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Research Article

Physiological Responses of Halophyte *Suaeda salsa* to Water Table and Salt Stresses in Coastal Wetland of Yellow River Delta

Soil salinity and waterlogging are two major environmental problems in estuarine wetlands. The objective of this study was to investigate the effects of salt stress, water table, and their combination on growth, chlorophyll content, antioxidant system, and ion accumulation in *Suaeda salsa* plant, which is the pioneer plant in coastal wetland of the Yellow River Delta (YRD). The results showed that plant height, number of branches, and biomass were significantly affected by water table and salt stress. With enhanced salt stress, the ratio of leaf to total biomass increased and the ratio of root to total biomass decreased. The contents of Chl-a, -b, Chl-a + b, and carotenoids (Car) decreased significantly with increasing soil salinity and the water table level. Salt stress enhanced the activity of superoxide dismutase (SOD) and catalase (CAT), but reduced the content of protein. With the lowering water table level, the activity of CAT and protein content increased, and activity of SOD decreased. Na⁺ and Cl⁻ content were up-regulated with increasing salt stress (NaCl), whereas, the contents of other cations (K⁺, Ca²⁺, and Mg²⁺) and anions (SO₄²⁻ and NO₃⁻) were decreased. In summary, the results indicated that the *S. salsa* plants could adapt to the adverse soil environments through modifying their growth and physiology status at the highly saline and intertidal zone, such as the YRD estuarine wetlands, and also could be used as a bio-reclamation plant to decline the high salt in saline soils.

Keywords: Antioxidant; Ion balance; Salt stress; *Suaeda salsa*; Water table

Received: December 5, 2010; *revised:* January 11, 2011; *accepted:* January 18, 2011

DOI: 10.1002/clen.201000557

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1 Introduction

Soil salinity is one of most important reasons for degradation of ecological environment in estuarine wetlands. Study on the response of plants to water-salt gradients in estuarine wetlands is also one of research hotspots in recent years [1–3]. The salt tolerate plants cultivation is one of the most promising strategies to ecologically and efficiently utilize salt affected lands [4–6]. Of various salt tolerant plants, *Suaeda salsa* (L.) has been ranked as most tolerance to salinity, which is a euhalophytic herb that naturally grows on highly saline soil and in the intertidal zone in Europe and East Asia, saline and alkaline soils of beaches and lakeshores in northern China [7]. The Yellow River Delta (YRD) is one of the three main estuarine wetlands in China. In recent decades, the coastal wetlands in the region were suffering ecological degradation and soil salinization due to discontinuous flow of Yellow River, marine denudation, and climate changes [8]. The habitat which was suitable to *S. salsa* was

degraded. As a matter of fact, both water table and soil salinity are important limited factors. Some researchers have studied the interactions between plant growth, community distribution, soil characteristics and water table, salt stress in the wetlands of YRD [2, 9–12], and the significant relationships between salt marsh vegetation distribution/diversity and soil chemical factors including salinity, nutrients, and pH in the Yellow River Estuary [13, 14]. Cui et al. [12] and Wang et al. [15] found that the texture of soil and the contents of salt, organic materials, and N, P changed regularly under the different vegetation types, which showed that the land use was restricted by the soil characters in the YRD, on the contrary, the land use types affected the soil characters, too. However, very few studies have performed on the morphological and physiological responses of plant to the interactions of salt stress and water table.

In this work, the interactive effects of water table and salt stress on *S. salsa* were characterized by the eco-physiological parameters including biomass of organs, leaf chlorophyll (Chl) content, ion balance, activities of antioxidant enzymes, the content of MDA, and protein in leaves. The objectives of this paper are to: (1) Investigate the adaptive mechanism of *S. salsa* to the environment with changeable salinity and water table in the YRD and (2) provide new knowledge for the restoration of degraded saline wetlands in the YRD.

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Abbreviations: CAT, catalase; Car, carotenoids; Chl, chlorophyll; LSD, least significant difference; MDA, malonaldehyde; SD, standard deviation; SOD, superoxide dismutase; YRD, Yellow River Delta

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2 Materials and methods

2.1 Experiment design

Seeds of *S. salsa* (L.) were collected from wetland of YRD in autumn 2009. After surface-sterilized with 3% sodium hypochlorite for 5 min, followed by a thorough rinsing with deionized water, seeds were kept in refrigerator at 4°C until the experiment began. In early April 2010, Seeds were sown in different heights (10–40 cm) of plastic pots containing native soils in greenhouse. The day and night temperatures in greenhouse were controlled at 30 ± 3 and 24 ± 3 °C, respectively. The seedlings were sufficiently watered every second day. The total nitrogen, available phosphorus, and potassium of the experiment soils in plastic pots were 1.12 g kg^{-1} , 12.9 mg kg^{-1} , and 203.6 mg kg^{-1} , and the total salt content were 2.22 g kg^{-1} , respectively.

