-tolerant plants have the potential to be employed in large scale in horticultural areas as green walls and bonsai, thereby reducing freshwater consumption.

Research questions:

1. What are the biological attributes to be a good candidate plant for saline horticultural conditions?

2. How can salt-tolerant horticulture plants conduct freshwater conservation?

3. What are the limitations and challenges in implementing salt-tolerant horticultural plants in agriculture?

2. Methodology

The literature search was performed on Web of Science Core Collection and Science Direct databases. Based on articles published in scientific journals, selected the period from 1990 to 20th of September 2023. An extensive search was initiated focusing on salt-tolerant plants. The search string used in each database were (Salt tolerant plants * OR (Salt-tolerant plants *) OR (SALT TOLERANT PLANT *) OR (SALT TOLERANT PLANTS*) OR (SALT-TOLERANT PLANT) OR (SALT-TOLERANT PLANTS) OR (Saline horticulture *) OR (Salinity resistant plants *) OR (Salt stress plant) OR (NaCl stress tolerance plants *) OR (Brackish *) OR (Halophytes) *). For the Web of Science Core Collection databases, we searched using a topic search. For Science Direct databases, we searched using the title- abstract- keyword search. The EndNote citation manager was utilized to deduplicate repeated references across databases. Selection criteria are summarized in Table 1.

Table 1. Selection criteria

Criteria	Inclusion	Exclusion
Timeline	1990-2023	<1990
Document Type	Review and research articles	Conference proceeding, and thesis
Language	English	Non-English

3. Result and Discussion

3.1 Classification of Biological Attributes

3.1.1 Morphological features

Adaption in root – Salt exclusion

The regulation of sodium exclusion is closely linked to a plant's salt tolerance. Plant roots undergo physiological and structural changes to mitigate exposure to high salt concentrations through salt exclusion (Balasubramaniam *et al.*, 2023; Guo *et al.*, 2022; Munir *et al.*, 2022). Root membranes play a crucial role in safeguarding against salt accumulation in the cytoplasm. This is achieved by excluding a significant portion of sodium and chloride from the soil solution or by accumulating salt at root and root/stem junctions (Figure 2) (Godfrey *et al.*, 2019；Munir *et al.*, 2021). In the presence of saline conditions, the increased accumulation of salt ions in roots is associated with structural alterations, particularly in the apoplastic exodermal barriers. These changes include the presence of preformed suberin lamellae, and the development of Casparian bands (Andersen *et al.*, 2015；Guo *et al.*, 2022；Krishnamurthy *et al.*, 2020). Furthermore, absorbed ions in root cells can be expelled via antiporters like SOS1(Gul *et al.*, 2022). Salt exclusion in plants primarily occurs at pericyclic parenchyma cells, xylem parenchyma cells, root cortex, and phloem cells. The inhibition of sodium (Na^+) influx into roots, a process crucial for salt exclusion, is carried out by transporters activated through the SOS (salt overly sensitive) signaling pathway and nonselective cation channels.This leads to heightened ion accumulation in roots and diminished transport of salt ions to shoots (Song *et al.*, 2012; Gao *et al.*, 2016; Guo *et al.*, 2022；Mohammadi *et al.*, 2019).

Absorbed salt ions, apart from being reduced through structural features, can be expelled from the xylem. The HKT1 gene, essential in this process (Guo *et al.*, 2022；Ali *et al.*, 2016), helps restrict Na^+ entry into plant roots (Guo *et al.*, 2022；Rus *et al.*, 2001). Noteworthy members of these channels include cyclic nucleotide-gated channels (CNGCs) and glutamate-activated channels (GLRs). In the Ca^{2+} insensitive pathway, nonselective cation channels (NSCCs) like HKT1, KUP, and HAK may also be involved (Munns, 2005; Tester and Davenport, 2003).

