Differences in Response of *Suaeda* spp. to Salt Stress between Two Habitats

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Abstract *Suaeda* spp. are a type of halophytes with salinity tolerance, and they have good bioremediation function on saline soil. Starting from relevant indicators such as seed germination, growth and development, photosynthetic characteristics, pigment content, ion content and absorption, this paper summarizes the research progress on the differences in response of *Suaeda* spp. to salinity between two habitats of inland saline-alkali land and intertidal zone, so as to elaborate the similarities and differences in the physiological mechanism of *Suaeda* spp. to salinity between two habitats and reveal their different salt tolerance mechanisms.

Key words Halophytes, Inland saline-alkali habitat, Intertidal zone habitat, Response to salinity

1 Introduction

Saline soil mostly refers to salty soil and alkaline soil. According to statistics, the saline soil in the world is about 954.38 million ha, among which, the area of saline soil in China accounts for 10%[1]. Due to the increase of salt content in the soil solution, the osmotic pressure of saline soil also increases, and the effectiveness of soil moisture decreases accordingly, making it difficult for plant roots to absorb moisture, eventually causing a large-scale reduction in crop production. Therefore, how to improve saline soil has become one of the biggest challenges facing agricultural workers in China[2]. The fundamental purpose of saline soil improvement is to control the salt content in the soil in a lower range to make it adapt to the growth of crops. The main characteristics of saline land are drought and high salinity. Therefore, comprehensive treatment must be carried out by a combination of drought resistance and desalination. Currently, at home and abroad, we mainly rely on planting halophytes such as *Suaeda* spp. to absorb excess salt in the soil, thus maintaining mineral nutrients and moisture in the soil. *Suaeda* spp. have also become a research hotspot due to their simple planting and high economic benefits.

Suaeda spp., as typical herbal euhalophytes, have been widely used in the biological improvement of saline land for its characteristics of salt tolerance, drought resistance, water absorption, *etc*[3]. *Suaeda* salsa is a plant of the genus *Suaeda*. It is also called Jiancong, Chijianpeng, Haiyingcai, Yanhao, *etc*. According to reports, at present, there are mainly two environments suitable for the growth of *S. salsa*: one is the intertidal habitat that is often covered by the tide, and the other is the inland saline habitat away from the sea[4-6]. The intertidal zone is a kind of "tidal flat" in geomorphology, and refers to the place which is submerged by seawater during high tide and exposed during low tide. The total area of coastal beaches in China is about 21 700 km^2, and each year it grows at a rate of 2×10^4 to 3×10^4 km^2, mainly distributed in the northeast and north of China and the coastal areas north of the Yangtze River[7]. The inland saline-alkali habitat refers to the saline-alkali land far away from the coast. Its formation is mostly closely related to climatic conditions, geographical conditions and soil texture. According to reports, inland saline-alkali land has an area of about 99.13 million hm^2 in China. It is concentrated in inland arid and semi-arid areas, Huanghuaihai Plain and coastal areas. Liu Yu compared the soil between the intertidal zone and the inland saline-alkali land. It was found that the moisture content of the intertidal soil was significantly higher than that of the inland saline-alkali soil. In addition, the Na^+ and Cl^- contents in the intertidal zone were higher than those in the inland saline-alkali land, and the K^+ and Ca^{2+} contents in the intertidal soil were lower than those in the inland saline-alkali habitat[8].

Studies in recent years have found that planting *Suaeda* spp. in two different habitats can not only effectively reduce the surface water content, increase the contents of N, P, K and other organic matter and significantly improve the fertility of the soil but also increase the number of microorganisms in the soil and improve the saline-alkali environment by affecting the microbial community, ultimately achieving good economic and ecological benefits. Therefore, *Suaeda* spp. are ideal halophytes for improving the environment of saline-alkali soil[9-11]. To this end, from the aspects of seed germination, growth and development, ion content and absorption, photosynthetic characteristics, pigment content, *etc.*, the differences in the response of *Suaeda* spp. to salt stress between two habitats are summarized, and the physiological and molecular mechanisms of salt tolerance of *S. salsa* in two different habitats are explored, in order to provide a reference for the future use of *Suaeda* spp. in repairing saline soil and the rational promotion of *Suaeda* spp. in different habitats.

