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The ecological adaptability of *Phragmites australis* to interactive effects of water level and salt stress in the Yellow River Delta

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Abstract Soil salinity and waterlogging are two major environmental problems in estuarine wetlands. To prevent the typical wetland plants from degradation by soil salinization and salt waterlogging and more effectively use the plants to provide wetland ecosystem services, we examined the ecological adaptability of *Phragmites australis*, a characteristic plant species in the Yellow River Delta, to the interactive effects of water level and salt stress. The results showed that *P. australis* adapts to salt and water table stressed environments through slowing down the growth rate, maintaining the tiller number, and adjusting the biomass allocation of different organs. The highest plant height and the largest leaf area were

at 0 cm water table treatment; the 0.5 % NaCl treatment increased the aboveground biomass; higher water table increased the fibrous root biomass allocation, but largely decreased the leaf biomass. The exclusion of toxic inorganic ions such as Na^+ and Cl^- and the accumulation of organic solutes are also important mechanisms to aid survival in saline wetlands. On average 35.1 % of Cl^- and 53.9 % of Na^+ accumulated in belowground organs. The study could provide fundamental guidance for wetland restoration projects and wetland sustainable use in coastal zones such as the Yellow River Delta.

Keywords *Phragmites australis* · Ion content · Biomass · Salt stress · Water table

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Introduction

Coastal wetlands, which are normally affected by both fresh and salt water, are important natural ecosystems that provide ecosystem services (Barbier et al. 2011). Plants in coastal wetlands, which play an important role in ecosystem services, tend to suffer a number of environmental stresses, including dramatic temperature fluctuation, strong winds, flooding, high salinity, and seawater inundation (Guan et al. 2011; Wang et al. 2012; Lucas and Carter 2013). Among those, soil salinity and flooding are often regarded as the most restrictive environmental factors affecting plant growth and distribution, and even the whole coastal wetland environment (Cui et al. 2008; Di Bella et al. 2014).

The Yellow River Delta (YRD) is one of the most active land–ocean interactive regions among the large river deltas in the world. The YRD is often called the “Golden Triangle” because massive sediment transport brings fertile soil from the Loess Plateau of central China to the river mouth, leading to the expansion of YRD by 20–25 km² per year (Ren and Walker 1998; Wang and Liang 2000). However, the annual discharge of the Yellow River has gradually decreased in the past decades due to climate change and anthropogenic influence (Wang et al. 2006). Consequently, the freshwater wetland of the YRD has degraded, and both biodiversity and soil quality have been threatened by water deficiency and increasing salt stress (Shan 2007; Yu et al. 2013). A number of studies have determined the influence of salt and water table on typical plants in the YRD. For instance, *Suaeda salsa* L. Pall (= *Suaeda maritima* subsp. *salsa* (L.) Soó.), a euhalophytic herb, can grow in high salt stress environments, but cannot withstand high water table levels (Cui et al. 2008; Guan et al. 2011); while *Tamarix chinensis* Lour, a natural secondary forest shrub species, shows strong physiological drought tolerance (Xia et al. 2015).

Phragmites australis (Cav.) Trin. ex Steud. (often known as common reed) is one of the most widespread perennial grasses in the temperate region of the world (Brix 1999). It can be found in both shallow freshwater swamps and coastal salt marshes across North America, Europe, Australia, and Asia (Burdick et al. 2001; Mauchamp and Mésleard 2001; Wang et al. 2012; Achenbach et al. 2013; Guo et al. 2013). In the YRD, there are about 2600 ha of *P. australis* wetland, which

provide staging, wintering and breeding sites for birds and may directly benefit ecological restoration of wetlands (Wu et al. 2009; Wang et al. 2012).

