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Article

Plant distribution can be reflected by physiological responses to salinity of three submerged macrophytes from the Modern Yellow River Delta

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With 4 figures

Abstract: Patterns of distribution vary greatly among species in the Modern Yellow River Delta, the largest estuarine wetland in China. Although salinity has been considered as the key factor determining plant distribution patterns in this delta, the intrinsic mechanisms accounting for distribution patterns are far from clear. To this end, three submerged macrophytes (*Ceratophyllum demersum* L., *Potamogeton perfoliatus* L. and *Myriophyllum spicatum* L.) were grown in 0.2 (control), 1.2, 2.4 and 3.6 psu salinity waters. The relative growth rate (RGR), content of MDA (malondialdehyde) and activities of the enzymes (SOD – superoxide; POD – peroxidase; CAT – catalase; APX – ascorbate peroxidase) in leaves were investigated. The RGR of *M. spicatum* decreased only in the 3.6 psu treatment, while those of *C. demersum* and *P. perfoliatus* declined significantly with increasing salinity. Compared to the control, RGR of *M. spicatum*, *C. demersum* and *P. perfoliatus* decreased by 31.8 %, 78.5 % and 71.0 % while the MDA content increased by 12.0 %, 35.9 % and 28.3 % in the 3.6 psu treatment, respectively, indicating that *M. spicatum* had a higher salinity tolerance ability than the other two species. The activities of four antioxidative enzymes increased with increasing salinity in *M. spicatum*. However, for *C. demersum* and *P. perfoliatus,* the four antioxidative enzymes increased in the 0.2 to 2.4 psu treatments, but decreased subsequently in the 3.6 psu treatment except for the activities of SOD and APX in *C. demersum*. It is concluded that antioxidative enzymes can protect *M. spicatum* from oxidative stress under higher salinity, but that this mechanism is absent in *C. demersum* and *P. perfoliatus*.

Key words: Antioxidative enzyme, estuarine wetland, salinity stress, MDA.

1 Introduction

In wetlands, plant zonation along environmental gradients such as flooding, nutrient and salinity is a common phenomenon (Verhoeven & Vierssen 1978, Luo et al. 2008). For example, in the Modern Yellow River Delta (MYR), the largest estuarine wetland in China, an obvious succession series closely related to water and soil salinities was found (Zhang et al. 2007). That is, only some halophytes, such as *Spartina alterniflora*, *Suaeda salsa* and *Ruppia maritima*, can occur in areas nearby the coastline, while with increasing distance from the coastline, the dominant communities have changed to *Phragmites australis*, *Myriophyllum spicatum*, and *Aeluropus sinensis* (Zhang et al. 2007). Even though much work has been done to investigate the relationship between salinity and plant distribution patterns in this delta (Zhang et al. 2007, Li et al. 2009),

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the intrinsic mechanisms accounting for the presence or absence of species along a salinity gradient are far from clear.

Tolerance is the ability of an organism to avoid displacement during a stress period, and a more tolerant organism usually undergoes small changes in a state or flux variable after disturbance (Fritz & Dodds 2004). In salt marsh and estuarine wetlands, differences in plant tolerance to salinity play an important role in vegetation distribution and development (Selig et al. 2007). A high salt concentration can cause ionic imbalance resulting in ion toxicity and osmotic stress, and can lead to oxidative stress through an increase in reactive oxygen species (ROS), such as superoxide ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH•) (Alscher et al. 1997, Mittler 2002, Masood et al. 2006). ROS are highly reactive and cause oxidative damage to lipids, proteins and nucleic acids, disrupting plant metabolism and ultimately affecting plant distribution (Alscher et al. 1997, de Azevedo Neto et al. 2006).

Niche separation, a basic theory for explaining plant distribution, in a stressful gradient is closely related to the variation in physiological traits of plants (Luo et al. 2008). De Azevedo Neto et al. (2006) have indicated that malondialdehyde (MDA), the decomposition product of polyunsaturated fatty acids of biomembranes, can accumulate under salt stress and a higher increment can be found in salt-sensitive plants than salt-tolerant plants. Therefore, MDA content can be used as an indicator of plant's salt-tolerance ability. Moreover, to alleviate oxidative damage, a complex antioxidative system, especially the antioxidative enzymes, such as superoxide, peroxidase, catalase, ascorbate peroxidase, is developed for ROS scavenging (Masood et al. 2006). A higher activity of antioxidative enzymes usually indicates higher salinity tolerance ability (de Azevedo Neto et al. 2006, Sekmen et