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2 Physiological differences of *Suaeda* spp. under salt stress in the two habitats

2.1 Seed germination Seeds of *S. salsa* have the characteristics of dimorphism. According to the color, they can be divided into brown seeds and black seeds. Episperm of brown seeds is soft, while that of black seeds is hard. In terms of seed germination, whether in the intertidal habitat or inland saline-alkali habitat, the germination rate, water absorption rate and emergence rate of seeds will be suppressed as the external salt concentration increases. It indicates that high salt can indeed affect the germination of *S. salsa* seeds. Gao Ben found that *S. salsa* has high salt tolerance during the germination stage of seeds[12]. In the two habitats, brown seeds have a faster seed germination rate and water absorption rate under salt stress due to their soft seed coat. Especially in the intertidal zone, the salt tolerance of *S. salsa* mainly refers to that of *S. salsa* grown from brown seeds. Taking seeds of different colors grown in the two habitats as experimental materials, Xu Yange conducted difference analysis combined with the transcriptome sequencing data. The results show that there were a total of 4 630 differential genes in black seeds in the two different habitats. Through GO (Gene ontology) gene function annotation and KEGG (Kyoto encyclopedia of genes and genomes) metabolic pathway analysis, it was found that these genes are mostly involved in the process of salt transport, metabolism and absorption. However, the above genes are rarely involved in brown seeds. It is speculated that brown seeds have higher salt tolerance, while black seeds need to start a series of gene expressions to complete the germination[13]. Shi Gongwei *et al.* studied the effects of high-salt and flooding conditions on the emergence rate of *S. salsa*. Whether in the intertidal zone or inland saline-alkali habitat, compared with black seeds, brown seeds showed a higher germination rate due to their higher ion content, while black seeds were more difficult to germinate[13]. It is speculated that this might be related to the more wax in the coat of black seeds. In the intertidal zone habitat, *S. salsa* has high salt tolerance during its seed germination stage, which might be because that the intertidal habitat itself contains less salt ions than the inland saline-alkali habitat[14]. Zhou Jiachao determined the germination rate of *S. salsa* seeds of dimorphism using salt and nitrogen interactive treatment, and it was found that the dormancy characteristic of black seeds may be due to the adaptation to low nitrogen conditions, and the application of nitrate nitrogen from outside sources may also act as a signaling molecule for the germination of black seeds[15]. This study can partially explain why brown seeds have a higher germination rate than black seeds. Therefore, it is speculated that nitrogen may participate in the germination process of *Suaeda* spp. seeds in the form of a signaling molecule.

2.2 Growth and development The growth and development of *S. salsa* is susceptible to salt stress. Peng Bin *et al.* studied the effects of different salinity treatments on the growth and development of *Suaeda* sp. in the intertidal zone and inland saline-alkali land. The results show that after treatment with 200 mmol/L of NaCl, the succulence degree, dry weight and shoot dry weight of *Suaeda* sp. increased to varying degrees[2]. However, Gao Ben found that the treatment with 200 mmol/L of NaCl had no significant effect on the biomass dry weights of roots and shoots of *Suaeda* sp. in inland saline-alkali land and intertidal zone. Regardless of habitat, *Suaeda* sp. shows strong salt tolerance[16]. As can be seen from the above research results, in a high-salt concentration environment, the growth and development of *Suaeda* spp. is determined by its own physiological characteristics, and also, it is easily affected by the external environment. In addition to the above-mentioned related research on root system and aboveground biomass, the agronomic traits such as the number of primary branches, the number of mature leaves per plant, the plant height, and the branch length of *Suaeda* spp. under different salt concentrations have also been comprehensively compared between saline-alkali land and intertidal habitat. It shows that the growth and development of *Suaeda* spp. in inland saline-alkali habitat under salt stress is significantly better than that in the intertidal zone, and the succulence degree of *Suaeda* spp. in the inland saline-alkali land is significantly higher than that in the intertidal zone. In summary, the growth and development of *Suaeda* spp. in the inland habitat is better than that in the intertidal zone[4, 8, 12, 14]. The adaptation of the halophytes *Suaeda* spp. to the saline environment mainly depends on the succulence of its leaves. The succulent leaves allow *Suaeda* spp. to store water and maintain the normal progress of photosynthesis under stress, eventually increasing the biomass content, leaf number, plant height, *etc.* of the root system and aboveground part, and ensuring the normal growth and development of *Suaeda* spp. in saline soil environment.