The treatments combined four levels of water table with four salt levels in an orthogonal design (water table \times salt). The pots were placed in sinks with 10 cm depth to control the water table of 0, –10, –20, and –30 cm (Fig. 1). Four salt levels of 0–3% NaCl were designed in different set of sinks.

The seedlings started watering with different levels of NaCl solutions after 3 wk incubation, while the average plant height was 6.35 ± 1.37 cm. About a week later, the soil salt concentrations reached to the desired treatment levels. Then the plots were placed into sinks which filled with different salt solution. Hereafter the salt solutions in sinks were replaced every third day to avoid significant changes of salt concentrations. The pots had drainage holes in the bottom. These holes were covered with nets to prevent the soil seepage and allowed water to enter into the pot easily. Forty-eight pots were divided into four sets according to salt gradient treatment, each set contained three replicates.

2.2 Morphological indices measurements

The experiment period was lasted for 5 wk. Seedlings were thinned to 15 per pot after 7 days of sowing. The plant height was measured every 1 wk. At the end of the experiments, the harvested plants were washed with distilled water. Roots, shoots, and leaves were separated and the fresh-weight was determined for each plant. Then the plant samples were oven-dried at 105°C for 15 min, then dried at 60°C to constant weight, and the dry-weight was recorded.

2.3 Physiological indices measurements

2.3.1 Determination of chlorophyll content

After 2 wk of treatment, 0.1 g of fresh leaf were crushed and extracted with acetone for 24 h. The absorbancy of extraction

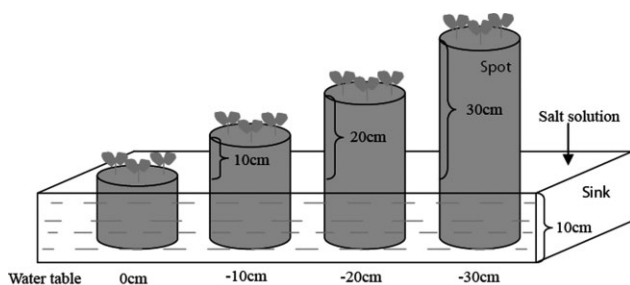


Figure 1. The sketch of experimental sink designed for controlling the water table and salt level.

solution was determined using spectrophotometer at 440, 645, and 663 nm, three replicates for each sample. The calculation methods for carotenoids (Car) and Chl-a and -b are given in Eqs. (1)–(4) [16]:

$$C_a = 12.7A_{663} - 2.69A_{645} \quad (1)$$

$$C_b = 22.9A_{645} - 4.68A_{663} \quad (2)$$

$$C_k = 4.7A_{440} - C_{a+b} \quad (3)$$

$$C_T = C_a + C_b = 8.02A_{663} + 20.21A_{645} \quad (4)$$

where C_a and C_b are the concentrations of Chl-a and -b, respectively, C_k the concentration of Car; C_T (C_{a+b}) the concentration of total Chl content, and A is the absorbancy of extraction solution.

2.3.2 Determination of enzyme activities and lipid peroxidation

For the determination of antioxidant enzyme activities, 0.2 g of fresh leaf were homogenized in 1 mL of the respective extraction buffer in a pre-chilled mortar and pestle. The homogenate was centrifuged at 15 000 rpm for 20 min at 4°C before determining the antioxidant enzyme activities. The soluble protein concentration was determined according to Bradford [17]. Activities of the antioxidant enzymes are expressed in units per gram of protein. The activities of superoxide dismutase (SOD), catalase (CAT), and malonaldehyde (MDA) content were assayed using corresponding detection kits (Jiancheng Biotechnology Companies, Nanjing, China).

2.3.3 Determination of ion contents

Dry samples of plant leaf (100 mg) were treated with 20 mL deionized water at 100°C for 20 min and the extract was taken to determine free anion contents. The contents of Cl^- , NO_3^- , and SO_4^{2-} in leaves were determined by ion chromatography (ICS-2000, Dionex, USA). A 400 mg dry sample of plant leaf was wet ashed with $\text{H}_2\text{SO}_4/\text{HClO}_4$ (10:1 v/v) digestion, then kept constant volume of 100 mL with deionized water. Atomic emission spectrometry (AA-6800, Shimadzu, Japan) were used for the determination of sodium (Na), potassium (K), calcium (Ca), and magnesium (Mg) concentrations.

2.4 Data analysis

Statistical analysis of the data, which involved data processing and variance analysis (ANOVA), was conducted using SPSS 11.5 (SPSS Inc., Chicago, IL, USA). Experimental data were subjected to two-way analysis of variance (salt stress and water table depth as main factors) and the means were separated by the least significant difference (LSD). All acquired data were represented by an average of at least three replicate measurements and standard deviation (SD). Significance was tested at the 5% level.