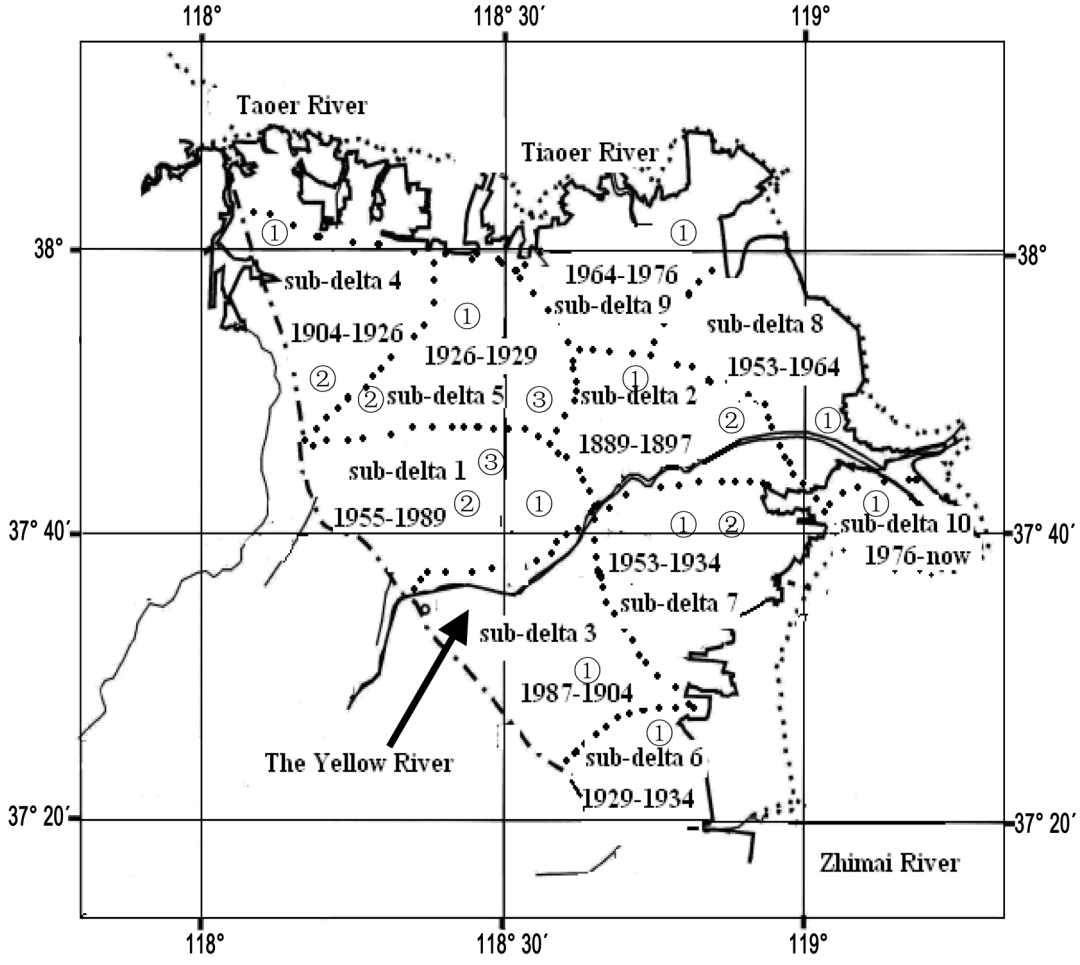

Fig. 1. The distribution of three species in the sub-deltas of the Modern Yellow River Delta. *Myriophyllum spicatum* (1) can be found in each sub-delta; *Potamogeton perfoliatus* (2) was found in sub-delta 1, 2, 4, 5 and 7; *Ceratophyllum demersum* (3) was only found in sub-delta 1 and 5. The dates in the figure indicate the forming time of each sub-delta.

al. 2007, Xue & Liu 2008). Therefore, the activities of antioxidative enzymes can also be used as an integrative indicator to estimate plant's ability to salinity tolerance, and differences among species might account for plant distribution patterns.

The Modern Yellow River Delta is located in the northern part of Shandong Province and is composed of 10 sub-deltas which were formed at different times due to changes in the rivers course (Fig. 1; Xu 2008). Aquatic macrophytes are sensitive to environmental changes, and have an important function in maintaining ecosystem health, such as stabilizing sediments and providing food and shelter for other organisms (Lacoul & Freedman 2006). To evaluate the role of antioxidative enzymes in accounting for plant distribution patterns in this delta, three submerged macrophytes with different distribution patterns were treated with four salinity levels. *Myriophyllum spicatum* is distributed widely in the whole delta over a salinity range from 0.57 to 9.37 psu, while *Potamogeton perfoliatus* and *Ceratophyllum demersum* were only found in the sub-delta that had formed a longer time ago (Fig. 1), where the salinity is 1.13–3.66 psu and 0.85–4.00 psu, respectively (Li et al. 2009). Moreover, these three species have different niche breadth (*M. spicatum*, 0.673; *P. perfoliatus*, 0.351; *C. demersum*, 0.100) in this delta (Li et al. 2009). Based on these different distribution patterns, we tested the following hypotheses: First, the relative growth rate will decrease more dramatically with enhancing salinity in *C. demersum* and *P. perfoliatus* than in *M. spicatum*. Second, MDA contents in *C. demersum* and *P. perfoliatus* will increase more markedly than those in *M. spicatum* in the high salinity environment. Third, the activities of antioxidative enzymes in response to salinity stress will be higher in *M. spicatum* than in *C. demersum* and *P. perfoliatus*.

