Abstract: Halophytes can survive and complete their life cycle in the presence of ≥200 mM NaCl. These remarkable plants have developed various strategies to tolerate salinity and thrive in high-salt environments. At the appropriate levels, salt has a beneficial effect on the vegetative growth of halophytes but inhibits the growth of non-halophytes. In recent years, many studies have focused on elucidating the salt-tolerance mechanisms of halophytes at the molecular, physiological, and individual level. In this review, we focus on the mechanisms, from the macroscopic to the molecular, underlying the successful growth of halophytes in saline environments to explain why salt has beneficial effects on halophytes but harmful effects on non-halophytes. These mechanisms include the specialized organs of halophytes (for example, ion compartmentalization in succulent leaves), their unique structures (salt glands and hydrophobic barriers in roots), and their salt-tolerance genes. We hope to shed light on the use of halophytes for engineering salt-tolerant crops, soil conservation, and the protection of freshwater resources in the near future.

Keywords: Hydrophobic barriers, Ion compartmentalization, Molecular, Salt gland, Salt tolerance

1 Introduction

Salt water accounts for approximately 97% of the Earth’s water supply, and humans can only use 1% of the fresh water found worldwide [1]. Saving fresh water and making good use of salt water pose new challenges, especially in arid and semi-arid countries. Halophytes naturally grow in saline environments [2,3], and some species, such as mangroves, can even grow in seawater [4]. Halophyte plants can be used as forage grasses, in medicines, as vegetables, and as papermaking materials [1]. Therefore, investigating the mechanisms by which halophytes tolerate saline environments is crucial for sustainable development.

Salt can damage plants through its osmotic effect (physiological drought under high-salinity conditions), ion toxicity (especially Na+ and Cl−), and secondary stresses such as oxidative stress [5,6]. Halophytes and non-halophytes show distinct differences in maximum salt tolerance [7-9]. Plants that can survive and complete their life cycle in a salt concentration of ≥200 mM NaCl are usually defined as halophytes [5,10,11-13]. Halophytes actively control the uptake, storage, exclusion, and secretion of ions under saline conditions [14-17]. The most salt-tolerant halophytes such as Suaeda salsa can complete their life cycle in soils containing 200 to 500 mM NaCl [18-20], whereas non-halophytes show limited salt tolerance and can be damaged in soils with NaCl concentrations <50 mM [21].

Halophytes do not simply tolerate high-salt conditions. True halophytes thrive at the appropriate salt concentrations and show optimal growth in the presence of significant amounts of NaCl, e.g., 200 mM for S. salsa [22,23], 150 mM for Chenopodium quinoa [24], and 100 mM for Cakile maritima [25]. The halophyte Plantago crassifolia exhibits highly efficient responses to salt stress during early seedling development [26,27]. Appropriate salt concentrations can promote the vegetative growth of halophytes and are conducive to the completion of their life cycle, as described by Flowers & Colmer [10]. Salt has a beneficial effect on halophytes, as they grow larger...
and more rapidly in the presence of the appropriate salt concentration, compared to conditions with little or no salt [20]. More specifically, the majority of halophytes benefit from the presence of high concentrations of salt during processes ranging from seed germination to seedling growth. For example, many halophytes such as *Cakile maritima* [25] and *Chloris virgata* [28] have been shown to have higher germination percentages at slightly elevated salinity levels (0.5% NaCl, or around 50–90 mM) vs. distilled water [28,29]. In addition to seed germination, appropriate NaCl concentrations also enhance the seedling growth of halophytes compared to non-salt conditions. This is evidenced by higher seedling biomass, larger leaf area [30], and enhanced photosynthetic efficiency [17,31] and yield, thus leading to increased seed production for the next generation [18,19].

By contrast, non-halophytes are salt sensitive and suffer from salt-induced damage. These plants are classified as salt-sensitive and salt-tolerant non-halophytes based on their level of salt tolerance. Plants in both categories show inhibited growth under saline conditions, but salt-sensitive non-halophytes, such as soybean and rice, may suffer irreparable damage in response to low concentrations of NaCl (less than 50 mM) [32,33], whereas salt-tolerant non-halophytes such as cotton, beets, and barley can tolerate higher salt concentrations (200–300 mM NaCl) [34-36]. However, all non-halophytes show decreased biomass when grown in the presence of salt with one exception: *Eutrema salsugineum* (formerly misclassified as *Thellungiella salsuginea*, Brassicaceae [37,38]). This plant is widely considered to be a model halophyte [39] because it has a certain degree of salt tolerance and was reported to survive under 250 mM NaCl conditions [40,41], although its growth sharply declines with increasing NaCl level [42,43]. Studies of *E. salsugineum* performed over the past 15 years have contributed to our understanding of salt tolerance mechanisms in halophytes.

Why does the appropriate salinity level enhance the vegetative growth of halophytes and inhibit the growth of non-halophytes? Do halophytes have special characteristics that allow them to adapt to saline environments? In the past decade, many studies have investigated possible underlying mechanism. In the current review, we focus on the vegetative growth of halophytes to illustrate the mechanisms underlying the robust growth of halophytes in saline environments, from the morphological to the cellular and molecular levels.

2 Morphological, cellular, and subcellular adaptations

All plants, including non-halophytes, compartmentalize excess ions into their vacuoles, which is considered the physiological foundation of salt tolerance in all plants [44]. Halophytes have evolved several specific structures or mechanisms to adapt to saline environments (Fig. 1). However, non-halophytes have not evolved the unique morphological features needed to cope with salt stress, and if forced to live in saline soil, their biomass is reduced and they cannot complete their life cycles. By contrast, halophytes can survive high-salt conditions due to leaf succulence and the functions of specialized organs (e.g., salt glands, as described below). There are three types of halophytes: euhalophytes, recretohalophytes, and pseudohalophytes [45]. Euhalophytes such as *Kalidium foliatum* and *S. salsa* are salt accumulators that can take up large amounts of ions and compartmentalize them in vacuoles to maintain cell turgor. These plants also develop leaf or stem succulence when the soil water potential is low [20].