2.3 Ion content and absorption The contents and absorption of ions in different parts of *Suaeda* spp. are different in the two habitats. Gao Ben *et al.* found that the salt ion content of *Suaeda* sp. leaves in the intertidal zone was significantly lower than that in the inland habitat. Therefore, it is speculated that *Suaeda* spp. in the intertidal zone may have a more complete salt resistance and salt tolerance mechanism to reduce the transport of salt ions from the root system to the aerial part[12]. What's more, Gu Yinyu *et al.* and Peng Bin *et al.* found in subsequent experiments that the aboveground part of *Suaeda* sp. in the intertidal zone usually absorbed a small amount of Na^+ and Cl^- to adapt to external stresses[2, 17]. In order to explore the transport mechanism of Na^+, Cl^- and other salt ions in *Suaeda* sp., Li *et al.* conducted related research and found that compared with inland saline-alkali habitat, in the intertidal zone habitat, more NO_3^- and K^+ and less Cl^- and Na^+ in *Suaeda* sp. leaves and stems were transferred to the embryo, and more Cl^- and Na^+ were allocated to the pericarp of *Suaeda* sp. in intertidal zone. This indicates that *Suaeda* spp. in different habitats have different preferences for the absorption and accumulation of salt ions. In terms of selective absorption of salt ions by episperm, *Suaeda* spp. growing in the intertidal zone has certain advantage[18]. With *Suaeda* sp. in two different habitats as test materials, Gao Ben also found that the *Suaeda* sp. in the intertidal habitat has a strong salt rejection ability, mainly manifested in the root system's accumulating more Na^+ and Cl^-. It is speculated that the cortical parenchyma cells and the pericycle cells of the root system may have a certain compartmentalization role for salt ions.

2.4 Photosynthetic characteristics Leaf photosynthetic pigments are an important part of granum chloroplast thylakoid. Their content is an important indicator of plant photosynthesis. There are three main types of photosynthetic pigments in plants: chlorophyll, carotenoids and phycobiliproteins. Among them, content of chlorophyll can directly affect the photosynthetic rate and yield of plants. In terms of photosynthetic characteristics, whether in inland habitat or intertidal habitat, the chlorophyll content and photosynthetic oxygen release rate of *S. salsa* leaves are significantly reduced under salt treatment. Peng Bin *et al.* studied the effect of salt treatment on chlorophyll a/b. The results show that after different concentrations of salt treatment, the chlorophyll a/b of the two habitats increased to different degrees, and the degradation rate of chlorophyll b was significantly higher than that of chlorophyll a; however, the contents of chlorophyll a and chlorophyll b in *Suaeda* sp. growing in intertidal habitat were significantly lower than those growing in saline-alkali habitat. Therefore, it is speculated that the higher photosynthetic oxygen release rate of *Suaeda* spp. in inland habitat may be caused by its higher chlorophyll content. Under high temperature and high salt stress, the leaves of *Suaeda* spp. in the inland habitat may rely on high stacking of its chloroplast thylakoids to enhance photosynthesis, increase chlorophyll content and ultimately increase the plant's ability to withstand stress[16]. Liu Yu comprehensively analyzed the accumulation of pigments in *Suaeda* sp. leaves under different habitats. It was also found that the contents of chlorophyll a and chlorophyll b in the leaves of *Suaeda* sp. growing in the inland habitat were significantly higher than those in the intertidal zone, but the contents of betanin and carotenoids in leaves of *Suaeda* sp. in the seaside habitat were significantly higher than those in the inland habitat. The above results show that salt stress can stimulate the accumulation of betanin and carotenoids and inhibit the synthesis of chlorophyll a and chlorophyll b in leaves of *Suaeda* spp., ultimately resulting in purple-red *Suaeda* spp. in the seaside habitat and green *Suaeda* spp. in the inland habitat[8]. On the other hand, different habitats also have significant effects on the photosynthetic parameters of *Suaeda* spp. leaves. The study found that the stomatal conductance of mature leaves of *Suaeda* spp. in inland saline-alkali land was significantly higher than that in seaside habitat, and the maximum photochemical efficiency, PS II actual photochemical efficiency, net photosynthetic rate and photosynthetic oxygen release rate in inland saline-alkali land were all higher than those in intertidal habitat. The above results show that the ability of mature leaves of *Suaeda* spp. to absorb light energy and convert light energy to PS II in inland habitat is better than that in intertidal zone[2, 12, 16]. Shi Gongwei *et al.* and Sui *et al.* have also reached similar conclusions. It is believed that the differences in these traits may be the result of long-term adaptation of *Suaeda* spp. to different habitats. In short, *Suaeda* spp. have different photosynthetic characteristics and pigment accumulation in different habitats[5, 14]. It may be the comprehensive performance of *Suaeda*'s adapting to multiple stresses such as salt damage, drought, waterlogging damage and low temperature.