2 Material and methods

2.1 Plant material

Shoots of the three species (*Myriophyllum spicatum*, *Potamogeton perfoliatus* and *Ceratophyllum demersum*) and the sediment (containing 1.08 g kg^{-1} organic matter, 0.79 g kg^{-1} total N, 0.06 g kg^{-1} total P and 3.4 g kg^{-1} NaCl) were collected from a typical pond (E:118° 25′ 5.7″; N: 37° 39′ 46.3″) in the Modern Yellow River Delta in June, 2008. After collection, shoots were put in three water-filled buckets (22 L), then transported to an outdoor net-house in the Institute of Subtropical Agriculture, the Chinese Academy of Sciences, and pre-incubated in tap water (containing 0.511 µg L^{-1} NH_4^+–N, 1.760 µg L^{-1} NO_3^--N and 0.527 µg L^{-1} PO_4^{3+}-P, pH 7.2) for 15 days. The net-house was covered with one layer nylon-net and the light was about 50 % of full sun. The average temperature was about 25.5 °C during the experimental period.

After pre-incubation, 88 apical shoots of each species with a length of 12 cm were planted in sediment-filled plastic pots (8 cm in diameter, 15 cm in height, one shoot per pot) with the lower 2 cm buried in the sediment. All pots were placed into 8 large plastic bins (78 cm × 56 cm × 60 cm, 11 pots per bin per species), in a water depth of 30 cm.

2.2 Experimental set-up

Experimental treatments were initiated one week after transplantation. Prior to the experiment, growth parameters of 8 seedlings (per plant per bin) for each species were measured for the calculation of relative growth rate. Four salinity levels (control, 1.2, 2.4, 3.6 psu) were used in the experiment. The salinity in the control treatment was 0.2 psu and the other three treatments were obtained by mixing different ratios of tap water with artificial seawater (to 1 L tap water 22.4 g NaCl, 2.6 g MgCl. $6H_2O$, 0.9 g $CaSO_4$. $2H_2O$, 1.9 g $MgSO_4$. $2H_2O$ and 0.8 g KCl were added). Each bin was evenly divided into three plots and ten pots of each species were distributed randomly in each plot. There were a total of eight bins and two bins were used for each salinity treatment. The highest salinity content was set up on the basis of a preliminary experiment, which showed that *P. perfoliatus* began to die in 4.29 psu salinity water. Salinity was measured by a portable multi-parameter water quality tester (HANNA HI98201, Italy), and was adjusted daily. Tap water was supplied according to plant growth and its salinity content was also adjusted depending on the designated treatment. The final water depth was 58 cm.

2.3 Harvest and relative growth rate (RGR)

The plants were harvested after an incubation period of 30 days. Six plants of each species were randomly selected from each bin and 1 g of fresh leaf samples from each plant were collected for the analysis of physiological traits. Then, plant roots were carefully dug out and cleaned with tap water. The plants were divided into leaves, stems and roots. Fresh weights of each part were determined before they were oven dried at 80 °C for 48 h and weighed. The biomass of the leaves used in the analysis of physiological traits was also added to the corresponding plant biomass by conversion of fresh weight to dry weight. RGR was calculated using the following equation: $RGR = (\ln w_2 - \ln w_1) / (t_2 - t_1)$, where w_1 is the initial dry mass, w_2 the dry mass at harvest time t_2, and $(t_2 - t_1)$ the experimental time.

2.4 MDA content

The content of MDA was measured using the method of Duan et al. (2005). 0.5 g fresh leaves were homogenized in 10 ml 10 % trichloroacetic acid (TCA) and centrifuged at 14,000 × g for 10 min. Then, 2 ml 0.6 % thiobarbituric acid (TBA) in 10 % TCA was added to an aliquot of 2 ml of the supernatant. The mixture was then heated for 30 min in boiling water, and cooled quickly in an ice bath. After centrifugation at 10,000 × g for 10 min, the absorbance of the supernatant was determined with a spectrometer at 450, 532 and 600 nm. The MDA concentration was calculated using the formula: $C\ (\mu mol\ L^{-1}) = 6.45(A_{532} - A_{600}) - 0.56A_{450}$ and was expressed as µmol g^{-1} FW (Yang et al. 2009).