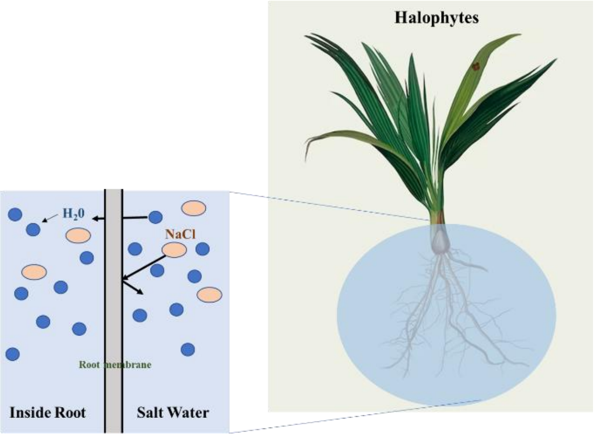

Figure 2. Salt exclusion mechanism (Modified from Krishnamurthy *et al*., 2011)

Adaption in shoot - Salt secretion

Plants possess specialized structures known as salt glands, which play a crucial role in managing the excess transport of salt ions to their aboveground parts (García-Caparrós *et al*., 2020；Sudhir *et al*., 2022). The function of the salt glands is to remove surplus salt through secretion, preventing potential damage to plant cells. In some halophytes, specialized salt glands are present and actively excrete additional salts onto the surface of leaves. The salt tolerant plants exhibit two divisions in salt secretions, including directly secreting salts to the surface of the leaf (exo-recretohalophytes), and those accumulating salt in the vacuole of a specialized bladder cell (endo-recretohalophytes) (Ding *et al*., 2010). The salt glands are distributed on every aboveground part of the plant and are abundant in mitochondria. These glands, known as transit cells, differ from storage cells as they lack central vacuoles. Water evaporates from these glands, leaving salts on the leaf surface in the form of crystals that are dispersed by wind or air currents (Flowers *et al*., 2010). The salt secretion through salt glands has been recorded in approximately 50 species (Munir *et al*., 2021；Santos *et al*., 2016) such as *Avicennia marina, Chenopodium quinoa,* and *Mesembryanthemum crystallinum.*

3.1.2 Physiological features

3.1.2.1 Photosynthesis

Photosynthesis plays a crucial role in plants by transforming solar energy into chemical energy. Increasing of salt concentration can interfere with stomatal conductance, leading to a gradual decline in both photosynthesis and transpiration (Balasubramaniam *et al*., 2023; Guo *et al*., 2022). The high level of salinity adversely impacts the leaf ability to retain water during photosynthesis and also decrease chlorophyll content. In *Rhizophora mangle* young plants exposed to high salt concentration (70 ppt), the leaf water potential was significantly lower than in the control exposed to low salt concentration(10 ppt). Additionally, the total chlorophyll content decreased, while accessory pigment concentrations increased (Silva *et al*., 2023). In *Dianthus caryophyllus* plant under high salinity, stomatal conductance, intercellular CO_2, and transpiration were significantly decreased (Kwon *et al*., 2019). Plenty of studies have similar results, including *Brassica juncea, Bruguiera gymnorrhiza*, and *Gossypium hirsutum* (Ashraf, 200；Burman *et al*., 2003；Takemura *et al*., 2000； Zhang *et al*., 2014).

Increasing accumulation of sodium (Na^+) and chloride (Cl^-) within the chloroplast will inhibit photosynthesis, including photophosphorylation and carbon metabolism. The disruption caused by salt stresses includes thylakoid membrane damage, alterations in the electron transport chain, changes in enzymatic activity and protein synthesis, and disturbances in the Calvin cycle, all of which affect the photosynthesis process (Batista *et al*., 2015). Under high salt concentration environments, the formation of reactive oxygen species (ROS) occurs, resulting in a decrease in photosynthesis (Khan *et al*., 2018). The diminished photosynthetic rate affects the activity of enzymatic antioxidants, sluch as catalase (CAT), superoxide dismutase (SOD), and various reactive oxygen species (ROS) (Balasubramaniam *et al*., 2023；Gul *et al*., 2022).

3.1.2.2 Osmotic adjustment and ionic homeostasis

Plants facing salt stress can adapt through osmotic adjustment, achieved by accumulating elevated levels of either inorganic ions, organic solutes, or a combination of both (Ashraf, 2004). In saline environments, a key obstacle arises from the diminished external water potential caused by the presence of salt ions. This hinders the absorption of water by plant roots and may lead to cellular dehydration. In response, plants counteract this challenge by accumulating both organic and inorganic solutes within the cytoplasm of root cells. This accumulation serves to decrease water potential, thereby enhancing the uptake of water and facilitating adaptation to conditions of salt stress (Feng *et al*., 2015；Guo *et al*., 2022；Han *et al*., 2012；Shao *et al*., 2014). The accumulation of inorganic ions serves as a strategy that consumes less energy than synthesizing organic substances for halophytes. Ions, such as Na^+ and $Cl^−$, mainly accumulate in the vacuole to be utilized for the osmotic adjustment of plant cells (Chen and Jiang, 2010；Guo *et al*., 2022).