To prevent the *P. australis* wetlands from degradation by soil salinization and salt water flooding, and more effectively use the *P. australis* wetland ecosystem services in the YRD, it is necessary to understand the mechanism of ecological adaptability of *P. australis* to the interactive effects of water level and salt stress. Most of the previous studies of the subject were focused on the niches of *P. australis* under gradients of water depth (He et al. 2008), the biodiversity of restored *P. australis* wetlands (Wang et al. 2012), and the vegetation distribution patterns corresponding to different water depths and soil salinities in the YRD (He et al. 2007). It is difficult to explain in depth the relationship between plant growth and certain factors such as salt stress and water table levels based on field investigation of the complicated environmental elements. In this study, the interactive impacts of water table levels and salt stress on the growth of *P. australis* seedlings and their physiological responses were studied in experimental greenhouse conditions. It was hypothesized that (1) a high water table treatment could reduce the growth of *P. australis*; (2) an appropriate water level has compensatory effects on the loss of growth induced by high salt stress; and (3) the adaptive mechanism involves morphological responses, such as biomass allocation, and physiological responses.

Materials and methods

Experimental design

Clones of *Phragmites australis* were collected from a brackish wetland of the Yellow River Delta. All the clones were collected from a reed community, which grew in uniformity and was within a small area of 9 m² and 10–30 cm vertical direction to maximize the probability of obtaining rhizomes originating from the clonal extension of a single genet (Deng et al. 2008). In order to produce similar-sized plants for the experiment, the clones were propagated by the layering of shoots in a pot filled with water in the greenhouse for 20 days, to initiate adventitious shoot growth at the stem nodes. Then, 5 similar-sized seedlings were planted in 15.7 L PVC pots (diameter 20 cm, height

50 cm) containing native sandy clay loam soils (48 cm from surface soil to the bottom), which was collected from the same reed community at the same time as the plant material. A permeable cloth was placed at the bottom of the PVC pots, to prevent soil leakage from the bottom. The concentrations of total nitrogen, available phosphorus, and potassium in the experimental soils were $1.40 \pm 0.21 \text{ g kg}^{-1}$, $13.4 \pm 2.5 \text{ mg kg}^{-1}$, and $222.1 \pm 13.8 \text{ mg kg}^{-1}$, respectively, and the total salt content was $2.22 \pm 0.52 \text{ g kg}^{-1}$. The day and night temperatures in the greenhouse were controlled at 30 ± 3 and $24 \pm 3 \text{ }^\circ\text{C}$, respectively. The plants were sufficiently watered every 4 days for seedling cultivation.

In total, 240 plants were used for the experiment. The treatments combined four levels of water table with three salt levels in an orthogonal design (water table \times salt). The pots were placed in sinks with a depth of 80 cm to control a water table of -30 , 0 , and 30 cm, respectively, and with a soil water content of 60–80 % as a control. Forty-eight pots were divided into 12 sets according to different water table and salt gradient treatments, and each set contained 4 replicates. Three salt levels, i.e., 0, 0.5, and 1 % NaCl, were designed in different sets of sinks.

The plants started to be watered with different levels of NaCl solutions after three weeks of recovery while the average plant height achieved 18.98 ± 2.27 cm. About a week later, the soil salt concentrations reached the desired treatment levels. Then the plots were placed into sinks which were filled with different salt solutions. Thereafter, the salt solutions in sinks were replaced every 2 weeks to avoid significant changes of salt concentrations. The pots had drainage holes in the side. These holes and the bottom of each pot were covered with permeable cloth to prevent soil seepage and allow water to enter into the pot easily.

Morphological indices measurements

The experiment lasted for 6 months. Plant height, stem diameter, tiller number (per plant), and leaf area (the second fully unfolded leaf from the top of the plant) were measured before harvest. At the end of the experiment, the harvested plants were washed with distilled water. Taproots, fibrous roots, shoots, and leaves were separated for each plant. The plant samples were oven-dried at $105 \text{ }^\circ\text{C}$ for 15 min, and

then dried at $60 \text{ }^\circ\text{C}$ to constant weight; the dry weight was recorded.

Determination of ion contents

Dry samples of plant leaves (100 mg) were treated with 20 ml of deionized water at $100 \text{ }^\circ\text{C}$ for one hour, and the extract was taken for determination of free ion contents. An atomic emission spectrometer (AA-6800, Shimadzu, Japan) was used to measure sodium (Na) concentrations, and ion chromatography (ICS-2000, Dionex, USA) was used for chloride (Cl) concentrations.

Determination of proline, soluble sugar and protein content

The concentration of proline and soluble sugar in the dry plant samples was measured, respectively, using ninhydrin and anthrone (Zhu et al. 1983).