2.5 Enzyme extractions and assays

For SOD, POD, CAT and APX extraction, fresh leaf samples (0.5 g) were homogenized with pre-chilled pestle and mortar in ice-cold 0.1 M phosphate buffer (pH 7.5, 5 ml) containing 0.5 mM EDTA, then centrifuged at 15000 × g (4 °C) for 20 min. The supernatant was used for enzyme activity analysis (Esfandiari et al. 2007).

SOD activity was estimated by measuring its ability to inhibit the photochemical reduction of nitro blue tetrazolium (NBT; Stewart & Bewley 1980). One unit of SOD activity was defined as the amount of enzyme, which causes 50 % inhibi-

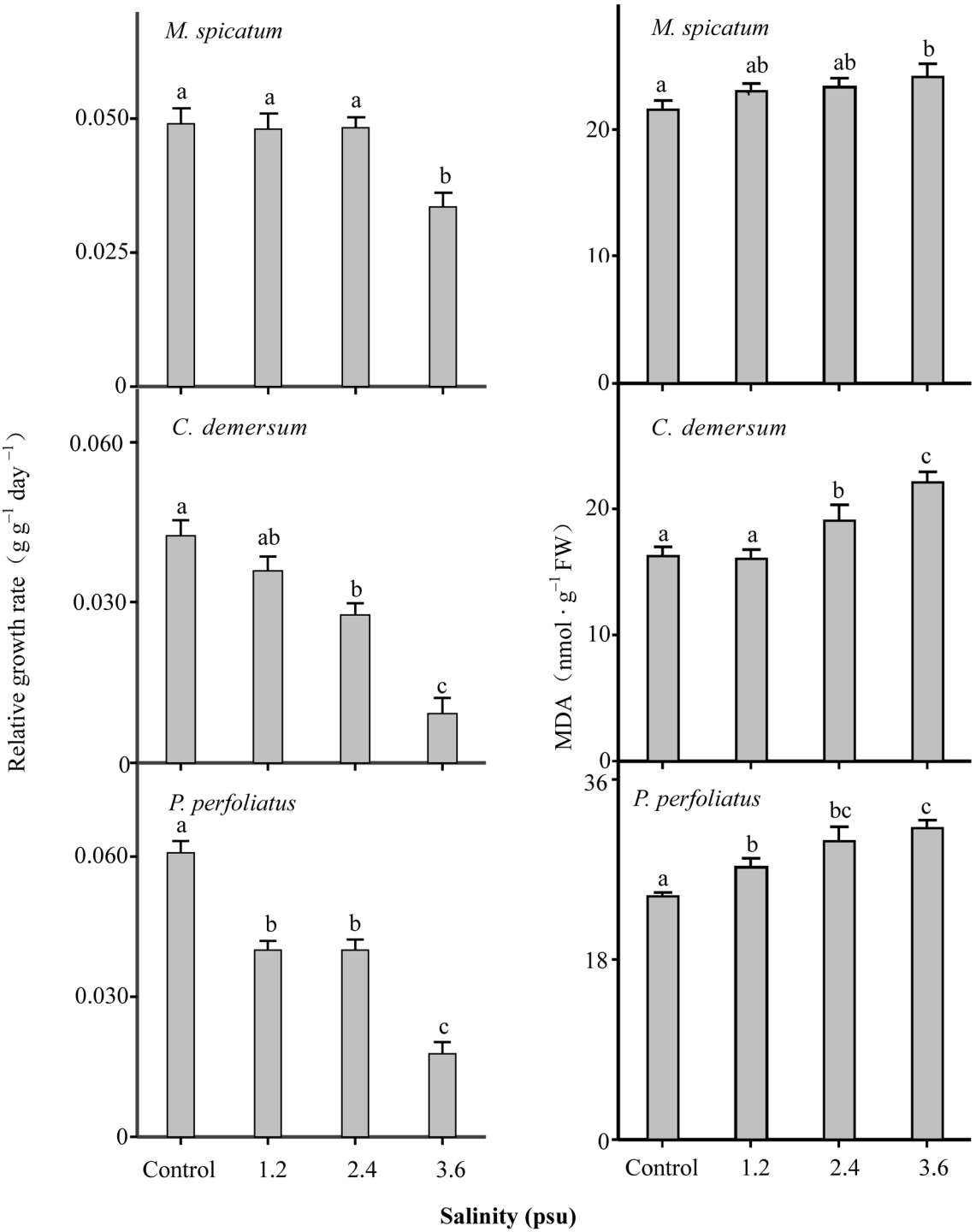

Fig. 2. The relative growth rate and MDA content of *Myriophyllum spicatum*, *Ceratophyllum demersum* and *Potamogeton perfoliatus* at four different salinity concentrations. Different letters indicate significant differences among treatments at the 0.05 significance level.