For optimal growth and development of plants in saline conditions, it is essential to maintain a proper ratio of cytosolic K^+ to other ions, including Ca^{2+}/Na^+ ratio.The homeostasis of Mg^{2+} and Fe^{2+} is equally crucial and serves as a reliable indicator of the plant salt tolerance level (Munns and Tester, 2008). Salt-tolerant plants uphold ionic homeostasis by employing mechanisms such as the exclusion of soil salt ions through roots, facilitated by Salt Overly Sensitive 1 (SOS1) and apoplastic barriers.

Consequently, fewer ions are translocated to or accumulate in aboveground plant parts, such as leaf cells. This is achieved by compartmentalizing salt ions into the vacuole and reducing the ionic concentration in the cytoplasm. Hence, the crucial pathways to bolster salt tolerance in plants within saline environments involve restraining ionic transport to the shoots and effectively compartmentalizing toxic ions in the vacuole (Gul *et al*., 2022；Guo *et al*., 2022).

3.1.2.3 ROS scavenging

Reactive oxygen species (ROS) are naturally produced during plant metabolism, playing vital roles in growth, development, and stress response. A delicate balance between ROS production and scavenging exists under normal conditions. However, under salt stress, ROS production increases. If production exceeds scavenging, ROS accumulates, causing harm to plant structures and metabolism (Guo *et al*., 2022；Pang *et al*., 2011). ROS under high salt concentration can damage lipids, proteins, and nucleic acids, leading to irreversible metabolic dysfunction. Plants counteract this through antioxidant defense mechanisms, involving enzymes such as Superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), and nonenzymatic molecules such as glutathione (GSH), ascorbates (ASC), and carotenoids (Azeem *et al*., 2023；Gupta and Huang, 2014). Increased ROS levels during salt stress, including H_2O_2, $^1O_2$, OH^-, and O_2^-, are neutralized by these antioxidants. The detoxification process begins with SOD production, followed by a cascade of antioxidants. This intricate defense system is crucial for plants to combat oxidative challenges from environmental stress (Balasubramaniam *et al*., 2023). In conclusion, plants with salt tolerance typically demonstrate improved ROS scavenging ability through both enzymatic and non-enzymatic processes. This can be considered an indicator for selecting salt-tolerant horticultural plants.

3.1.3 Genetic features

Salt tolerance is a complex genetic trait influenced by multiple genes and numerous physiological mechanisms. The regulation of this trait involves hundreds of thousands of genes, and the response to salt stress can be observed at both the RNA and protein levels. It is suggested that enhancing the expression of a single gene has the potential to enhance the salt tolerance of transgenic plants (Munir *et al*., 2022).

The plant's ability to maintain K^+ and Na^+ balance is a critical indicator to determine of salt tolerance. The Salt Overly Sensitive (SOS) regulatory pathway plays an essential role in maintaining ionic homeostasis by regulating the activity of Na^+/H^+ antiporters during salt stress (Balasubramaniam *et al*., 2023；Yang *et al*., 2009; Ji *et al*., 2013). This pathway effectively manages Na^+ homeostasis by transporting excess Na^+ from the cytosol to the apoplast, thereby preventing the accumulation of Na^+ to toxicity (Halfter *et al.*, 2000; Yang *et al.*, 2009; Quintero *et al.*, 2011). The SOS signaling pathway contains *SOS1*, *SOS2*, and *SOS3* genes. Among three key genes, *SOS1* controls ion homeostasis for K^+ and $Ca_2{}^+$ and contributes to achieving salt tolerance. *SOS1* encodes a plasma membrane localized Na^+/H^+ antiporter that exports Na^+ in exchange for a proton. Numerous studies have shown that overexpression or co-overexpression of *SOS1* gene along with other salt-tolerant genes can lead to significantly enhanced salt stress tolerance, like *Triticum aestivum* (Jiang *et al.*, 2021) and *Oryza sativa* (Kumar *et al.*, 2014).