Leaf succulence is a typical visible characteristic of euhalophytes such as *S. salsa* under high-salinity conditions (Fig. 2) [46,47], although this feature is not unique to halophytic plants as certain xerophytes, such as cacti and *Kalanchoe daigremontiana*, also have succulent leaves under drought conditions. However, halophytes and xerophytes have evolved different strategies leading to the formation of succulence. Under saline conditions, ion accumulation in vacuoles results in succulence, which may be caused by the presence of carbon as a driving force and ion compartmentalization to relieve salt damage. For example, *S. salsa* actively accumulates ions and proline in its vacuoles and cytosol to reduce plant water potential [48]. A possible mechanism underlying leaf succulence in *S. salsa* is suggested by the finding that the presence of aquaporins in the plasma membrane is correlated with Na⁺ accumulation in the vacuole [23,49,50]. Under drought conditions, however, succulence is induced by the accumulation of organic compounds such as malate via a carbon gradient [51].

Halophytes and non-halophytes show distinct differences in ion compartmentalization. Photosynthesis and chloroplasts in non-halophytes are markedly damaged by salinity due to a weak ion compartmentalization [52]. For example, in *Arabidopsis thaliana*, electron transport though photosystem II is dramatically inhibited and nonphotochemical quenching of chlorophyll fluorescence increases in response to 150 mM NaCl [39]. By contrast,
Figure 1 Salt-tolerance mechanisms in halophytes. Seeds that rapidly germinate under saline conditions benefit from dimorphism or mobilization. Vegetative growth is maximal and reproductive growth is stimulated under appropriate salt concentrations because of the following salt-tolerance mechanisms: 1) ion compartmentalization; 2) salt secretion; and 3) ion intraveinal recycling and the root apoplastic barrier. In the first mechanism- ion compartmentalization- Na$^+$ actively accumulates in the vacuoles, thus preventing protoplast damage. The second mechanism- salt secretion- is described in Yuan et al. [3], which showed the typical multi-cellular salt gland and salt bladder. SC, secretory cell; AC, accessory cell; IC, inner cup cell; OC, outer cup cell; MC, mesophyll cell; EC, epidermal cell. The third mechanism- the root apoplastic barrier- includes the Casparian strip and suberin lamellae, which can effectively block the apoplastic pathway. Ions can only enter endothelial cells via passage cells (PC), i.e., the symplastic pathway. XY, xylem; CO, cortex; EN, endodermis; PC: passage cell. The plant was drawn with Photoshop CS6.

Figure 2 The succulent blades of euhalophyte Suaeda salsa grown in intertidal zone (left, red leaves) and inland saline soils (right, green leaves) of the Yellow River Delta (N 37°25′; E 118°54′).
the chloroplasts and mitochondria of halophytes are protected under salt-stress conditions due to a strong ion compartmentalization. The ultrastructure of thylakoids in the chloroplasts of two euhalophytic species *Haloxylon ammodendron* and *Suaeda physophora* showed no observable damage when treated with 700 mM NaCl [17]. In the halophyte *Artemisia anethifolia*, the thylakoids in chloroplasts were intact, and the number of cristae in the mitochondria did not decrease until the plants were treated with 200 mM NaCl [53]. The halophyte *Suaeda altissima* also retained normal chloroplast function under 750 mM NaCl conditions [31].

The two other types of halophytes are considered to be salt regulators. Recretohalophytes can secrete excessive ions via specific salt-secreting structures, e.g., salt bladders in *Atriplex centralasiatica* [54] and salt glands in *L. bicolor* [55,56]. These unique epidermal structures distinguish these plants from other halophytes and all non-halophytes [3,57]. Vesicle transport is the main pathway for salt secretion [2,58]. The subcellular structures of recretohalophytes also exhibit specific characteristics. Most reports have focused on salt-secretory ultrastructures such as highly developed plasmodesmata, mitochondria, vesicles, the lack of chloroplasts, cuticles, and so on (this information can be found in Yuan *et al.* [3] and Shabala *et al.* [54]). A review by Dassanayake [59] discusses the morphology and evolution of salt glands, suggesting that these structures emerged independently at least 12 times in recretohalophytes.

The roots of non-halophytes and halophytes behave quite differently. In root cells of the non-halophyte common bean (*Phaseolus vulgaris*), the addition of 80 mM NaCl leads to membrane vesiculation and increased solute leakage [60]. By contrast, the roots of pseudohalophytes such as mangroves in the Rhizophoraceae family and reeds in the *Gramineae* family show high salt exclusion ability, thereby protecting the shoots from salinity. The possible mechanism underlying salt exclusion in plants such as reeds is described as interveinal recycling and apoplastic barriers in the roots. During interveinal recycling, the Na⁺ absorbed by roots is transported into the shoots through xylem vessels and is then loaded into the phloem by HKT1 (a high-affinity K⁺ transporter) [61,62]. Finally, this Na⁺ is unloaded back into the soil by SOS1 (a plasma membrane Na⁺/H⁺ antiporter) [63,64] in roots cells [65,66] (detailed in the “Salt-tolerance genes” section). In recent years, lignin and suberin lamellae in the root endodermis have also been shown to be involved in the salt exclusion pathway. Root hydrophobic barriers play an important role in salt exclusion in *Avicennia officinalis* [4]. The same group reported that, although rice is a representative non-halophyte, it can also tolerate low concentrations of salt (50–100 mM NaCl), mainly due to the presence of apoplastic transport barriers in the roots [67].

As mentioned in the Introduction, *E. salsugineum* is a special type of halophyte that has been used as a model plant to unravel the molecular mechanisms of salt tolerance in halophytes [68,69]. Although this plant does not possess the typical characteristics of halophytes (such as salt glands or salt bladders) and shows a marked decrease in vegetative growth under high salinity, studies of *E. salsugineum* have shed light on the mechanisms underlying salt tolerance. Under high-salt conditions, *E. salsugineum* undergoes differential regulation of Na⁺/K⁺ ions and re-establishes Na⁺/K⁺ homeostasis [70], including a reduction in Na⁺ absorption [71] and an increase in Na⁺ compartmentalization [72,73]. The genes controlling Na⁺ absorption are described in the following section and listed in Table 1. The osmotic balance in *E. salsugineum* can also be maintained by proline accumulation in addition to ion accumulation [74], which helps this plant survive in saline environments.