tion of the photochemical reduction of NBT (Masood et al. 2006). The reaction mixture (3 ml) contained 13 mM methionine, 75 mM NBT, 100 mM EDTA and 50 µl of enzyme extract in 50 mM phosphate buffer (pH 7.8). After addition of 2 mM riboflavin, the reaction took place when the mixture was exposed to 15 W fluorescent lamps for 15 min (a non-irradiated reaction mixture served as black). The absorbance was measured at 560 nm.

POD activity was measured by the H_2O_2-dependent oxidation of guaiacol. One unit POD activity was defined as the change in absorbance of 0.01 per minute at room temperature. Reaction mixture contained 1 ml of 3 % H_2O_2, 1.95 ml of 0.2 % guaiacol, 1 ml of 0.05 mol·L^{-1} phosphate buffer (pH = 7.0) and 0.05 ml enzyme extract, and the absorbance was measured at 470 nm (Hao et al. 2004).

CAT activity was measured by monitoring the decomposition rate of H_2O_2 at 240 nm for 1 min. The reaction mixture contained 2 mL of 3 % H_2O_2, 1.9 ml of distilled water and 0.1 ml extract. Reaction was started by addition of 0.1 ml enzyme extract (Hao et al. 2004).

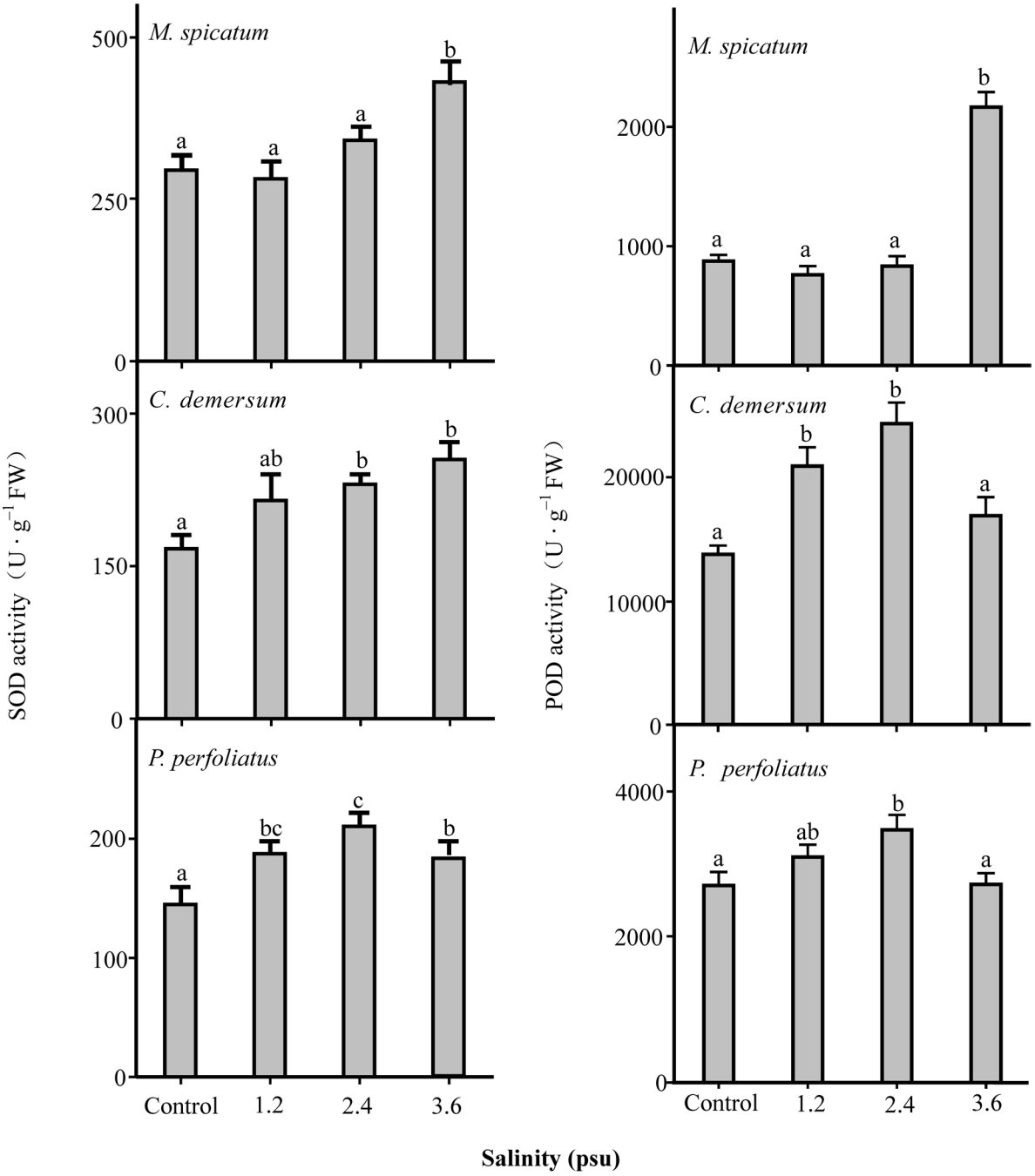

Fig. 3. SOD and POD activity of *Myriophyllum spicatum*, *Ceratophyllum demersum* and *Potamogeton perfoliatus* grown at four salinity concentrations. Different letters indicate significant differences among treatments at the 0.05 significance level.

APX activity was measured by monitoring the rate of ascorbate oxidation at 290 nm ($\varepsilon = 2.8\ mM^{-1}\ cm^{-1}$) for 1 min (Nakano & Asada 1981). The reaction mixture contained 25 mM phosphate buffer (pH 7.0), 0.1 mM EDTA, 1.0 mM H_2O_2, 0.5 mM AsA (ascorbic acid) and 50 µl enzyme sample. The reaction was started by the addition of H_2O_2 (de Azevedo Neto et al. 2006).

2.6 Data analysis

Two split-plot ANOVAs were applied to test the effects on the RGR, MDA content and enzyme activities. An ANOVA with salinity as main plot and bin as the sub-plot was performed to identify the effect of bin on the RGR, MDA content and enzyme activities. If bin had insignificant effects, a second