High-Affinity Potassium Transporters (HKTs) have been demonstrated to play a pivotal role in salt tolerance by excluding Na^+ ions from sensitive shoot tissues of plants (Balasubramaniam *et al.*, 2023). The structural characteristics of HKTs consist of four repetitions of MPM, where M denotes the transmembrane segment and P denotes the pore-loop domain. The arrangement of the repetition M1A-PA-M2A–M1D-PD-M2D and the structural determinant located in the first P domain, PA, delineate two categories of HKTs: HKT1 and HKT2 type (Hauser and Horie, 2010). HKT1 is known to enhance salt tolerance by mitigating Na^+ accumulation in shoot tissues, thereby shielding leaves from Na^+ toxicity. Tissue-specific manifestations of HKT1, such as in the pericycle or vascular bundle, contribute to improved salt tolerance in the entire plant. HKT1 facilitates the distribution of Na^+ between roots and shoots by translocating Na^+ from the root to the shoot xylem (Gul *et al.*, 2022; Tester and Davenport, 2003).

The increased accumulation of Na+ in vacuoles may also serve as an osmoticum, enhancing the plant's ability to tolerate salt. NHXs, identified as putative Na^+/H^+ exchangers, play a crucial role in transporting Na^+ from the cytoplasm to the vacuole, contributing to the plant's resistance to salt stress (Gul *et al.*, 2022; Su *et al.*, 2020). The increased accumulation of Na^+ in vacuoles might also act as an osmoticum, enhancing salt tolerance ability. NHXs are putative Na^+ /H^+ exchangers that transport Na^+ from the cytoplasm to the vacuole, holding plant resistance to salt stress (Su *et al.*, 2020). The NHX family in Arabidopsis consists of eight members classified based on their subcellular localization. *AtNHX7*/*SOS1* and *AtNHX8* are localized to the plasma membrane, *AtNHX1-4* are localized to the vacuolar membrane, and the remaining members, *AtNHX5* and *AtNHX6*, are localized to the trans-Golgi network (with *AtNHX5* on the Golgi membrane aiding in trafficking Na^+ into the vacuole). Numerous studies have demonstrated that overexpression of NHX imparts salinity tolerance in various plant species. For instance, the constitutive overexpression of *AtNHX1* significantly enhances salt tolerance in rice, wheat, tomato, and cotton (Gul *et al.*, 2022).

The NAC family represents one of the largest groups of stress-responsive transcription factors in plants, with NAC standing for NAM (No Apical Meristem), AATAF, and CUC (Cup-Shaped Cotyledon). This combination forms a transcription factor (Hu *et al*., 2006). NAC transcription factors exhibit organ-specific expression, and their expression levels are influenced by various stress stimuli. During abiotic stresses, NAC transcription factors play a important role in both ABA-dependent and ABA-independent pathways. NAC proteins, along with their corresponding cis-acting elements (NACRS), contribute to the formation of NAC regulons(Munir *et al*., 2022)

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3.2 Applications of salt-tolerant horticultural plants in reducing freshwater usage in horticulture

3.2.1 Adaptability of salt-tolerant plants

Plants can be divided into two types, glycophytes (salt-sensitive plants) and halophytes (salt-tolerant plants), based on how well they can withstand high salt concentrations. Most mangroves are considered as salt-tolerant. The capability to utilize salt water is the individual outstanding quality of the mangrove plants. Sreelekshmi *et al*. (2018) recorded the distribution and zonation of mangrove species in the SW coast of India related to its salinity tolerance, the result showed that *Bruguiera sexangula*, *B. gymnorrhiza*, *B. cylindrica*, *Acrostichum aureum*, and *Excoecaria agallocha* were distributed in low saline area. *Excoecaria indica was* distribution in both low and intermediate saline area. *Avicennia officinalis* and *Lumnitzera racemosa* were distributed in intermediate saline area. *Sonneratia alba*, *S. caseolaris*, and *Kandelia candel* were distributed in both intermediate and high saline area. *Rhizophora mucronata*, *R. apiculata*, *Avicennia alba*, and *Ceriops tagal* were distributed in high saline area (Figure 3, Figure 4).