In short, halophytes have evolved several structural or ultrastructural adaptations to salt stress, whereas non-halophytes do not develop these adaptive structures, and their ultrastructure is significantly injured under low-salt conditions. Therefore, specific cellular and subcellular structures facilitate the strong growth of halophytes under the appropriate salt concentrations.

### 3 Salt-tolerance genes

All traits, including salt tolerance and salt sensitivity, are ultimately controlled by genes. Certain salt tolerance genes are constitutively expressed in halophytes while other genes are induced by salt [75], exhibiting increased expression under salt treatment [76,77]. Although many reports involving salt-tolerance genes have focused on non-halophytes such as *Arabidopsis* [64,78,79] and rice [80], we will concentrate on salt-tolerance genes in halophytes. Table 1 lists the genes involved in Na⁺ transport across the membrane and the three salt-tolerance mechanisms used by halophytes (also see Fig. 1). Na⁺ flux occurs from root to leaf in halophytes based on the genes described to date. Na⁺ may enter the cell by HKT1, KT, KUP/HAK/KT-type transporters, AKT1-type channels, and NSCCs (nonselective cation channels). To avoid salt damage to the cytoplasm, many genes involved in the three salt-tolerance mechanisms are upregulated, such as *NHX* (encoding a vacuolar-type Na⁺/H⁺ antiporter that participates in ion compartmentation in vacuoles);
SOS pathway genes such as *SOS1; PIP* (aquaporin involved in salt secretion); and *cytochrome P450* (*AQP* and *TIP* aquaporin genes) encode proteins involved in ion compartmentation and root hydrophobic barriers.

Table 1. Genes involved in Na\(^+\) influx and the three salt tolerance mechanisms of halophytes

| Salt-tolerance mechanism | Gene | Likely function in salt tolerance | Halophyte species | References |
|-------------------------|------|-----------------------------------|-------------------|------------|
| Na\(^+\) influx         | *HKT1* | High-affinity K\(^+\) transporter 1 | *Suaeda salsa*    | [92]        |
|                         |       |                                   | *Salicornia dolichostachya* | [111]      |
|                         |       |                                   | *Leptochloa fusca*   | [112]      |
|                         |       |                                   | *Aeluropus lagopoides* | [113]      |
|                         | *AKT1* | Inward-rectifying K channel 1     | *Suaeda maritima*   | [114]      |
|                         | *KUP/HAK/KT* | KUP/HAK/KT type transporter | *Suaeda maritima* | [115]      |
|                         | *KT* | Potassium transporter             | *Eutrema salignum*  | [71]       |
|                         |       |                                   | *Reaumuria trigyna* | [104]      |
|                         |       |                                   | *Limonium bicolor*  | [56]       |
| 1) Ion compartmentation  | *NHX* | Encodes a vacuolar-type Na\(^+\)/H\(^+\) antiporter that is located on the vacuolar membrane and pumps excessive Na\(^+\) into the vacuole to avoid toxic Na\(^+\) concentrations in the cytoplasm. | *Limonium gmelinii* | [116]      |
|                         |       |                                   | *Karelinia caspica* | [81]       |
|                         |       |                                   | *Salicornia brachiata* | [117]      |
|                         |       |                                   | *Aeluropus littoralis* | [118,91] |
|                         | *CLC* | Chloride channel on vacuolar membrane | *Mesembryanthemum crystallinum* | [119] |
|                         | *AQP* | Encodes aquaporin                  | *Sesuvium portulacastrum* | [76]       |
|                         |       |                                   | *Suaeda salsa*      | [50]       |
| 2) Salt secretion       | *SOS1* | Encodes a Na\(^+\)/H\(^+\) antiporter located on the plasma membrane that pumps excess Na\(^+\) out of the cell. | *Avicennia marina* | [120]      |
|                         | *HA1* | PM H\(^+\)-ATPase                   | *Avicennia marina* | [120]      |
|                         | *NHX* | Na\(^+\)/H\(^+\) antiporter on the vacuolar membrane | *Avicennia marina* | [120]      |
|                         | *VAMP* | Vesicle-associated membrane protein | *Limonium bicolor* | [56]       |
|                         | *CLC* | Chloride channel on the plasma membrane | *Limonium bicolor* | [56]       |
|                         | *PIP and TIP* | Aquaporin genes | *Avicennia officinalis* | [121] |
| 3) Intravein recycling  | *SOS1* | Encodes a Na\(^+\)/H\(^+\) antiporter located on the plasma membrane that plays a role in Na\(^+\) efflux from roots | *Salicornia dolichostachya* | [111]      |
| root hydrophobic barriers| *AoCYP86B1* | Encodes cytochrome P450 that regulates suberin biosynthesis and prevents some Na\(^+\) from entering the roots | *Avicennia officinalis* | [6]        |

SOS pathway genes such as *SOS1; PIP* (aquaporin involved in salt secretion); and *cytochrome P450* (*AQP* and *TIP* aquaporin genes) encode proteins involved in ion compartmentation and root hydrophobic barriers.

To date, to the best of our knowledge, only one halophyte gene has been tested in a halophyte to verify its function. Silencing *KcNHX1* in the halophyte *Karelinia caspica* led to reduced tolerance to high concentrations of NaCl, suggesting that *KcNHX1* plays an essential role in the response of *K. caspica* to salt stress [81]. Most of the same genes may be present in halophytes and non-halophytes but exhibit different expression patterns due to different long-term survival strategies [82]. Therefore, all salt-tolerance genes that have been cloned in halophytes to date have been tested by heterologous expression in non-halophytes to explore their functions [83-88]. The highest concentration of NaCl that these transgenic plants could tolerate was reported as 400 mM [89,90]. For example, transgenic tobacco (*Nicotiana tabacum*) transformed with *AlNHX* (encoding a vacuolar-type Na\(^+\)/H\(^+\) antiporter) from the halophyte *Aeluropus littoralis* exhibited high salt tolerance (400 mM NaCl) [91]. Transgenic tobacco also compartmentalized more Na\(^+\) in its roots than wild type tobacco to maintain a relatively high K\(^+\)/Na\(^+\) ratio in its leaves [91]. Overexpression of a similar gene *SsNHX1* (encoding a putative vacuolar Na\(^+\)/H\(^+\) antiporter) from *Salsola soda* allowed *Medicago sativa* to survive in high concentrations of NaCl (up to 400 mM) due to improved Na\(^+\) sequestration in the vacuole [90]. In addition to the role of NHX genes in ion compartmentation, studies in non-halophytes have also verified the functions of many other groups of halophyte genes controlling primary salt-tolerance traits, showing that heterologous expression of these genes significantly improved the salt tolerance of these plants. The first group of genes includes *HKT1* (encoding a high-affinity K\(^+\) transporter) and *SOS1* (encoding a plasma membrane Na\(^+\)/H\(^+\) antiporter). Transgenic *Arabidopsis* transformed with *SsHKT1;1* from *S. salsa* showed enhanced salt tolerance and increased K\(^+\) concentrations in shoots [92]. Transgenic tobacco harboring *SbSOS1* from *Salicornia brachiata*...
showed a high degree of salt tolerance, growing in 200 mM NaCl [93].