3 Results

3.1 Plant growth

The plant height and number of branches were affected significantly by both salt and water table ($p < 0.001$), with increasing salinity and decreasing water table, the plant height increased dramatically (Fig. 2A and B). For same NaCl concentrations treatment, the number

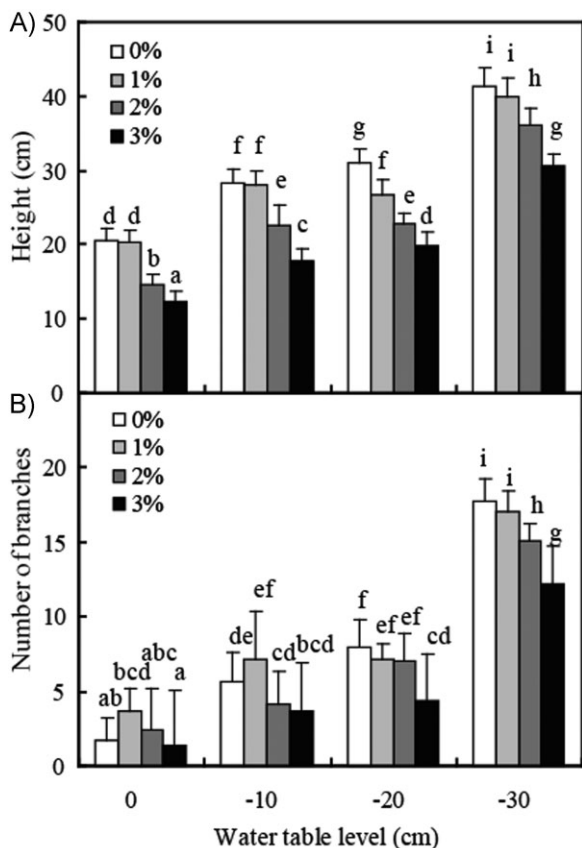


Figure 2. The plant height (A) and number of branches (B) of *S. salsa* seedlings in different treatments of water table and salt. In each column, the data markers identified with the same letters are not significantly different ($p < 0.05$) from different treatment according to a LSD test. The error bars represent \pm SD ($n = 10$) of 10 replicates.

of branches increased significantly with lowering the water table (Fig. 2B).

The total biomass of *S. salsa* seedlings increased markedly with the lowering of water table at none salt treatment (Fig. 3A). At 2 and 3%

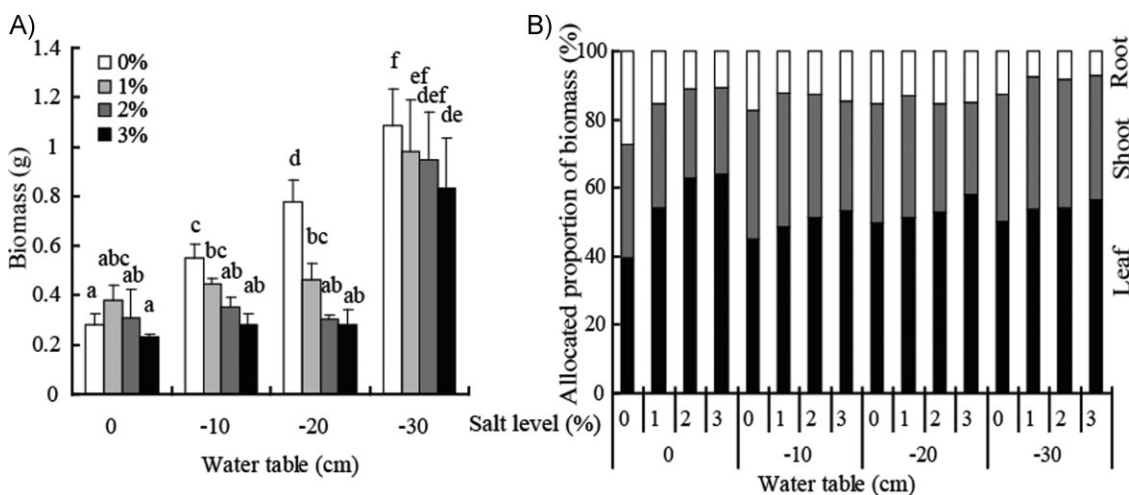


Figure 3. Total biomass (A) and allocated proportion of biomass (B) of *S. salsa* seedlings in different salt and water table treatments. Different letters indicate significant difference ($p < 0.05$) from different treatments in (A).

NaCl concentrations treatment, a significant difference of biomass could not be observed between 0, -10, and -20 cm water table, but a sharp increase of biomass was found at low water table of -30 cm (Fig. 3A). The ratio of leaf to total biomass increased with salt stress, on the contrary, the ratio of root to total biomass decreased (Fig. 3B).