For protein measurement, 0.1 g of fresh leaves was homogenized with 0.9 ml of ice-cold normal saline. Homogenates were then centrifuged at 2500 rpm at $4 \text{ }^\circ\text{C}$ for 10 min. The supernatants were used for the determination of the soluble protein contents (Bradford 1976).

Data analysis

Statistical analysis was performed using IBM SPSS 20.0. Experimental data were subjected to two-way analysis of variance (salt stress and water table level as main factors), and the means were separated by the least significant difference (LSD). All acquired data were represented by the average of four replicate measurements and standard deviation (SD). Significance was tested at the 5 % level.

Results

Effect of salt and water table on plant morphology

Plant heights were affected significantly by both salt ($p < 0.01$) and water table ($p < 0.001$) (Fig. 1; Table 1). As the salt stress increased, the plant height decreased significantly. Plants in the three water table treatments (-30 , 0 , and 30) were taller than the control. The tallest plant was at 0 % NaCl treatment

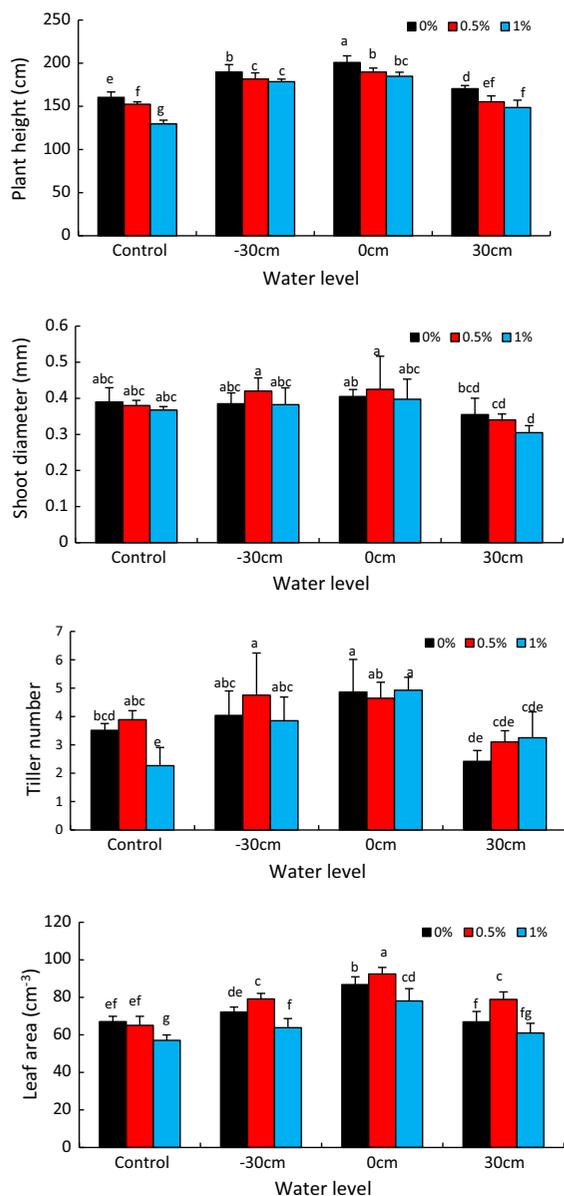


Fig. 1 Plant height, shoot diameter, tiller number, and leaf area of *P. australis* in different water table level and salt treatments. In each column, the data markers identified with the same letters are not significantly different ($p < 0.05$) according to a least significant difference test

under 0 cm water table depth. Among different water table treatments, the plant height decreased significantly with increasing or decreasing water table depth from 0 cm water table.

Shoot diameters and tiller numbers were significantly affected by water table (Fig. 1; Table 1), but no significant differences were observed between

different salt stresses. The lowest shoot diameter appeared in the combination of 1 % NaCl and 30 cm water table, and the lowest tiller number in the combination of 1 % NaCl and control water table treatment.

Leaf area, which was stimulated by 0.5 % NaCl in all three water table treatments, (−30, 0, and 30), was higher than in 0 and 1 % NaCl treatments. Water table levels also significantly affected plant leaf area (Table 1). The highest leaf area appeared in the combination of 0.5 % NaCl and 0 cm water table treatment.