The second group of genes, including H\(^-\)pyrophosphatase and vacuolar ATPase genes, is involved in energy supply. For example, transgenic Arabidopsis transformed with StVP (encoding a vacuolar H\(^-\)pyrophosphatase) from S. Sals [94] or KfVP1 (encoding H\(^-\)pyrophosphatase) from Kalidium foliatum [95] showed increased salt tolerance due to enhanced V-ATPase and V-PPase activity. Transgenic rice transformed with SaVHAc1 (a vacuolar H\(^-\)ATPase subunit c1 gene) from the halophyte Spartina alterniflora performs better under salt stress than control [96].

The third group of genes is involved in the ROS scavenging system. Transgenic tobacco transformed with SbpAPX (encoding Peroxisomal Ascorbate Peroxidase) from S. brachiata showed enhanced vegetative growth compared to wild type when grown at 300 mM NaCl [97]. Transformation with Ss.sAPX (encoding a stromal ascorbate peroxidase) from S. salsa improved the growth of Arabidopsis plants under high-salt conditions [84].

The remaining groups of genes are related to plant hormones and aquaporin. Transgenic tobacco expressing high levels of SbASR-1 (encoding abscisic acid stress ripening-1) from S. brachiata showed better germination and seedling growth than wild type when grown on 400 mM NaCl [89]. Transgenic tobacco harboring SpAQPI (aquaporin-related gene induced by salt) from Sesuvium portulacastrum showed enhanced seed germination and root growth under high-salt conditions due to increased antioxidant enzyme activity [76].

The heterologous expression of halophytic salt-tolerance genes improves salt resistance in non-halophytes to some degree, but transgenic plants often cannot finish their life cycles in naturally saline soils due to the great spatial and temporal variation of salt content. Moreover, to the best of our knowledge, no transgenic non-halophytes show typical halophyte characteristics such as improved growth under the appropriate salt concentration. In general, salt-tolerance traits are controlled by a series of genes rather than one or two genes. Therefore, it might be necessary to identify salt-tolerance gene networks and explore their effects under controlled conditions.

4 Conclusions and Perspective

The vegetative growth of halophytes can benefit from appropriate salt concentrations. Although different halophytes have evolved diverse salt-tolerance mechanisms, these can primarily be divided into three categories: the use of specialized organs (succulent leaves via ion compartmentalization), unique structures (salt glands and hydrophobic barriers in roots), and salt-tolerance genes. In this review, we focused on the mechanisms that could explain the beneficial effects of salt on vegetative growth in halophytes (i.e., better and more rapid growth than under non-salt conditions, resulting in increased seed production), including the morphological, cellular, and molecular aspects of these mechanisms. Additional reviews about various salt-tolerance mechanisms can be found in [82,98,99,100]. Many reports emphasize the important role of halophytes in improving saline soil conditions and the cultivation of salt-tolerant crops [1,3,20,44,82,100,101]. Several researchers have proposed a series of possible ways to realize these dreams, such as transforming non-halophytes with salt-tolerance genes to improve their salt resistance [82]. Indeed, salt-tolerance genes isolated from halophytes are often used to transform non-halophytes.

However, it is still difficult to apply these solutions to plants grown in the field and these solutions face many challenges. To date, no glycyphytes/non-halophytes transformed with salt-tolerance genes have been successfully grown in natural saline environments. On the one hand, all known salt-tolerance genes have been heterologously overexpressed in non-halophytes to clarify their functions, which is not a very precise method. The functions of salt-tolerance genes should be verified in the halophyte itself via silencing or knockout, but this type of experiment has only been reported for the halophyte K. caspica [81]. On the other hand, salt tolerance in halophytes is a complex trait that is controlled by gene families or networks. Transforming one or several related genes into glycyphytes may not cause radical changes in salt tolerance; instead, the transformed genes must function coordinately. Nevertheless, these solutions appear feasible, but additional time is needed to carry out such experiments.

For the discovery of salt-tolerance genes and networks, high-throughput RNA-seq has been used in several halophytes such as L. bicolor [13], M. crystallinum [102,103], and Reaumuria trigyna [104]. Although many salt-tolerance genes have been identified in halophytes, which genes should we focus on first? Perhaps we can focus on the genes controlling primary salt-tolerance traits as mentioned in this review (such as succulent leaves, salt glands, and root hydrophobic barriers), followed by regulatory genes (such as transcription factor genes) that control these traits (e.g., Table 1) by transforming the halophyte itself. Using this procedure, we can target the key traits directly involved in salt tolerance and the
corresponding phenotypes, allowing a single trait to be improved in non-halophytes via the transformation of these genes. Good transformation systems are clearly needed for this strategy and, therefore, there is an urgent need to establish such systems for use in various halophytes, such as *Leymus chinensis* and *L. bicolor* [105,106]. Based on this system, CRISPR/Cas9-mediated genome editing will likely prove to be a useful tool for verifying target gene function [107]. In addition, many recent studies have found that long non-coding RNAs play an important role in salt tolerance in plants [108-110]. Therefore, more attention should be paid to non-coding RNAs that participate in the unique salt-tolerance strategies of halophytes via high-throughput RNA sequencing.