In addition to the above photosynthetic parameters, there are also research results showing that stomatal conductance is highly correlated with the salt tolerance of plants, and the closing of the stomata is the main reason for the decrease of the photosynthetic rate of *Suaeda* spp. The decrease in photosynthetic efficiency under salt stress is mainly due to stomatal limitation due to stomatal closure and non-stomata limitation caused by decreased chlorophyll photosynthetic activity. Kao *et al.* believe that the decrease in net photosynthetic rate of *Suaeda* spp. in the intertidal zone may be due to the decrease in osmotic potential, which causes the stomatal closure or NaCl-caused non-stomatal inhibition of photosynthetic organs that are not affected by stomatal closure[19]. Liu Yu found that the intercellular CO_2 concentration of mature leaves of *S. salsa* in the inland habitat was significantly lower than that in the seaside habitat, but the stomata conductance in inland habitat was higher than that of seaside habitats[8]. Based on the above results, it could be concluded that under long-term stress, the photosynthetic rate and stomatal conductance of *Suaeda* spp. in intertidal zone habitat are significantly lower than those in inland habitat, and the intercellular CO_2 concentration of *Suaeda* sp. in intertidal habitat is higher than that in inland habitat. Therefore, it is believed that the difference in the stomatal conductance of *Suaeda* spp. leaves in two habitats determines the different photosynthetic rates in the two habitats, which ultimately affects the growth and development of *Suaeda* spp.

3 Response mechanism of *Suaeda* spp. to saline environment

From the perspective of adaptability of *Suaeda* spp. to salt stress, in the 1970s, the famous British botanist Flowers began to explore the physiological mechanism of *Suaeda* spp. under salt stress[20]. The domestic research on the salt tolerance of *Suaeda* spp. started in the 1990s. Most of the work mainly focused on the physiological response of *Suaeda* spp. under salt stress, including leaf structure (degree of succulence), ion distribution and osmotic adjustment. However, the research on the salt tolerance mechanism of *Suaeda* spp. at the molecular level is not deep enough. In particular, there are few studies on the difference in response of *Suaeda* spp. to salt stress on the molecular level.