Effect of salt and water table on plant biomass

Salt stress ($p < 0.05$, Table 1) and water table ($p < 0.01$, Table 1) had significant effects on plant leaf biomass, which was highest (4.49 g/plant) in the −30 cm water table level and 0.5 % NaCl treatment and lowest (1.13 g/plant) in the 30 cm water table level and 0 % NaCl treatment. Shoot biomass, taproot biomass, fibrous root biomass, and total plant biomass were significantly affected by water table and the combination of water table and salt stress, but no significant differences were observed between different salt stresses (Table 1). Similar to leaf biomass, the biomass of shoot (8.50 g/plant), taproot (13.09 g/plant), and total plant (30.16 g/plant) were highest in the combination of −30 cm water table level and 0.5 % NaCl treatment. The fibrous root biomass showed a difference, the highest of which was 6.51 g/plant under the combination of 0 cm water table level and 0.5 % NaCl. More biomass accumulated in aboveground organs with the increasing of salt stress. The highest ratio of leaf, shoot, taproot, and fibrous root to total biomass occurred in the combination of control and 1 % NaCl stress, 30 cm water table level and 0.5 % NaCl stress, −30 cm water table level and 1 % NaCl stress, and 0 cm water level and 0 % NaCl stress, respectively (Fig. 2).

Effect of salt and water table on Na⁺, Cl[−] contents

Na⁺ content significantly increased with increasing salt stress ($p < 0.05$) and also was affected dramatically by the combination of salt stress and water table level ($p < 0.05$) (Fig. 3; Table 1). No significant differences of Na⁺ content were observed between different water table levels. When belowground and

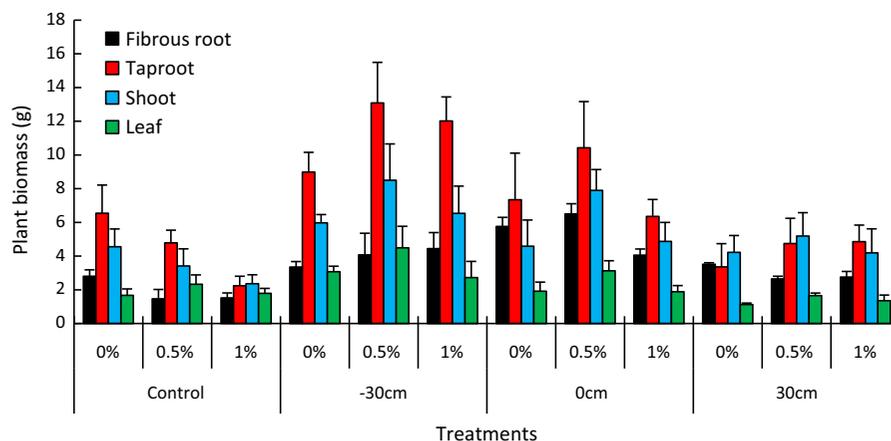
Table 1 Relationships between growth parameters of *P. australis* plants and treatments of salt and water level

	Salt	Water level	Salt × water level
Plant height (cm)	14.479**	47.252***	3.797**
Shoot diameter (mm)	4.390	16.996**	0.447
Tiller number	1.110	8.469*	1.654
Leaf area (cm ²)	27.483**	42.203***	1.247
Biomass (g)			
Leaf	9.219*	16.19**	1.303
Shoot	2.819	5.83*	2.444*
Taproot	1.378	9.949**	3.672**
Fibrous root	0.725	9.751*	3.984**
Total plant	2.160	9.992**	3.745**
Na ⁺ content (mg/g)			
Leaf	7.843*	2.507	11.006***
Shoot	9.698*	1.366	8.869***
Taproot	12.766**	0.669	2.947*
Fibrous root	16.345**	0.276	4.692**
Cl ⁻ content (mg/g)			
Leaf	11.989**	3.736*	1.975
Shoot	7.428*	0.327	13.986***
Taproot	17.976**	0.041	2.873*
Fibrous root	11.462**	1.141	4.141**
Proline content (mg/g)	8.335*	2.500	10.046***
Soluble sugar content (mg/g)	18.554**	3.852	1.152
Protein content (mg/g)	1.279	2.656	5.331**