Overall, given that the expanding saline lands threaten human existence, there are two ways to make good use of halophytes to preserve soils and fresh water: 1) increasing the planting areas of halophytes in arid and semi-arid areas to help prevent water loss and 2) transforming non-halophytes with salt-tolerance genes to enable them to tolerate irrigation with full-strength or diluted seawater in the near future.

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**References**

[1] Abd El-Hack M E, Samak D H, Noreldin A E, et al. Towards saving freshwater: halophytes as unconventional feedstuffs in livestock feed: a review. Environmental Science and Pollution Research, 2018; 1-10.

[2] Feng Z, Sun Q, Deng Y, et al. Study on pathway and characteristics of ion secretion of salt glands of *Limonium bicolor*. Acta Physiologiae Plantarum, 2014; 36(10): 2729-2741.

[3] Yuan F, Leng B Y, Wang B S. Progress in Studying Salt Secretion from the Salt Glands in Recretohalophytes: How Do Plants Secrete Salt? Frontiers in Plant Science, 2016; 7(977): 977.

[4] Krishnamurthy P, Jyothi-Prakash P A, Qin L, et al. Role of root hydrophobic barriers in salt exclusion of a mangrove plant *Avicennia officinalis*. Plant Cell & Environment, 2014; 37(7): 1656-1671.

[5] Flowers T J, Munns R, Colmer T D. Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. Annals of Botany, 2015; 115(3)

[6] Yang Y, Guo Y. Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytologist, 2018; 217(2): 523-539.

[7] Leng B Y, Yuan F, Dong X X, et al. Distribution pattern and salt excretion rate of salt glands in two recretohalophyte species of *Limonium* (Plumbaginaceae). South African Journal of Botany, 2018; 115: 74-80.

[8] Wang F, Xu Y G, Wang S, et al. Salinity affects production and salt tolerance of dimorphic seeds of *Suaeda salsa*. Plant Physiology & Biochemistry, 2015; 95: 41.

[9] Zhou J, Zhao W, Yin C H, et al. The role of cotyledons in the establishment of *Suaeda physophora* seedlings. Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology, 2014; ahead-of-print: 1-7.

[10] Flowers T J, Colmer T D. Salinity tolerance in halophytes. New Phytologist, 2008; 179(4): 945-963.

[11] Santos J, Al-Azzawi M, Aronson J, et al. eHALOPH a database of salt-tolerant plants: helping put halophytes to work. Plant and Cell Physiology, 2015; pcv155.

[12] Yuan F, Chen M, Yang J C, et al. The optimal dosage of 60Co gamma irradiation for obtaining salt gland mutants of *Exo-recretohalophytes Limonium bicolor* (Bunge) O. Kuntze. Pak. J. Bot, 2015; 47(0): 71-76.

[13] Yuan F, Lyv M J, Leng B Y, et al. Comparative transcriptome analysis of developmental stages of the *Limonium bicolor* leaf generates insights into salt gland differentiation. Plant, Cell & Environment, 2015; 38: 1637–1657.

[14] Ma Q, Yue L-J, Zhang J-L, et al. Sodium chloride improves photosynthesis and water status in the succulent xerophyte *Zygophyllum xanthoxylum*. Tree Physiology, 2011; 32(1): 4-13.

[15] Song J, Shi W, Liu R, et al. The role of the seed coat in adaptation of dimorphic seeds of the euhalophyte *Suaeda salsa* to salinity. Plant Species Biology, 2017; 32(2)

[16] Song J, Zhou J, Zhao W, et al. Effects of salinity and nitrate on production and germination of dimorphic seeds applied both through the mother plant and exogenously during germination in *Suaeda salsa*. Plant Species Biology, 2016; 31(1): 19-28.

[17] Zhang S, Song J, Wang H, et al. Effect of salinity on photosynthesis and chloroplasts ultrastructure in cotyledons of desiccated seeds of halophytes or xerophyte growing in central Asia. Journal of Plant Ecology, 2010(3): 259-267.

[18] Guo J, Li Y, Han G, et al. NaCl markedly improved the reproductive capacity of the euhalophyte *Suaeda salsa*. Functional Plant Biology, 2018; 44(3): 350-361.

[19] Guo J, Luo S, Wang B S. Sodium chloride improves seed vigour of the euhalophyte *Suaeda salsa*. Seed Science Research, 2015; 25(3): 335-344.

[20] Song J, Wang B. Using euhalophytes to understand salt tolerance and to develop saline agriculture: *Suaeda salsa* as a promising model. Annals of Botany, 2015; mcu194.

[21] Galvan-Ampudia C, Christa T. Salt stress signals shape the plant root. Current Opinion in Plant Biology, 2011; 14: 296-302.

[22] Liu Q Q, Liu R R, Ma Y C, et al. Physiological and molecular evidence for Na+ and Cl- exclusion in the roots of two *Suaeda salsa* populations. Aquatic Botany, 2018; 146: 1-7.

[23] Yang M F, Song J, Wang B S. Organ-Specific Responses of Vacular H+-ATPase in the Shoots and Roots of C3 Halophyte *Suaeda salsa* to NaCl. Journal of Integrative Plant Biology, 2010; 52(3): 308-314.
[24] Shabala L, Mackay A, Tian Y, et al. Oxidative stress protection and stomatal patterning as components of salinity tolerance mechanism in quinoa (*Chenopodium quinoa*). Physiologia Plantarum, 2012; 146(1): 26–38.

[25] Debez A, Hamed K B, Grignon C, et al. Salinity effects on germination, growth, and seed production of the halophyte *Cakile maritima*. Plant & Soil, 2004; 262(1/2): 179-189.

[26] Alhassan M, Pacurar A, Gaspar A, et al. Growth and reproductive success under saline conditions of three *Plantago* species with different levels of stress tolerance. Notulae Botanicae Horti Agrobotanici Cluj-Napoca, 2014; 42(1): 180-186.

[27] Boscaiu M, Soriano E E, Vicente O. Effects of salt stress on the reproductive biology of the halophyte *Plantago crassifolia*. Biologia Plantarum, 2005; 49(1): 161-163.

[28] Zhang H, Irving L J, Tian Y, et al. Influence of salinity and temperature on seed germination rate and the hydrome model parameters for the halophyte, *Chloris virgata*, and the glycophyte, *Digitaria sanguinalis*. South African Journal of Botany, 2012; 78(3): 203-210.