The succulence of leaves is an important means for *Suaeda* spp. to resist high salt stress. The specific manifestation is that the plant parenchyma cells proliferate in large numbers, the cell volume becomes larger, and the water content of cells increases per unit volume, thus improving the salt resistance of plants by diluting the salts in the body. Qi *et al.* found that the aquaporins (AQPs) in *Suaeda* sp. are induced by salt stress, whether at the transcriptional or protein level, up-regulation of AQPs expression can enhance cell membrane permeability. By increasing the succulence degree of leaves, the ability of the leaves to store water is improved, eventually achieving the purpose of resisting stress[21]. In addition, the proteomic analysis of *Suaeda* spp. leaves after salt treatment found that actin (Profilin) may be associated with the succulence formation of leaves, and Proflin may regulate the migration of microtubules and filaments of organelle components, ultimately affecting cell succulence[22]. Peng Bin *et al.* studied effects of different concentrations (0, 200 and 400 mmol/L of NaCl and 0, 200 and 400 mmol/L of KCl) of salt treatments on the growth and development of *S. salsa* of different seed provenances (saline-alkali land and intertidal zone). The results show that, 200 mmol/L of NaCl significantly increased the succulence degree of *S. salsa*, while 400 mmol/L of NaCl and different concentrations of KCl significantly reduced the relevant parameters[2]. Therefore, it is believed that the salt content in the soil will affect the growth and development of *Suaeda* spp. Generally, low concentration of salt promotes growth while high concentration of salt inhibits growth of plants. The specific internal physiological and molecular mechanisms still need to be further explored. In short, the succulence degree of aboveground part of *Suaeda* spp. in the inland saline-alkali land is better than that in the intertidal zone. The highly developed succulentization allows *Suaeda* spp. in inland habitat to store a large amount of water available for absorption and utilization, thereby maintaining normal physiological processes.

In addition to the structural characteristics of the blade itself, the compartmentalization of ions is another important way for *Suaeda* spp. to respond to high-salt environments. Compartmentalization refers to isolating excess salt that affects the ion balance and growth of plants to organelles with low activity such as vacuole and vesicle, in order to achieve the purpose of salt rejection and salt discharge. According to reports, *S. salsa* can transfer salt ions such as Na^+ and Cl^- in the cytoplasm to storage in plant vacuoles through compartmentalization, effectively reducing the toxic effects of salt ions on cells, and reducing the osmotic pressure and increasing the resistance to high salt stress as well[23-24]. Further analysis finds that after salt stress, the expression of Na^+/H^+ antiporter and function-related H^+-ATPase and H^+-Ppase located on the vacuole membrane is significantly increased[25-27]. It shows that the three play an important role in the compartmentalization of the vacuole. Other ion transporters such as the Ca^{2+}/H^+ antiporter have also been discovered in *Suaeda* spp. ZHAO *et al.* found that after transferring the gene *SsNHX*1 that encodes Ca^{2+}/H^+ antiporter into rice, the salt tolerance of rice was significantly improved[28]. Yan Liuhua *et al.* found that compared with that in the inland saline-alkali habitat, the seed development of *Suaeda* sp. in the intertidal zone is obviously affected by the compartmentalization of ions in seed coat, and most of Cl^- and Na^+ accumulate in organelles such as vacuole to avoid their transfer in embryos. This has a positive effect on the seeds absorbing moisture from the soil solution and rapidly sprouting[29].

In addition, the ability of osmotic adjustment is also considered to be a basic feature of plants' salt tolerance. Osmotic adjustment refers to the active accumulation of various organic or inorganic ions in *Suaeda* spp. under salt stress conditions to cope with the stress brought about by high concentration of salt ions. Under high salt conditions, the above-ground part of *Suaeda* spp. in intertidal habitat contains less salt ions, in particular, the contents of Na^+ and Cl^- are significantly lower than those in inland saline-alkali habitat. However, the root system contains more Na^+ and Cl^-. Therefore, it is speculated that on the one hand, the root system may have a more complete absorption mechanism, so that salt ions accumulate more in the roots and transfer less to the ground; on the other hand, Na^+ and Cl^- accumulated in the root system can effectively reduce the osmotic pressure, allowing *Suaeda* spp. in the intertidal zone to efficiently absorb water from the soil. Finally, it appears that the ability to transport salt ions to the ground is inhibited. In the high-salinity environment, *Suaeda* spp. can maintain normal growth and development[16]. This phenomenon also appears in other plants. For example, Yao Ruiling *et al.* reported that as the concentration of NaCl applied externally increases, most of the salt ions absorbed by the root system of *Cyclocarya paliurus* accumulate in the root epidermal layer but rarely enter the pericycle cells, so it is speculated that *Suaeda* spp. in the intertidal zone may also adsorb more Na^+ on the root surface to prevent it from entering the central cylinder, thereby inhibiting the ability of to transporting ions upward[30]. Research shows the anion NO_3^- plays a significant role in adjusting the penetration potential and improving the salt tolerance of *Suaeda* spp. Compared with inland habitat, leaves of *Suaeda* spp. in the intertidal zone will use NO_3^- for osmotic adjustment[31]. Song *et al.* compared the osmotic pressure in *Suaeda* sp. under different salt treatment conditions. It was found that the NO_3^- content in *Suaeda* sp. leaves increased significantly under the high concentration of salinity, and the increase was more obvious in the intertidal zone near the sea, indicating that NO_3^- can effectively reduce the cell water potential and promote water absorption. During the period, nitric oxide, as a signaling molecule, also participates in this process[32]. However, the molecular mechanism of NO_3^- to participate in the osmotic balance of *Suaeda* spp. under salt stress is unclear and needs to be further studied in the future. Of course, small molecular organic substances also participate in the osmotic adjustment process of *Suaeda* spp. in response to environmental changes. The most common are mainly betaine, proline, organic acids and soluble carbohydrates. In recent years, scientists have constructed a cDNA library of *Suaeda* spp. under high salt stress at the molecular level, and screened a variety of salt tolerance genes related to the synthesis of the above organic substances. As a result, more than 10 kinds of related proteins have been successfully separated and identified, resistance genes such as *SsP5CS*[6], *SsBADH*[6], *SsCMO*[33], *SsINPS*[34] and *SsMBTF*[35] have been cloned, and the salt tolerance of these genetically modified crops has been improved significantly.