3.2 Leaf chlorophyll content

The effects of water table and salt stress on content of Chl-a, -b, Chl-a + b, and Car in leaf of *S. salsa* were similar. The content of the four parameters decreased significantly with increasing both salinity and water table level (Tab. 1). The leaf Chl content was highest at the interactions of 0% salt level and water table of -20 and -30 cm, and lowest at the interactions of 3% salt stress and 0 cm water table level.

3.3 Antioxidant enzyme activities and lipid peroxidation

Salt stress enhanced the activity of SOD (Tabs. 2 and 3). For the same water table level, the activity of SOD increased significantly with salt stress. Under the condition of high salt stress, the activity of SOD decreased with the water table (Tabs. 2 and 3). The trend of the activity of CAT was similar with SOD. At the same salt stress level, the activity of CAT at water table of -30 cm was significantly higher compared to the other three water table treatments (Tab. 2). The content of MDA increased with salt stress at 0 cm water table treatment, while it peaked at salt stress of 1% for water table of -10 and -20 cm, and 2% for water table of -30 cm. The protein content in leaves increased significantly with decreasing of salt stress. At 0 and 1% salt stress levels, the protein content increased with water table level, on the contrary, the protein content decreased with the increasing of water table at 2 and 3% salt levels (Tab. 2).

3.4 Cations and anions

The content of Na^+ was very low at 0% NaCl level and increased significantly with salt stress (Fig. 4A). At same salinity treatment, the content of Na^+ increased with water table level (Fig. 4A). On the

Table 1. The effects of different water table and salt treatments on leaf Chl-a, -b, Chl-a + b, and Car content of *S. salsa* seedlings

Index	NaCl (%)	Water table depth			
		0 cm	–10 cm	–20 cm	–30 cm
Chl-a ($\mu\text{g g}^{-1}$ FW)	0	224.0 \pm 27.1 ^{Ac}	302.0 \pm 14.6 ^{Bb}	356.0 \pm 55.3 ^{Cb}	348.3 \pm 10.7 ^{Cc}
	1	139.4 \pm 14.2 ^{Ab}	162.3 \pm 28.4 ^{Aa}	217.3 \pm 9.8 ^{Ba}	247.2 \pm 59.6 ^{Bb}
	2	77.8 \pm 15.6 ^{Aa}	172.8 \pm 8.2 ^{Ba}	176.5 \pm 27.1 ^{Ba}	251.6 \pm 30.2 ^{Cb}
	3	64.9 \pm 9.4 ^{Aa}	174.8 \pm 23.5 ^{Ba}	195.7 \pm 10.9 ^{Ba}	188.3 \pm 43.6 ^{Ba}
Chl-b ($\mu\text{g g}^{-1}$ FW)	0	76.9 \pm 8.4 ^{Ac}	104.5 \pm 5.9 ^{Bb}	120.1 \pm 19.5 ^{BCb}	128.1 \pm 8.9 ^{Cb}
	1	51.1 \pm 6.4 ^{Ab}	58.5 \pm 9.2 ^{Aa}	71.2 \pm 2.6 ^{ABa}	87.1 \pm 19.6 ^{Ba}
	2	39.3 \pm 6.9 ^{Ab}	59.2 \pm 4.5 ^{Ba}	61.5 \pm 8.3 ^{Ba}	92.4 \pm 11.3 ^{Ca}
	3	24.0 \pm 4.3 ^{Aa}	64.6 \pm 7.9 ^{Ba}	68.3 \pm 4.0 ^{Ba}	67.9 \pm 13.8 ^{Ba}
Car ($\mu\text{g g}^{-1}$ FW)	0	69.3 \pm 4.2 ^{Ac}	88.5 \pm 4.1 ^{Bb}	99.2 \pm 15.0 ^{Bb}	88.4 \pm 6.0 ^{Bb}
	1	45.3 \pm 2.6 ^{Ab}	51.4 \pm 8.1 ^{ABa}	67.0 \pm 2.0 ^{BCa}	73.6 \pm 12.7 ^{Cb}
	2	29.5 \pm 4.1 ^{Aa}	52.9 \pm 5.3 ^{Ba}	51.2 \pm 7.3 ^{Ba}	71.8 \pm 9.5 ^{Cb}
	3	27.2 \pm 1.9 ^{Aa}	52.6 \pm 5.4 ^{Ba}	54.0 \pm 0.5 ^{Ba}	55.4 \pm 7.5 ^{Ba}
Chl-a + b ($\mu\text{g g}^{-1}$ FW)	0	300.9 \pm 35.5 ^{Ac}	406.5 \pm 20.3 ^{Bb}	476.0 \pm 74.7 ^{Bb}	476.4 \pm 18.3 ^{Bb}
	1	190.5 \pm 20.5 ^{Ab}	220.8 \pm 37.6 ^{Aa}	288.6 \pm 12.4 ^{ABa}	334.3 \pm 79.2 ^{Ba}
	2	117.1 \pm 21.8 ^{Aa}	232.1 \pm 12.1 ^{Ba}	238.0 \pm 35.3 ^{Ba}	344.0 \pm 41.3 ^{Ca}
	3	88.8 \pm 13.4 ^{Aa}	239.4 \pm 31.1 ^{Ba}	264.0 \pm 14.9 ^{BCa}	256.2 \pm 57.3 ^{Ca}

The values are means (\pm SD) of three replicates.