[29] Qu X X, Huang Z Y, Baskin J M, et al. Effect of temperature, light and salinity on seed germination and radicle growth of the geographically widespread halophyte shrub *Halocnemum strobilaceum*. Annals of Botany, 2007; 101(2): 293-299.

[30] Yuan F, Liang X, Li Y, et al. Methyl Jasmonate Improves Salinity Tolerance in *Limonium bicolor* by Enhancing Photosynthesis and Abaxial Salt Gland Density. Functional Plant Biology, 2018; Online

[31] Balinokin Y V, Kurkova E B, Myasoedov N A, et al. Structural and Functional State of Thylakoids in a Halophyte *Suaeda altissima* before and after Disturbance of Salt-Water Balance by Extremely High Concentrations of NaCl. Russian Journal of Plant Physiology, 2004; 51(6): 815-821.

[32] Kaneda Y, Tabei Y, Nishimura S, et al. Combination of thidiazuron and basal media with low salt concentrations increases the frequency of shoot organogenesis in soybeans (*Glycine max* (L.) Merr.). Plant Cell Reports, 1997; 17(1): 8-12.

[33] Kawasaki S, Borchert C, Deyholos M, et al. Gene expression profiles during the initial phase of salt stress in rice. Plant Cell, 2001; 13(4a): 889.

[34] Farooq M, Hussain M, Wakeel A, et al. Salt stress in maize: effects, resistance mechanisms, and management. A review. Agronomy for Sustainable Development, 2015; 35(2): 461-481.

[35] Golan-Goldhirsh A, Hankamer B, Lips S H. Hydroxyproline and proline content of cell walls of sunflower, peanut and cotton grown under salt stress. Plant Science, 1990; 69(1): 27-32.

[36] Wang B, Ho T H D, Wu R. Expression of a Late Embryogenesis Abundant Protein Gene, *HVA1*, from Barley Confers Tolerance by Enhancing Photosynthesis *Limonium* *altissima*. Annals of Botany, 2007; 101(2): 293-299.

[37] Qi C H, Chen M, Wang B S. NaCl increases the activity of the plasma membrane H+-ATPase in C3 halophyte *Suaeda salsa* callus. Acta Physiologiae Plantarum, 2010; 32(1): 27-36.

[38] Sui N, Han G L. Salt-induced photoinhibition of PSII is alleviated in halophyte *Thellungiella halophila* by increases of unsaturated fatty acids in membrane lipids. Acta Physiologiae Plantarum, 2014; 36(4a): 983-992.

[39] Guo Y H, Jia W J, Song J, et al. *Thellungiella halophila* is more adaptive to salinity than *Arabidopsis thaliana* at stages of seed germination and seedling establishment. Acta Physiologiae Plantarum, 2012; 34(4a): 1287-1294.

[40] Guo Y H, Wang D, Jia W J, et al. Effects of seed vernalisation and photoperiod on flowering induction in the halophyte *Thellungiella halophila*. Australian Journal of Botany, 2012; 60(8): 743.

[41] Flowers T J, Galal H K, Bromham L. Evolution of halophytes: multiple origins of salt tolerance in land plants. Functional Plant Biology, 2010; 37(7): 604-612.

[42] Bremcle S. How do halophytes overcome salinity. Biology of Salt Tolerant Plants, 1995; 23: 199-203.

[43] Li X, Liu Y, Chen M, et al. Relationships between ion and chlorophyll accumulation in seeds and adaptation to saline environments in *Suaeda salsa* populations. Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology, 2012; 146(sup1): 142-149.

[44] Song J, Shi G, Gao B, et al. Waterlogging and salinity effects on two *Suaeda salsa* populations. Physiologia Plantarum, 2011; 141(4): 343-351.

[45] Song J, Chen M, Feng G, et al. Effect of salinity on growth, ion accumulation and the roles of ions in osmotic adjustment of two populations of *Suaeda salsa*. Plant and Soil, 2009; 314(1-2): 133-141.

[46] Chen M, Song J, Wang B S. NaCl increases the activity of the plasma membrane H+-ATPase in C3 halophyte *Suaeda salsa* callus. Acta Physiologiae Plantarum, 2010; 32(1): 27-36.

[47] Qi C H, Chen M, Song J, et al. Increase in aquaporin activity is involved in leaf succulence of the euhalophyte *Suaeda salsa*, under salinity. Plant Science, 2009; 176(2): 200-205.

[48] North G B, Nobel P S. Water uptake and structural plasticity along roots of a desert succulent during prolonged drought. Plant Cell & Environment, 1998; 21(7): 705-713.

[49] Schröppelmeier G, Kaiser W M. Ion Homeostasis in Chloroplasts under Excess or Deficiency of Sulfate, Phosphate, or Magnesium. Plant Physiology, 1988; 87(4): 828-832.

[50] Fan H, Dong K H, Hoo Y P, et al. Effect of NaCl Stress on Ultrastructure of Halophytes *Artemisia anethifolia*. Acta Agrestia Sinica, 2011; 19(3): 482-486.

[51] Shabala S, Bose J, Hedrich R. Salt bladders: do they matter? Trends in Plant Science, 2014; 19(11): 687–691.

[52] Yuan F, Chen M, Leng Y B, et al. An efficient autofluorescence method for screening *Limonium bicolor* mutants for abnormal salt gland density and salt secretion. South African Journal of Botany, 2013; 88: 110-117.
Alemán F, Nieves-Cordones M, Martínez V, et al. Differential regulation of the HAK5 genes encoding the high-affinity K+ transporter in the salt gland of Limonium bicolor. Plant Physiology, 1993; 97: 20-27.

Deng Y, Feng Z, Yuan F, et al. Identification and Functional Analysis of the Autofluorescent Substance in Limonium bicolor Salt Glands. Plant Physiology and Biochemistry, 2015; 84: 145-157.

Feng Z, Deng Y, Zhang S, et al. K+ accumulation in the cytoplasm and nucleus of the salt gland cells of Limonium bicolor accompanies increased rates of salt secretion under NaCl treatment using NanoSIMS. Plant Science, 2015; 238: 286-296.