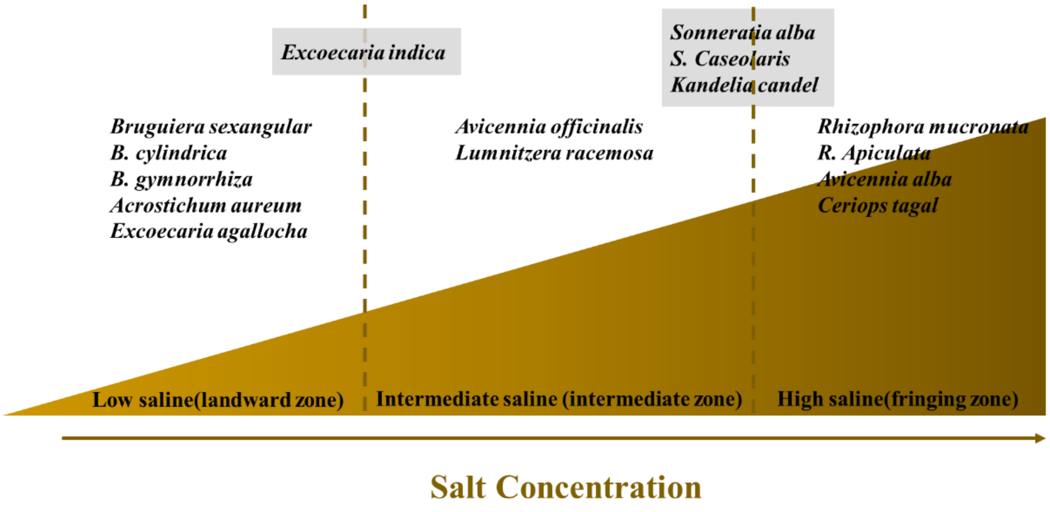

Figure 3. Adaptability of mangroves in different salt concentration (Modified from Sreelekshmi *et al*., 2018)

Figure 4. High salt tolerance mangrove species. (A) *Rhizophora mucronate*(by Martin Mergili), (B) *R. apiculate* (by J. B. Friday), (C) *Avicennia alba* (source: https://uk.inaturalist.org/taxa/189583-Avicennia-alba), and (D) *Ceriops tagal*(by Gerard Chartier).

3.2.2.Successful application cases in horticulture

Protection through vegetation and greening is one of the most effective and feasible biological methods for conserving fresh water usage. Planting salt-tolerant ornamental crops is a viable and sustainable greening strategy. Farieri *et al*. (2016) conducted a salt spray experiment using fifteen ornamental shrubs for potential use in urban and peri-urban coastal areas. In the end, *Raphiolepis umbellata* exhibited all three ideal morphological traits, as the epigeous dry matter, total leaf area, and leaf damage showed less reduction than in other species. Therefore, it could be considered of ornamental value under salt sprays. *Lumnitzera rosea* is commonly used as a green hedge in Vietnam. It grows to a height of 2.46 meters from the base to the top, featuring numerous branches. The flowers are pink and hermaphroditic (Tomlinson, 1986). *Pemphis acidula* is valued as a bonsai species. Its morphology can vary from a scrambler to a tall shrub and grows on raised coral and rocky or sandy beaches above the intertidal zone (Lewis and Rao,1971)(Figure 5, Figure 6). *Halimione*, *Plantago*, *Frankenia*, *Camphorosma*, *Halocnemum and Acantholimon* are used as ground cover and are highly preferred in high salt lands and can be used as turf grasses (Ungar, 1987).

Figure 5. Salt tolerance ornamental plants. (A) *Raphiolepis umbellate* (by A. Barra), (B) *Lumnitzera rosea* (by Jean Yong；Boo *et al*., 2014), (C) *Lumnitzera littorea* (by Jean Yong；Boo *et al*., 2014), (D) *Westringia fruticose* (by Fabrizio), (E) *Sonneratia ovata* (by Ron Yeo), (F) *Pemphis acidula*(by Leon Perrie).

Figure 6. Successful application cases of salt-tolerance species used in horticulture. (A)The *Lumnitzera racemosa* was used as a green hedge in Vietnam (by Jean Yong), (B) *Ceriops zippeliana* Blume was used as green wall in Vietnam (by Jean Yong), (C) *Pemphis acidula* was used as bonsai (website: bonsai-bci.com).