Different capital letters indicate significant differences from different water table levels and different lowercase letters indicate significant differences from different salt levels ($p < 0.05$).

Table 2. The effects water table and salt treatments on leaf antioxidant enzymes and protein (Prot.) content of *S. salsa* seedlings

Index	NaCl (%)	Water table depth			
		0 cm	–10 cm	–20 cm	–30 cm
SOD (U mg^{-1} Prot.)	0	55.00 \pm 2.75 ^{Aa}	65.24 \pm 2.48 ^{Ba}	73.43 \pm 2.52 ^{Ca}	70.54 \pm 4.18 ^{BCa}
	1	70.71 \pm 5.18 ^{Ab}	82.92 \pm 1.67 ^{Bb}	95.57 \pm 2.57 ^{Cb}	75.33 \pm 4.81 ^{ABa}
	2	137.21 \pm 5.55 ^{Bc}	99.93 \pm 6.60 ^{Ac}	106.09 \pm 2.40 ^{Ac}	99.12 \pm 3.81 ^{Ab}
	3	151.58 \pm 9.18 ^{Bd}	109.29 \pm 3.69 ^{Ad}	102.27 \pm 4.78 ^{Abc}	101.62 \pm 5.31 ^{Ab}
CAT (U mg^{-1} Prot.)	0	17.09 \pm 2.81 ^{Aa}	22.51 \pm 0.10 ^{Aab}	18.54 \pm 3.86 ^{Aa}	32.53 \pm 3.59 ^{Ba}
	1	16.27 \pm 0.61 ^{Aa}	21.26 \pm 2.12 ^{ABa}	18.74 \pm 1.61 ^{Aa}	27.60 \pm 0.53 ^{Ba}
	2	19.41 \pm 1.90 ^{Aab}	27.05 \pm 3.34 ^{Bcb}	22.47 \pm 3.08 ^{BCb}	29.17 \pm 1.87 ^{Ca}
	3	22.77 \pm 1.59 ^{Ab}	26.59 \pm 0.60 ^{Ab}	27.89 \pm 2.30 ^{Ab}	38.06 \pm 2.62 ^{Bb}
MDA (mmol g^{-1} Prot.)	0	1.01 \pm 0.18 ^{ABa}	0.93 \pm 0.02 ^{Aa}	1.11 \pm 0.09 ^{Bab}	0.68 \pm 0.14 ^{Ab}
	1	2.17 \pm 0.82 ^{Bab}	1.59 \pm 0.18 ^{ABb}	1.61 \pm 0.19 ^{ABb}	0.65 \pm 0.14 ^{Ab}
	2	3.32 \pm 0.42 ^{Bb}	1.06 \pm 0.31 ^{Aab}	0.92 \pm 0.29 ^{Aa}	0.92 \pm 0.13 ^{Ab}
	3	3.82 \pm 0.65 ^{Bb}	1.41 \pm 0.15 ^{ABb}	1.11 \pm 0.28 ^{Aab}	0.26 \pm 0.11 ^{Aa}
Protein (mg g^{-1})	0	5.12 \pm 0.11 ^{Cd}	4.29 \pm 0.29 ^{Bd}	3.80 \pm 0.17 ^{Ab}	4.03 \pm 0.19 ^{ABc}
	1	3.75 \pm 0.27 ^{Cc}	3.33 \pm 0.06 ^{Bc}	2.82 \pm 0.24 ^{Aa}	3.39 \pm 0.11 ^{BCb}
	2	1.47 \pm 0.04 ^{Aa}	2.40 \pm 0.05 ^{Ba}	2.61 \pm 0.06 ^{Ca}	3.01 \pm 0.16 ^{Da}
	3	1.93 \pm 0.16 ^{Ab}	2.96 \pm 0.12 ^{Bb}	2.81 \pm 0.18 ^{Ba}	2.83 \pm 0.14 ^{Ba}

The values are means (\pm SD) of three replicates.