*** Significantly different at $p < 0.001$

** Significantly different at $p < 0.01$

* Significantly different at $p < 0.05$

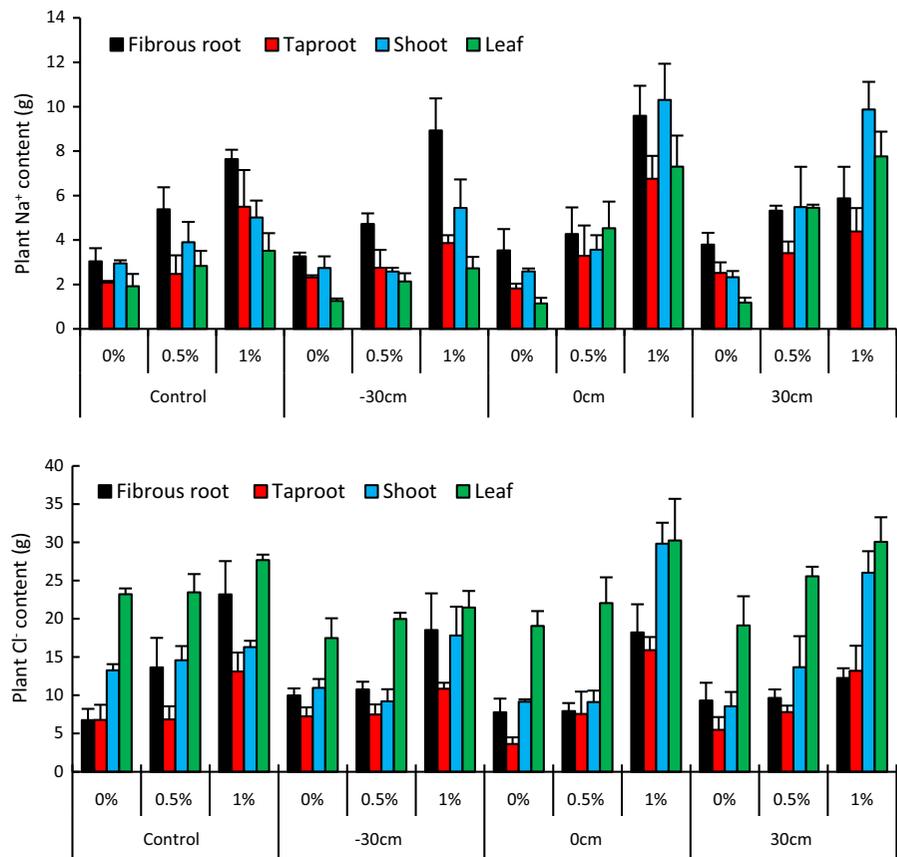
**Fig. 2** Leaf, shoot, taproot and fibrous root biomass of *P. australis* in different salt and water table level treatments

aboveground plant portions were compared, an average 53.9 % of Na⁺ accumulated in the belowground portion. The percentage of Na⁺ in roots (taproot and fibrous root) slightly increased with increasing soil salt when the water level was below ground (control and -30 cm water table), but as the plant was inundated

with water (0 cm and 30 cm water table), the aboveground plant (leaf and shoot) accumulated more Na⁺ with the increasing salt stress (Fig. 3).

A similar trend was observed in Cl⁻ content, which was also increased significantly by salt stress ($p < 0.001$, Fig. 3; Table 1). No remarkable

Fig. 3 Na^+ and Cl^- content in leaf, shoot, taproot and fibrous root of *P. australis* in different salt and water table level treatments



differences in the Cl^- contents of leaf occurred between different water table levels (Table 1). The average Cl^- allocation in the leaf was about 40 %, and on average less than 40 % of Cl^- accumulated in root (taproot and fibrous root), which was different from Na^+ allocation (Fig. 3).

Effect of salt and water table on osmotic parameters

Proline is a typical organic osmolyte closely related to osmotic stress intensity. When there was no salt stress, proline concentrations increased significantly with increasing water table (Fig. 4). At the same water table level, proline concentrations increased dramatically with the increasing of salt stress. However, no significant differences were observed at the 30 cm water table treatment among different salt stresses.