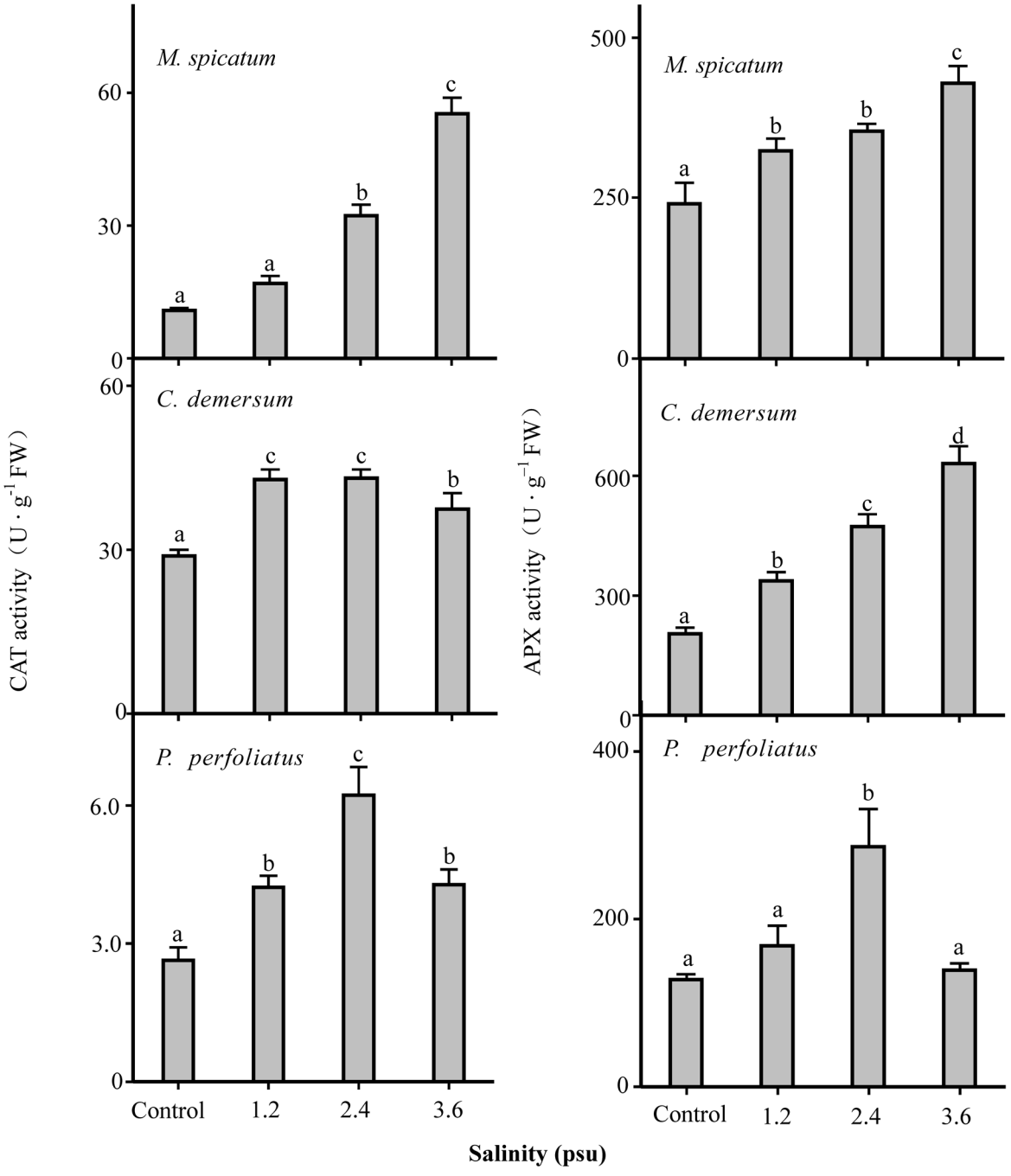

Fig. 4. CAT and APX activity of *Myriophyllum spicatum*, *Ceratophyllum demersum* and *Potamogeton perfoliatus* grown at four salinity concentrations. Different letters indicate significant differences among treatments at the 0.05 significance level.

ANOVA with salinity as the main plot and species as the subplot was applied to test for the combined effects on the RGR, MDA content and enzyme activities. Multiple comparisons of means were performed using Tukey's test at the 0.05 significance level and a Bonferroni correction for multiple comparisons was made where necessary. Data were $\log_{10}$-transformed if necessary to reduce heterogeneity of variances. Normality and homogeneity were tested using Liljefors test and Levene's test respectively. All analyses were performed using the software SAS V8.2 (SAS institute Inc. USA).

3. Results

3.1 Relative growth rate (RGR)

Bin had no significant effect on the RGR, MDA and enzyme activities of three species ($p > 0.05$). However, both salinity ($p < 0.001$; $F = 58.177$) and species ($p < 0.001$; $F = 34.929$), and the interaction of both factors ($p < 0.001$; $F = 6.343$) significantly affected RGR. The RGR of *C. demersum* and *P. perfoliatus* decreased significantly along with the increasing salinity, while in *M. spicatum* RGR declined only in the 3.6 psu treatment.. Compared to the control, the RGR in *M. spicatum*, *C. demersum* and *P. perfoliatus* decreased 31.8 %, 78.5 % and 71.0 % in the 3.6 psu treatment, respectively (Fig. 2).

3.2 MDA content