Dassanayake M, Larkin J C. Making Plants Break a Sweat: the regulation of the HKT5 genes encoding the high-affinity K+ transporter in the salt gland of Limonium bicolor. Plant Physiology, 2015; 173(1): 47-57.

Cachorro P, Olmos E, Ortiz A, et al. Salinity-induced changes in the structure and ultrastructure of bean root cells. Biologia Plantarum, 1995; 39(3): 119-131.

Horie T, Hauser F, Schroeder J I. HKT transporter-mediated salinity resistance mechanisms in Arabidopsis and monocot crop plants. Trends in Plant Science, 2009; 14(12): 660-668.

Deng Y, Feng Z, Yuan F, et al. Identification and Functional Analysis of the Autofluorescent Substance in Limonium bicolor Salt Glands. Plant Physiology and Biochemistry, 2015; 84: 145-157.

Dassanayake M, Larkin J C. Making Plants Break a Sweat: the regulation of the HKT5 genes encoding the high-affinity K+ transporter in the salt gland of Limonium bicolor. Plant Physiology, 2015; 173(1): 47-57.

Cachorro P, Olmos E, Ortiz A, et al. Salinity-induced changes in the structure and ultrastructure of bean root cells. Biologia Plantarum, 1995; 39(3): 119-131.

Horie T, Hauser F, Schroeder J I. HKT transporter-mediated salinity resistance mechanisms in Arabidopsis and monocot crop plants. Trends in Plant Science, 2009; 14(12): 660-668.

Lan W Z, Wang W, Wang S M, et al. A rice high-affinity potassium transporter (HKT) conceals a calcium-permeable cation channel. Proceedings of the National Academy of Sciences of the United States of America, 2010; 107(15): 7089-7094.

Shi H Z, Ishitani M, Kim C, et al. The HKT transporter-mediated salt secretion of salt gland. Plant Molecular Biology, 2015; 97: 20-27.

Deng Y, Yuan F, Lyu M J A, Leng B Y, et al. The transcriptome of Thellungiella halophila. Plant Molecular Biology Reporter, 2015; 37(2): 273-283.

Horie T, Hauser F, Schroeder J I. HKT transporter-mediated salinity resistance mechanisms in Arabidopsis and monocot crop plants. Trends in Plant Science, 2009; 14(12): 660-668.

Lan W Z, Wang W, Wang S M, et al. A rice high-affinity potassium transporter (HKT) conceals a calcium-permeable cation channel. Proceedings of the National Academy of Sciences of the United States of America, 2010; 107(15): 7089-7094.

Shi H Z, Ishitani M, Kim C, et al. The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na+/H+ antiporter. Proceedings of the national academy of sciences, 2000; 97(12): 6896-6901.

Deng Y, Yuan F, Lyu M J A, Leng B Y, et al. The transcriptome of Thellungiella halophila. Plant Molecular Biology Reporter, 2015; 37(2): 273-283.

Horie T, Hauser F, Schroeder J I. HKT transporter-mediated salinity resistance mechanisms in Arabidopsis and monocot crop plants. Trends in Plant Science, 2009; 14(12): 660-668.

Lan W Z, Wang W, Wang S M, et al. A rice high-affinity potassium transporter (HKT) conceals a calcium-permeable cation channel. Proceedings of the National Academy of Sciences of the United States of America, 2010; 107(15): 7089-7094.

Shi H Z, Ishitani M, Kim C, et al. The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na+/H+ antiporter. Proceedings of the national academy of sciences, 2000; 97(12): 6896-6901.

Deng Y, Yuan F, Lyu M J A, Leng B Y, et al. The transcriptome of Thellungiella halophila. Plant Molecular Biology Reporter, 2015; 37(2): 273-283.

Horie T, Hauser F, Schroeder J I. HKT transporter-mediated salinity resistance mechanisms in Arabidopsis and monocot crop plants. Trends in Plant Science, 2009; 14(12): 660-668.

Lan W Z, Wang W, Wang S M, et al. A rice high-affinity potassium transporter (HKT) conceals a calcium-permeable cation channel. Proceedings of the National Academy of Sciences of the United States of America, 2010; 107(15): 7089-7094.

Shi H Z, Ishitani M, Kim C, et al. The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na+/H+ antiporter. Proceedings of the national academy of sciences, 2000; 97(12): 6896-6901.

Deng Y, Yuan F, Lyu M J A, Leng B Y, et al. The transcriptome of Thellungiella halophila. Plant Molecular Biology Reporter, 2015; 37(2): 273-283.

Horie T, Hauser F, Schroeder J I. HKT transporter-mediated salinity resistance mechanisms in Arabidopsis and monocot crop plants. Trends in Plant Science, 2009; 14(12): 660-668.
[90] Li W, Wang D, Jin T, et al. The Vacuolar Na⁺/H⁺ Antiporter Gene SsNHX1 from the Halophyte Salsola soda Confers Salt Tolerance in Transgenic Alfalfa (Medicago sativa L.). Plant Molecular Biology Reporter, 2011; 29(2): 278-290.

[91] Zhang G H, Su Q, An L J, et al. Characterization and expression of a vacuolar Na⁺/H⁺ antiporter gene from the monocot halophyte Aeluropus littoralis. Plant Physiology & Biochemistry, 2008; 46(2): 117-126.

[92] Shao Q, Han N, Ding T, et al. SsHKT1;1 is a potassium transporter of a C3 halophyte Suaeda salsa involving in salt tolerance. Functional Plant Biology, 2014; 41: 790-802.

[93] Yadav N S, Shukla P S, Jha A, et al. The SbSOS1 gene from the extreme halophyte Salicornia brachiata enhances Na⁺ loading in xylem and confers salt tolerance in transgenic tobacco. Bmc Plant Biology, 2012; 12(1): 188.

[94] Guo S, Yin H, Zhang X, et al. Molecular cloning and characterization of a vacuolar H⁺-pyrophosphatase gene, SsVP, from the halophyte Suaeda salsa and its overexpression increases salt and drought tolerance of Arabidopsis. Plant Molecular Biology, 2006; 60(1): 41-50.