3.3 Limitations and challenges of implementing salt-tolerant horticultural plants in agriculture

The growing demand for freshwater, driven by climate change and population growth, poses a challenge to the sustainable development of horticulture. With these perspectives, saline horticulture is emerging as a crucial solution. However, few new species have been developed that are resistant to high salt concentrations. Hence, plant breeding through gene editing techniques could be the solution. Additionally, there is a lack of comprehensive research on the optimal conditions for cultivating halophyte species for industrial-level production, including considerations of consumer preferences. The economic aspects of utilizing saline water irrigation require consideration of three main factors: a thorough analysis of soil reclamation for saline and sodic soils before cultivation, an understanding of the implications of continuous saline water use for irrigation, and an examination of the potential for reusing drainage water for irrigation along with the optimization of drainage installations, which is crucial for sustainable practices (Ladeiro, 2012). Overall, a more concerted effort is required in studying the potential use of halophytes in saline horticulture, along with their economic value. This includes economic analyses, irrigation practices, and efficient drainage systems.

3.4 The opportunities for sustainable agriculture and water resource conservation

Salt-tolerant plants are highly valuable for agriculture, horticulture, and ecological purposes, particularly in regions facing freshwater shortages. These plants play a crucial role in maintaining ecological balance while also contributing to economic outcomes. Salt tolerant plants, in particular, can be exploited for their important bioactive metabolites, offering significant commercial value. The halophytes of mangroves serve as a natural barrier against storms, tsunamis, waves, and coastal erosions, making them the primary defense in protecting coastal areas (Asari *et al.*, 2021). The salt glands in the leaves of *Avicennia germinans* play a crucial role in defending against fungal attacks. This mangrove species experienced significantly less damage from foliar diseases compared to *Laguncularia racemosa* or *Rhizophora mangle* (Gilbert *et al.*, 2002). Additionally, they can be cultivated for various purposes such as food crops, animal feeds, and creating green hedges, walls, and bonsai on lands using salty water irrigation (Farieri *et al.*, 2016). To address the salinity problem, there are opportunities to assess halophytes for landscaping purposes. Species capable of tolerating 0.5% NaCl or more are potential candidates for ornamental purposes. Recommending the cultivation of halophytes for industrial purposes is prudent, given their capacity to thrive on saline-degraded lands. This not only brings about economic benefits but also contributes to environmental sustainability in our society (Munir *et al.*, 2021). Certain Poaceae species, including *Spartina alterniflora, Thinopyrum ponticum, Puccinellia ciliate, Imperata cylindrica, Spartina patens, Leymus racemosus, Leymus chinensis, and Spartina townsendii,* have been used for have been used for cultivating salt-affected soil or for irrigation with salty water. (Chaieb and Boukhris, 1998；Eid and Eisa, 2010；Li *et al*., 2009; Manousaki *et al*., 2008；Meudec *et al*., 2007; Shamsutdinov and Shamsutdinov, 2008；Sun *et al*., 2008). This practice contributes to enhancing both the biological and physicochemical properties of degraded soils, fostering an increase in soil organic matter and nutrient contents. Moreover, some salt-tolerant species have been utilized in large-scale environmental cleanup initiatives targeting metal-contaminated soils. In summary, harnessing the potential of salt-tolerant plants in horticulture can facilitate the establishment of crop production. The re-greening of natural saline soils proves to be a valuable strategy for valorizing and reclaiming salt-affected areas, presenting a promising solution to address water shortage issues (Atia *et al*., 2019；Munir *et al*., 2021).

4. Conclusion

Horticultural plants with salt tolerance can resist salt stress through cellular, tissue-specific, and whole-plant mechanisms by adapting their morphology (such as salt glands), physiology (photosynthesis, osmotic adjustment, ionic homeostasis, and ROS scavenging), and genes (*SOS1*, *HKTs*, *NHX*, and *NAC*). Planting halophytes is a feasible and sustainable greening strategy that can solve water scarcity problems. Mangrove plants are well-adapted to salt concentrations that exceed those tolerated by most other plant species. Among them, *Rhizophora mucronata*, *R. apiculata*, *Avicennia alba*, and *Ceriops tagal* mangroves can survive in highly saline environments, making them suitable candidates as salt-tolerant plants for use in green hedges or bonsai in the future. Currently, there have been successful applications in Southeast Asia, such as *Lumnitzera rosea* used as a green hedge and *Ceriops zippeliana* Blume employed as a green wall in Vietnam. Additionally, *Pemphis acidula* has been utilized as a valuable bonsai. In conclusion, it is possible to use salt-tolerant horticultural plants to at least partially solve the freshwater shortage problem. Looking ahead, it is important to continue selecting salt-tolerant species and researching their cultivation characteristics for practical applications.

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