Different capital letters indicate significant differences from different water table levels, and different lowercase letters indicate significant differences from different salt levels ($p < 0.05$).

contrary, contents of K^+ , Ca^{2+} , and Mg^{2+} decreased with salt stress at same water table treatment (Fig. 4B–D). With the increasing of water table (>10 cm), the K^+ content increased significantly, but at the interactions of 0 cm water table depth and 2 and 3% salt stress, the K^+ content was lowest. At low salt stress (0 and 1%), the Ca^{2+} content decreased with the water table level. The Ca^{2+} content lowered at high salt stress (2 and 3%), but at –30 cm water table treatment, there was no significant difference among different salt levels. The content of Mg^{2+} decreased significantly with water table level (Fig. 4D).

The trends of Cl^- content was similar with Na^+ , it was lowest at none salt stress, and increased significantly with the increasing of NaCl stress (Fig. 5A). At same salt stress, the content of Cl^- increased with water table level (Fig. 5A). Salt stress lowered the content of

SO_4^{2-} and NO_3^- and water table level lowered the SO_4^{2-} and NO_3^- content significantly in leaves of *S. salsa* seedlings (Fig. 5B and C). At the 0% NaCl treatment, the content of NO_3^- was highest at –30 cm water table level, but the SO_4^{2-} content was highest at water table level of –20 cm.

4 Discussion

4.1 Plant growth

It is an adaptive strategy that plant changes the morphological characteristics in different soil environment, such as plant height, number of branches, leaf area, and plant biomass [18–20]. Irving and Nathan [21] also proved that sediments subsidy could be used for

Table 3. Relationships between growth parameters of *S. salsa* seedlings and treatments of water table and salt

Index	Water table	Salt	Water table × Salt
Height (cm)	648.889 ^{a)}	197.127 ^{a)}	2.585 ^{b)}
Number of branches	223.000 ^{a)}	15.197 ^{a)}	1.879(0.06)
Biomass (g)			
Leaf	53.379 ^{a)}	3.417(0.029)	1.764(0.115)
Shoot	76.193 ^{a)}	12.506 ^{a)}	1.479(0.198)
Root	13.856 ^{a)}	45.608 ^{a)}	1.243(0.305)
Chl (mg g ⁻¹ FW)			
-a	38.266 ^{a)}	60.200 ^{a)}	1.534(0.168)
-b	35.475 ^{a)}	55.362 ^{a)}	1.670(0.128)
-a + b	37.888 ^{a)}	59.650 ^{a)}	1.525(0.172)
Car (mg g ⁻¹ FW)	31.850 ^{a)}	64.470 ^{a)}	2.330 ^{c)}
SOD (U mg ⁻¹ Prot.)	24.246 ^{a)}	231.110 ^{a)}	28.916 ^{a)}
CAT (U mg ⁻¹ Prot.)	57.522 ^{a)}	15.879 ^{a)}	5.129 ^{a)}
MDA (mmol g ⁻¹ Prot.)	14.600 ^{a)}	1.914(0.146)	2.546 ^{c)}
Protein (mg g ⁻¹ FW)	8.812 ^{a)}	257.537 ^{a)}	35.237 ^{a)}

a) F-values means significantly different at $p < 0.001$.

b) F-values means significantly different at $p < 0.01$.

c) F-values means significantly different at $p < 0.05$.

elevating salt marsh surface, which could generate a favorable environment for plant growth and potentially, marsh sustainability. So an understanding of plant response to the changes of water table depths and salt stress is important for the ecological restoration, as a strategy in dealing with salinity problem in coastal wetland. In the present study, salt stress and water table depth significantly influenced the ecological characteristics of *S. salsa*. At the same salt level, the plant height, branch number, and plant biomass under lower

water table level was greater than that under higher water table (Fig. 2A and B and Fig. 3A). This injurious effect might be caused not only by ion toxicities, but also the lack aeration in the root zone [1, 22]. The biomass allocation to leaves increased with salt stress (Fig. 3B), because leaves of *S. salsa* can absorb much more salt ions, which made them sustain high salt environment [23].

4.2 Leaf chlorophyll content

Several reports have shown that the Chl content reduced with increasing concentrations of NaCl [24, 25]. Wei et al. [25] found that NaCl induced decrease in F_v/F_m ratio in *Lycium barbarum*, which is an index of the photochemical efficiency of photosystem II (PS-II), might have resulted from a decrease in Chl concentration. In our study, a parallel trend of Chl-a and -b was found with the increasing salt stress, but at same salt stress treatment, the Chl content decreased with water table level (Tab. 1). These results indicated that the lowering salt water table level could reduce harmful effects of ion toxicities and waterlogging.