Salinity ($p < 0.001$; $F = 21.07$) and species ($p < 0.001$; $F = 115.70$), and the interaction of both factors ($p < 0.05$; $F = 2.25$) had significant effects on the MDA content. Salinity led to higher MDA content in all species, but species responded differently. The MDA content of *M. spicatum* in the 3.6 psu treatment was much higher than that in the other three treatments, while MDA content of *C. demersum* and *P. perfoliatus* had already increased at 2.4 psu and 1.2 psu, respectively. Compared to the control, MDA contents in *M. spicatum*, *C. demersum* and *P. perfoliatus* increased 12.0 %, 35.9 % and 28.3 % in the 3.6 psu treatment, respectively (Fig. 2).

3.3 Antioxidant enzyme activities

SOD activities were significantly affected by both salinity ($p < 0.001$; $F = 11.27$) and species ($p < 0.001$; $F = 66.36$), and the interaction of both factors ($p < 0.05$; $F = 2.72$). SOD activities increased significantly with enhancing salinity in *M. spicatum* and *C. demersum*, and the highest SOD activities of these two species occurred in the 3.6 psu treatment. However, SOD activity of *P. perfoliatus* increased firstly from control to 2.4 psu treatment, but decreased subsequently in the 3.6 psu treatment (Fig. 3).

Enhanced salinity ($p < 0.001$; $F = 18.43$) led to significantly increased POD activity in the three species. However, the patterns varied among different species ($p < 0.001$; $F = 902.43$). The highest POD activity of *M. spicatum* occurred in the 3.6 psu treatment, which was 2.79 times higher than control. However, the POD activity in *C. demersum* and *P. perfoliatus* increased significantly from control to 2.4 psu treatments (highest in the 2.4 psu treatment), but decreased subsequently in the 3.6 psu treatment (Fig. 3).