The response of soluble sugar concentrations to salt stress was observed differently compared to the responses of proline concentrations. With the increase

in salt stress, the soluble sugar concentrations decreased significantly at all levels of water table (Fig. 4). No obvious trends were observed between different water tables.

The protein content was the lowest in the interaction of control water treatment and 0 % salt treatment. With the increasing of salt stress and water table level, the protein content increased dramatically (Fig. 4).

Discussion

As one of the important, widespread and constructive wetland plant species over the YRD, *P. australis* is often the first choice for wetland restoration. So it is essential to understand the ecological responses of *P. australis* to the interactive effects of water table level and salt stress. The present study showed that 0 cm water table is the most suitable level for the growth of *P. australis*, with plant height, shoot diameter, tiller number, and leaf area all showing better performance

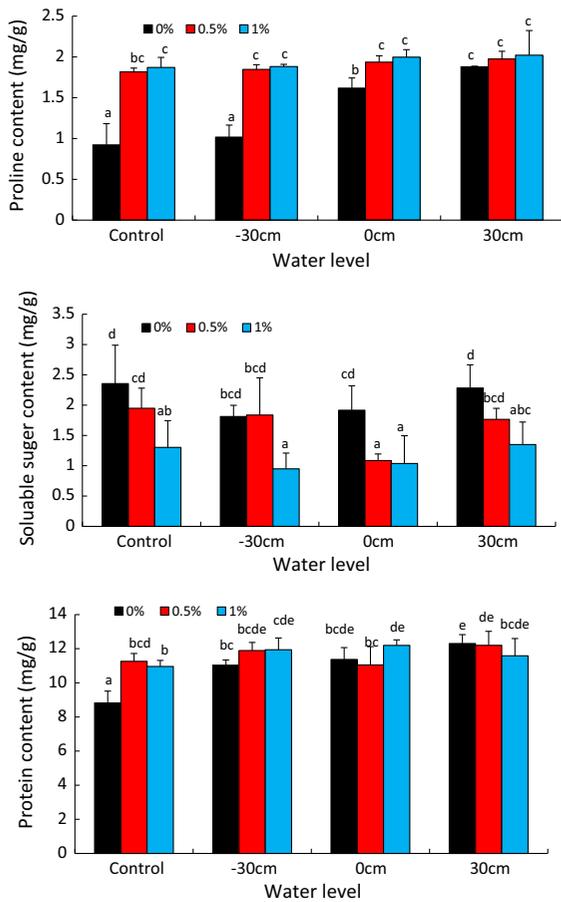


Fig. 4 Effect of salt stress and water level on proline contents, soluble sugar content and protein contents in leaves of *P. australis*. In each column, the data markers identified with the same letters are not significantly different ($p < 0.05$) according to a least significant difference test

compared to other water tables. Similar relationships were also reported by previous studies. *Suaeda salsa*, which is the main pioneer plant species in the YRD, showed significant increases in both plant height and branch number with decreasing water table depth (Guan et al. 2011). Similarly, the shoot biomass response of *Asteriscus maritimus* (L.) Less (= *Pallenis maritima* (L.) Greuter), which is often planted in saline agricultural land, is severely affected by a combination of salt and waterlogging treatments (Rodríguez et al. 2005), which confirmed that, in general, the first symptoms of environmental stress in plants are the restriction of plant shoot growth and leaf expansion (Sánchez-Blanco et al. 1998; Rodríguez et al. 2005). Based on our results, we can speculate that a moderate

growth strategy, such as a slowing down of growth rate and consistent tiller number under saline conditions (as occurs at 1 % salt solutions), strongly determines higher tolerance to a saline waterlogging environment, such as the intersection of Yellow River freshwater and Bohai seawater in the YRD.