4.3 Antioxidant enzyme activities and lipid peroxidation

In order to avoid the damage of reactive oxygen species (ROS), species have developed a defensive mechanism during the process of evolution, the accumulation of harmful ROS depends on an imbalance between the rates of production and elimination through several biochemical and chemical reactions [26]. Saline stress can disrupt

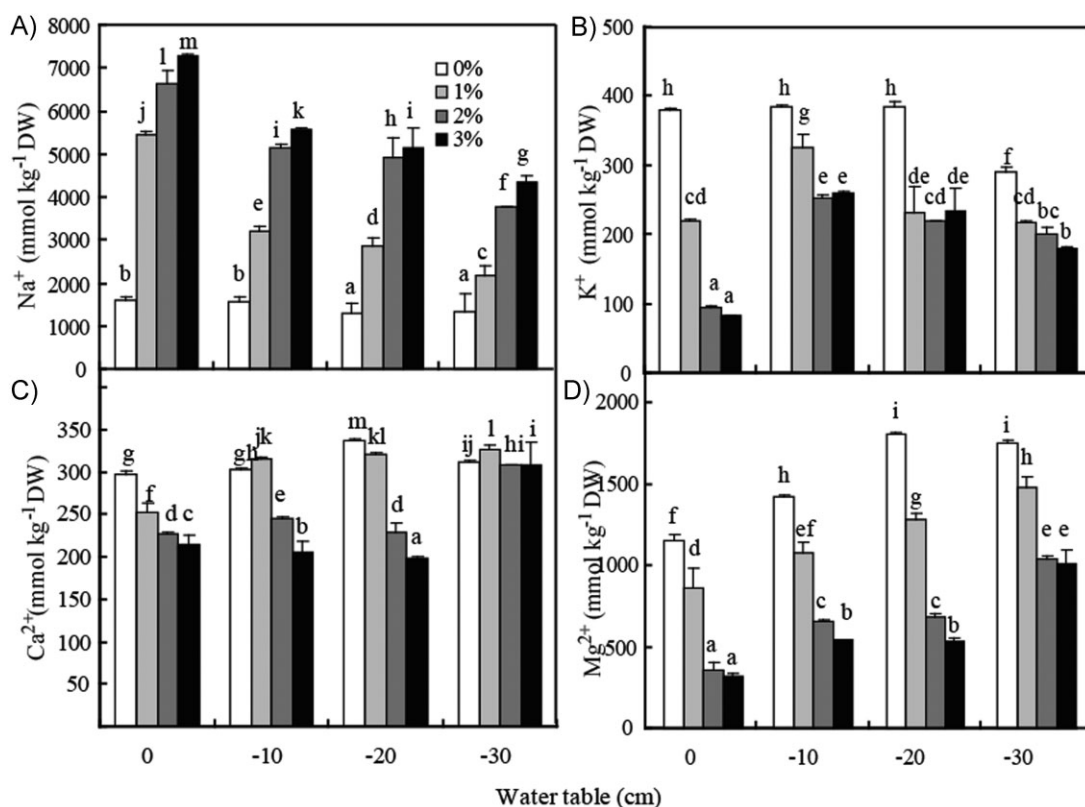


Figure 4. Effects of water table and salt stress on Na⁺ (A), K⁺ (B), Ca²⁺ (C), and Mg²⁺ (D) in leaves of *S. salsa* (L.) seedlings. The data markers identified with the same letters are not significantly different ($p < 0.05$) from different treatment according to a LSD test.