4 Research prospects of *S. salsa* in two different habitats

Practice has proved that traditional physical chemistry and other methods are gradually being eliminated due to the characteristics of high cost and long cycle[36-37]. The improvement of saline soil is inseparable from salt-resistant plants. *S. salsa* is an ideal salt-resistant plant[38-39]. In recent years, a series of studies have been carried out on the physiological characteristics of salt tolerance of *S. salsa* under different habitats[40-42], which lays a foundation for understanding the salt tolerance mechanism of halophytes. But whether at home or abroad, cognition about the molecular mechanism of salt tolerance of *S. salsa* is still very limited. Therefore, it is recommended to continue relevant research in the following areas. First of all, most of the current research is focused on the aboveground part of *Suaeda* spp. It is well known that the root system is the primary part of the plant directly in contact with soil nutrients and water. Therefore, it is necessary to first study the response mechanism of *Suaeda* root system to stress factors in soil and the difference in sensing mechanism under different salt stress in different habitats. Secondly, combining the above research results, *Suaeda* sp. of the same genotype differs in salt tolerance under 2 different habitat stresses. Whether this difference is caused only by different environments or the result of interaction between environment and genotype needs further research. In addition, the current research on the salt tolerance of *Suaeda* spp. mainly reflects the measurement of some physiological indicators. In fact, the adaptation of plants to salt stress is an extremely complex process and the root perception and internal transduction system of *Suaeda* spp. needs to be studied deeply to reveal the regulatory networks and molecular mechanisms that respond to and adapt to salt stress in different habitats. Finally, with the rapid development of high-throughput technologies such as genomics, transcriptomics, proteomics and epigenetics, it has been possible to study the differences in *Suaeda* spp. of the same genotype under salt stress in different habitats at the molecular level. This provides new ideas for exploring the salt tolerance mechanism of *Suaeda* spp.

This study has identified differences in the performance of seed germination, growth and development, photosynthetic characteristics, pigment content and ion content of *Suaeda* spp. between the intertidal zone and inland saline-alkali habitat. It is recommended to excavate the traits that perform well in the intertidal zone and the inland saline-alkali land, clone the genes that control the expression of these traits and introduce them into rice, wheat and other crops, and plant these crops in the corresponding habitats to make them reach the best condition in different environments, thereby increasing the planting area and yield of the crops. Simultaneously, it is needed to further understand the physiological characteristics of *S. salsa* under salt stress in different habitats, study the internal molecular mechanism deeply, and explore the adaption mechanism of *S. salsa* populations to soil salinity combining plant physiology and molecular biology, so as to provide a reference for the improvement of saline soil in the future and the cultivation of highly salt-tolerant varieties.

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