Interestingly, the 0.5 % NaCl treatment increased the aboveground biomass (both shoot and leaf) of *P. australis*, with the exception of shoot biomass in control water treatment. This indicated a positive response from *P. australis* growth to mild salt stress when compared to no salt and high levels of salt stress, especially within a suitable water table conditions. The biomass accumulation results confirmed our first and second hypothesis, which predicted that in higher saline condition, an appropriate water table level could increase plant biomass when compared with control or higher water table treatment. One primary reason could be the low oxygen status under higher water table levels and concomitant energy shortage (Mommert et al. 2006; Rodríguez et al. 2005). When a seedling is exposed to a high water table, anaerobic respiration and reserved carbohydrates will be used to tolerate long-term anoxic conditions (Gibbs and Greenway 2003). Voeselek reported that plants can elongate the shoot organs out of water to restore contact with the atmosphere (Voeselek et al. 2003). Similar results were observed in this study, showing the shoot biomass allocation increased at the high water table level compared to lower water table treatments. Moreover, we also found that the fibrous root biomass allocation increased in higher water table treatments (0 and 30 cm), whereas leaf biomass largely decreased. One point of view believes that the developed fibrous root system in flooding is not the most crucial requirement for survival, and furthermore, these roots need a continuous oxygen supply (Vartapetian and Jackson 1997). However, results similar to this study were obtained elsewhere (Banach et al. 2009). It is generally believed that more tolerant species can photosynthesize under water and also possess an efficient within-plant system of gas transport (Blom et al. 1994; Banach et al. 2009).

Previous studies have shown that as a salt tolerant plant, when *P. australis* is exposed to saline conditions, ion exclusion from plant tissues is the first attempt to protect the plant against salt stress, and the ion uptake is most likely isolated in the vacuoles (Achenbach et al. 2013; Achenbach and Brix 2014).

After 6 months of exposure to saline conditions in this study, the Na⁺ and Cl⁻ contents of *P. australis* increased substantially, and water table treatments had no significant effects on ion contents. The allocation of Na⁺ and Cl⁻ in different organs showed different trends, with 53.9 % of Na⁺ being accumulated in belowground organs, while about 64.9 % of Cl⁻ accumulated in aboveground organs. Similar results were also found by a previous study (Achenbach and Brix 2014). This could be attributed to a decrease in the Na⁺ release rate from xylem parenchyma cells to xylem, and/or an occurrence of Na⁺ retranslocation from shoot to root (Matsushita and Matoh 1991).

Organic solutes, such as proline, may accumulate in the cytoplasm and organelles to balance the low osmotic potential in the vacuole when in stress environments such as salt or flooding (Hasegawa et al. 2000). This is consistent with the results obtained in this study, in which the accumulation of proline was clearly a response to osmotic stress to salt and the combination of salt and water table. Previous studies have demonstrated that proline could preserve protein structure and activity and reduce enzyme denaturation by inactivating hydroxyl radicals and other reactive chemical species (Saradhi et al. 1995; Yang et al. 2007). This finding was verified by our experimental results. The protein content of leaves in different treatments showed similar trends with proline content (Fig. 4). Soluble sugar is another important organic osmotic compound, which can contribute to up to 50 % of the total osmotic potential in some glyco-phytes subject to salt stress (Ashraf and Harris 2004; Cram 1976). However, salinity may increase soluble sugar in some plant species (De Lacerda et al. 2003) or decrease it in others (Agastian et al. 2000). The soluble sugar in the leaves of this study showed a significant decrease with increasing salt stress. No significant effects were observed in water table treatments or from the combination of salt stress and water table levels.

Conclusions

In summary, understanding the mechanism of the typical dominant plants in resisting different saline and water table stresses is important for the ecological recovery and exploitation of the newly accreted coastal wetland soil in regions of active biogeochemical

interactions between land and ocean waters. *P. australis* plant could adapt to the different saline and water table depth environments in the YRD through the slowing down of growth rate, keeping a consistent tiller number and adjusting the biomass allocation of different organs. The plant traits of osmoregulation are another important survival mechanism in saline wetlands, which include the exclusion of inorganic ions dominated by Na⁺ and Cl⁻, and the accumulation of organic solutes dominated by proline. The results elucidated the adaptive mechanism of the typical *P. australis* clone plant in response to saline and water table stress from ecophysiological aspects. The study could provide fundamental guidance for wetland restoration projects and wetland sustainable use in coastal zones such as the YRD.

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