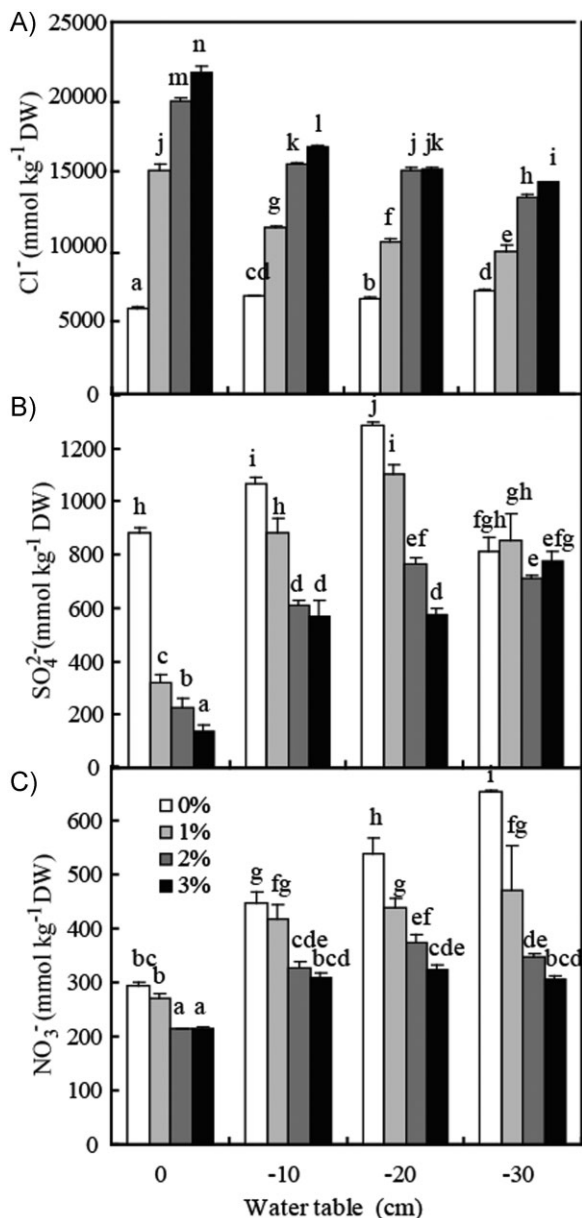


Figure 5. Effects of water table and salt stress on Cl⁻ (A), SO₄²⁻ (B), and NO₃⁻ (C) in leaves of *S. salsa* (L.) seedlings. The data markers identified with the same letters are not significantly different ($p < 0.05$) from different treatment according to a LSD test.

the cellular homeostasis of ROS and enhance the production of ROS, resulting in intracellular oxidative stress [27]. As part of defensive mechanism, the activities of antioxidant enzymes increased under salt stress [23, 27]. Our results showed that water table also significantly affected the antioxidant enzyme activities. At 2 and 3% salt stress levels, the activities of SOD decreased with the water table level (Tab. 2). These results indicated that high water table level reduced the aeration in the root zone and increased the accumulation of harmful ROS. The content of MDA, which is an indicator of intracellular oxidative stress, increased significantly with the increasing salt stress at 0 cm water table treatment, which may be caused by the interaction of salt stress and waterlogging. But at -30 cm water table depth, the content of MDA decreased with the

salt stress (Tab. 2). This result indicated that 3% salt stress could not lead to severe intracellular oxidative stress. The metabolic regulation of ROS under different salt and water table levels may be very complex. Enzyme activity can be regulated at the level of synthesis (transcription, translation, and modification of new polypeptides) or after synthesis by the action of activators and inhibitors [28].

4.4 Cations and anions

As a salt accumulator, *S. salsa* plant accumulated much more Na⁺ and Cl⁻ with the increasing salt stress (NaCl), while the content of other cations (K⁺, Ca²⁺, and Mg²⁺) and anions (SO₄²⁻ and NO₃⁻) decreased for the ion balance (Figs. 4 and 5). Although high K⁺/Na⁺ selectivity in plants under saline conditions is considered as one of the selection criteria for salt tolerance [4, 19], the accumulation of osmotic adjustments (Na⁺ and K⁺) into the vacuole is also a salt tolerance mechanism for some halophytes such as *S. salsa* [18] and *Cakile maritime* [29]. Furthermore, some other osmoregulators such as proline and amino acids can also be accumulated by plants [30]. Based on this mechanism, some researchers stated that the plantation of salt tolerant plants such as halophytes in saline soils showed an effective decline in soil salinity [30]. The accumulation of Cl⁻ in the leaves was markedly higher than that of Na⁺. Such pattern of accumulation of the toxic ions has earlier been reported in a number of plant species [18, 19, 31]. When the water table level lowered, the content of Na⁺ and Cl⁻ decreased significantly, which suggested that waterlogging could influence the salt tolerance of *S. salsa* plant. Ca²⁺ is also an important factor in the battle of Na⁺ and K⁺, increasing calcium supply has a protective effect on plants under sodium stress [32]. In the present study, compared with high water table, the Ca²⁺ content remained high at -30 cm water table, especially at 2 and 3% salt stress, which might be one of the important salt-tolerant mechanisms for *S. salsa* that can live in high saline coastal wetland in the YRD.

S. salsa plant could change its morphological characteristics, biomass allocation, activities of antioxidant enzymes, and absorb Na⁺ and Cl⁻ to adapt highly saline environments and intertidal zone, such as the YRD estuarine wetlands. Furthermore, the mechanism of accumulating salt ions into *S. salsa* plant could be an effective way to decline soil salinity, thus, plantation of *S. salsa* can also be used as bio-reclamation method to restore of degraded saline wetlands.

Acknowledgments

We are grateful for support from the Chinese Academy of Sciences (Grant # kzcx2-yw-223); The National Commonweal (Agricultural) research project (200903001); the CAS/SAFEA international partnership program for creation research team; the National Natural Science Foundation of China (30770412 and 40873062); the 100 Talents Program of the Chinese Academy of Sciences and the Science and Technology Planning Program of Shandong Province (nos. 2008GG20005006 and 2008GG3NS07005); the National Science and Technology Supporting Program of China (Grant # 2006BAC01A13); National Key Science and Technology item in "11th Five Year" period (no. 2006BAC01A13). We would like to thank the editor and the two anonymous reviewers for their helpful comments.

The authors have declared no conflict of interest.

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