The activities of CAT were significantly influenced by salinity ($p < 0.001$; $F = 46.36$), species ($p < 0.001$; $F = 302.03$), and the interaction of both factors ($p < 0.001$; $F = 32.23$). Higher salinity led to higher CAT activity in *M. spicatum* and the highest activity occurred in the 3.6 psu treatment, which was 5.14 times higher than control. Both *C. demersum* and *P. perfoliatus* had the highest CAT activities in the 2.4 psu treatment and lowest in the control treatment (Fig. 4).

Salinity ($p < 0.001$; $F = 37.45$) and species ($p < 0.001$; $F = 73.64$), and the interaction of both factors ($p < 0.001$; $F = 12.95$) had significant effects on the activities of in 40 of APX. Compared to the control, the contents of APX in *M. spicatum* and *C. demersum* increased significantly with rising salinity. However, *P. perfoliatus* had the highest APX activity in the 2.4 psu treatment, which was 2.23 and 2.05 times higher than that in the control and 3.6 psu treatment, respectively (Fig. 4).

4. Discussion

The changes of RGR in the three species is consistent with our hypothesis 1, which predicts that the relative growth rate decreased more dramatically with rising salinity in *C. demersum* and *P. perfoliatus* than in *M. spicatum*. Furthermore, the increments of MDA content in the three species in the 3.6 psu treatment support our hypothesis 2, which suggests that MDA contents in *C. demersum* and *P. perfoliatus* increased more pronouncedly than that in *M. spicatum* in the high salinity environment. These results suggest that oxidative damage was less severe in *M. spicatum* compared to the other two species. Additionally, our results are consistent with previous studies. Twilley (1990) found that *M. spicatum* can survive at 15.7 psu salinity, and is a widely distributed species in the southern Baltic Sea

Coast where the salinity is around 8–10 psu (Selig et al. 2007). However, the highest salinity found for survival of *C. demersum* was 7.9 psu (Wang & Ji 2007), and *P. perfoliatus* is not usually considered as a species that can tolerate brackish waters (Hynes 1960). Therefore, *M. spicatum* is better able to grow in high salinity water than the other two species.

SOD catalyses the conversion of the superoxide anion to O_2 and H_2O_2, and performs the first step in the removal of ROS (Rahnama & Ebrahimzadeh 2005). In this work, SOD activities of *M. spicatum* and *C. demersum* increased along with rising salinity, and the activity was stronger in *M. spicatum* than that in *C. demersum*. However, the SOD activity of *P. perfoliatus* first increased at lower salinities (1.2 psu and 2.4 psu), then declined in the 3.6 psu treatment. These results suggest that *M. spicatum* had a better superoxide radical scavenging ability than the other two species, which can also be reflected by their different RGR. A higher SOD activity in salinity-tolerant species was also found by Masood et al. (2006) and Sekmen et al. (2007). The decline in SOD activity in *P. perfoliatus* might be caused by inactivation due to the large amount of ROS (Tao et al. 2007).

POD activity increased significantly in *M. spicatum* with rising salinity whereas it increased firstly at the low salinity treatment, but declined significantly in the high (3.6 psu) treatment in *C. demersum* and *P. perfoliatus*, indicating that the 3.6 psu treatment might have resulted in H_2O_2 accumulation in these two species. CAT and APX are also important enzymes in converting H_2O_2 to H_2O and O_2, but CAT has a lower affinity for H_2O_2 than APX, and is absent from the chloroplasts (Graham & Patterson 1982, Sekmen et al. 2007, Xue & Liu 2008). Our results suggest that the activities of CAT and APX show similar patterns to the other two enzymes (SOD and POD) in *M. spicatum*, suggesting that these enzymes can work together to help *M. spicatum* escape from salinity stress. However, these two enzymes decreased significantly in the 3.6 psu treatment in the other two species, except for APX in *C. demersum*, indicating that CAT and APX are less efficient in helping *C. demersum* and *P. perfoliatus* to acclimate to higher salinity environments. The decrease of POD, CAT and APX at higher salinity environments were also found in other salt-sensitive species (Masood et al. 2006, de Azevedo Neto et al. 2006). All together, these results are in agreement with our hypothesis 3, which suggests that the activities of antioxidative enzymes in response to salinity stress will be higher in *M. spicatum* than in *C. demersum* and *P. perfoliatus*.

In conclusion, our study suggests that the salinity tolerance is higher in *M. spicatum* than in the other two species due to its higher activity of antioxidative enzymes and these results are in agreement with our hypothesis, which suggested that different distributions of plant species in the Modern Yellow River Delta can be reflected by their different physiological responses to salinity. However, plant distribution also can be determined by other environmental variables (e.g. competition, nutrient, pH). Therefore, more studies are still needed to further understand the mechanisms structuring plant distributions in this delta.

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