[95] Yao M, Zeng Y, Liu L, et al. Overexpression of the halophyte Kalidium foliatum H⁺-pyrophosphatase gene confers salt and drought tolerance in Arabidopsis thaliana. Molecular Biology Reports, 2012; 39(8): 7899-7996.

[96] Baisakh N, RamanaRao M, Rajasekaran K, et al. Enhanced salt stress tolerance of rice plants expressing a vacuolar H⁺-ATPase subunit c1 (SaVHAc1) gene from the halophyte grass Spartina alterniflora Löisel. Plant Biotechnol J., 2012; 10(4): 453-464.

[97] Singh N, Mishra A, Jha B. Over-expression of the Peroxisomal Ascorbate Peroxidase (SbpAPX) Gene Cloned from Halophyte Salicornia brachiata Confers Salt and Drought Stress Tolerance in Transgenic Tobacco. Marine Biotechnology, 2014; 16(3): 321-332.

[98] Flowers T, Troke P, Yeo A. The mechanism of salt tolerance in halophytes. Annual review of plant physiology, 1977; 28(1): 89-121.

[99] Flowers T J, Munns R, Colmer T D. Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. Annals of Botany, 2014; 115(3).

[100] Ozfidankonakci C, Uzilday B, Ozgur R, et al. Halophytes as a source of salt tolerance genes and mechanisms: a case study for the Salt Lake area, Turkey. Functional Plant Biology, 2016; 43(7).

[101] Wang F X, Yin C H, Song Y P, et al. Reproductive allocation and fruit-set pattern in the euhalophyte Suaeda salsa in controlled and field conditions. Plant Biosystems, 2017: 1-10.

[102] Barkla B J, Vera-Estrella R. Single cell-type comparative metabolomics of epidermal bladder cells from the halophyte Mesembryanthemum crystallinum. Frontiers in Plant Science, 2015; 6: 435.

[103] Tsukagoshi H, Suzuki T, Nishikawa K, et al. RNA-seq analysis of the response of the halophyte, Mesembryanthemum crystallinum (ice plant) to high salinity. Plos One, 2015; 10(2).

[104] Dong Z H, Zheng L L, Wang J, et al. Transcriptomic profiling of the salt-stress response in the wild recrétolophyte Rumuria trigyna. BMC Genomics, 2013; 14(1): 29.

[105] Sun Y L, Hong S K. Agrobacterium tumefaciens -Mediated Transformation of the Halophyte Leymus chinensis (Trin.). Plant Molecular Biology Reporter, 2012; 30(5): 1253-1263.

[106] Yuan F, Chen M, Yang J C, et al. A system for the transformation and regeneration of the recrétolophyte Limonium bicolor. In Vitro Cellular & Developmental Biology-Plant, 2014; 50: 610-617.

[107] Duan Y B, Li J, Qin R Y, et al. Identification of a regulatory element responsible for salt induction of rice OsRAV2 through ex situ and in situ promoter analysis. Plant Molecular Biology, 2016; 90(1-2): 49-62.

[108] Huanca-Mamani W, Arias-Carrasco R, Cár-N S, et al. Long Non-Coding RNAs Responsive to Salt and Boron Stress in the Hyper-Arid Lluteño Maize from Atacama Desert. Genes, 2018; 9(3): 170.

[109] Qin T, Zhao H, Cui P, et al. A Nucleus-localized Long Non-Coding RNA Enhances Drought and Salt Stress Tolerance. Plant Physiology, 2017; 175(3): 1321.

[110] Song Y, Zhang D. The Role of Long Noncoding RNAs in Plant Stress Tolerance. Methods Mol Biol, 2017; 1631: 61-68.

[111] Katschnig D, Bliek T, Rozema J, et al. Constitutive high-level SOS1 expression and absence of HKT1;1 expression in the salt-accumulating halophyte Salicornia dolichostachya. Plant Science, 2015; 234: 144-154.

[112] Rauf M, Shahzad K, Ali R, et al. Cloning and characterization of Na⁺/H⁺ antiporter (jinHXX1) gene from a halophyte grass Leptochloa fusca for drought and salt tolerance. Molecular Biology Reports, 2014; 41(3): 1669-1682.

[113] Sanadhyya P, Agarwal P, Khedia J, et al. A Low-Affinity K⁺ Transporter AlHKT2;1 from Recretohalophyte Aeluropus lagopoides Confers Salt Tolerance in Yeast. Molecular Biotechnology, 2015; 57(6): 489-498.

[114] Wang S M, Zhang J L, Flowers T J. Low-Affinity Na⁺ Uptake in the Halophyte Suaeda maritima. Plant Physiology, 2007; 145(2): 559-571.

[115] Zhang J L, Flowers TJ, Wang S M. Differentiation of low-affinity Na⁺ uptake pathways and kinetics of the effects of K⁺ on Na⁺ uptake in the halophyte Suaeda maritima. Plant & Soil, 2013; 368(1-2): 629-640.

[116] Zhou L L, Miao J K, Zhu J B, et al. Cloning and sequence analysis of a Na⁺/H⁺ antiporter gene in the halophyte Limonium gmelini. Acta Prataculture Sinica, 2009

[117] Jha A, Joshi M, Yadav N S, et al. Cloning and characterization of the Salicornia brachiata Na⁺/H⁺ antiporter gene SbNHX1 and its expression by abiotic stress. Molecular Biology Reports, 2011; 38(3): 1965-1973.

[118] Khan M S. Role of sodium and hydrogen Na⁺/H⁺ antiporters in salt tolerance of plants: Present and future challenges. African Journal of Biotechnology, 2011; 10(63): 13693-13704.

[119] Wissing F. Vacuolar chloride transport in the extreme halophyte Mesembryanthemum crystallinum, of University of Oxford, 1999.

[120] Chen J, Xiao Q, Wu F, et al. Nitric oxide enhances salt secretion and Na⁺ sequestration in a mangrove plant, Avicennia marina, through increasing the expression of H⁺-ATPase and Na⁺/H⁺ antiporter under high salinity. Tree Physiology, 2010; 30(12): 1570-1585.

[121] Tan W K, Lin Q, Lim T M, et al. Dynamic secretion changes in the salt glands of the mangrove tree species Avicennia officinalis in response to a changing saline environment. Plant, Cell & Environment, 2013; 36: 1410-1422.