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# Effects of growing conditions on the growth of and interactions between salt marsh plants: implications for invasibility of habitats

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## Abstract

A common but often less tested explanation for the successful invasion of alien species is that invasive alien species outcompete their co-occurring natives, which may not always be the case. In this study, we established artificial environmental gradients in a series of pot experiments with controlled environments to investigate the effects of salinity, sediment type and waterlogging on the performance of and interactions between *Phragmites australis* (native) and *Spartina alterniflora* (alien), which generally co-exist in the saline intertidal zones of Chinese and American coasts. Significant effects of salinity and waterlogging were detected on biomass production and morphological characteristics of *S. alterniflora* and *P. australis*, and the competitive interactions between the two species were found to vary with all three environmental factors in our experiments. Relative Neighbor Effect (RNE) analyses indicate that competitive dominance of *S. alterniflora* occurred under the conditions of high salinity, sandy sediment and full immersion, whereas *P. australis* showed competitive dominance under the conditions of low salinity and non-immersion. Our results suggest that *S. alterniflora* might outcompete *P. australis* under conditions present in early salt marsh succession, which support the viewpoint that the outcomes of competition between co-occurring native and invasive alien plants depend on the growing conditions. The implication of this study is that in response to the environmental changes expected from seawater intrusion and sea-level rise, the range of *S. alterniflora* is expected to expand further in the Yangtze River estuary in the future.

## Introduction

The invasions of alien plant species are a serious threat to native ecosystems and regional economy (Pimentel et al. 2000, 2001), which drive native plant species to extinction (Marco and Paez 2000; Pimentel et al. 2001; Rodriguez 2001), and cause considerable economic loss. Many invasive plants often dominate the ecosystems they invade, and may form their monocultures by excluding co-occurring native plants. Thus plant invasions may alter the structure and functions of the native ecosystems. Many hypotheses have been proposed to explain the success of plant invasions. For example, a common but less tested explanation is that invasive species outcompete their co-occurring natives – debate still continues. Alpert et al. (2000) have proposed that the competitive balance between invasive and native species could be shifted by environmental stresses. Daehler (2003) has more recently reviewed 119 published papers containing comparative performance data of co-occurring native and invasive alien plants, concluding that the invasive alien species are not statistically more likely to have higher growth rates, competitive ability, or fecundity than the co-occurring natives, but the relative performance of invasive species and co-occurring natives often depends on their growing conditions. These recent views suggest that the invaders are not necessarily born competitive. Therefore, studying the competitive relations between co-occurring native and invasive alien plants under varying environmental conditions might help to reveal the invasion mechanisms in relation to competition, and provide important information for the management of invasive species and restoration of the invaded habitats by manipulating the environmental factors.

Coastal ecosystems are extremely variable in many ways as they are affected by the processes of marine, terrestrial and sometimes riverine ecosystems. Ecologists have recognized that environmental factors play important roles in structuring and functioning of coastal salt marshes (Hemminga and Buth 1991; Vernberg 1993; Grace and Pugesek 1997). The zonation of plant communities on many salt marshes has been interpreted as reflecting stages in a successional sequence associated with the environmental gradient (Brereton 1971; Scholten and Rozema 1990). Therefore, the composition and distribution of plant communities along the elevational gradients of coastal salt marshes are related to the variation in environmental conditions that are associated with the tidal inundation which varies in frequency and duration over time. Many previous studies have shown that the performance and distribution of salt marsh plant species are affected by salinity, sediment type and waterlogging, which are all associated with the tidal inundation gradient (Bertness and Ellison 1987; Flynn et al. 1995; Brewer et al. 1997; Christiansen et al. 2000). Huckle's study (2000) indicates that the growth and interactions between two graminoid species (*Puccinellia maritima* and *Spartina anglica*) vary with the above three abiotic factors.

Many coastal marshes in the world are now under the serious threat of invasive alien species such as *Phragmites australis* Cav. Trin Ex Steud (common reed, hereafter referred to as *Phragmites*) and *Spartina alterniflora* (smooth cordgrass, hereafter referred to as *Spartina*) (Grosholz 2002; Chen et al. 2004). *Phragmites* and *Spartina* both are tall perennial graminoid grasses that grow in the intertidal zones of estuaries in dense monocultures. *Phragmites* has been moving from high to low marshes and has replaced the native *Spartina* in many marshes along the Atlantic Coast of the US (Marks et al. 1994; Windham and Lathrop 1999). The dramatic spread of *Phragmites* into the lower marshes has caused some major ecological and economical problems in North America. *Phragmites* is therefore considered a weedy invader because it outcompetes other plant species, lowers plant and bird species richness, causes accumulation of sediments, alters patterns of water flow, and reduces habitat heterogeneity (Buttery and Lambert 1965; Benoit and Askins 1999; Weinstein and Balletto 1999; Meyerson et al. 2000). *Spartina*, native to the East and Gulf coasts of North America, has become a highly invasive weed in some Pacific coastal marshes across the world including those in the Yangtze River estuary in eastern China. *Spartina* was first introduced to China from North America in 1979. Now *Spartina* flourishes in the coastal intertidal areas from Guangxi northward to Tianjin mainly by intentional introductions (Chung 1993). Introduced *Spartina* spp. have clear negative effects on some native plants species (Daehler and Strong 1996), and some indications that invertebrate communities and shorebird populations may also be negatively affected by *Spartina* invasion (Sayce 1991). In the Yangtze River estuary, native *Phragmites* and *Scirpus mariqueter* in the marshes are replaced rapidly by invasive *Spartina*, and the expanding *Spartina* is seriously threatening the native ecosystems and coastal aquaculture in China (Chen et al. 2004).

As invasive species, both*Phragmites* and *Spartina* also have tremendous impact on the invaded ecosystems, and their invasions in the non-native habitats are often considered as ecological disasters (Callaway and Josselyn 1992; Daehler and Strong 1996; Able and Hagan 2000). It is interesting to note that *Phragmites* is invading *Spartina*-dominated ecosystems in North America (Marks et al. 1994; Chambers et al. 1999; Windham and Lathrop 1999), whereas *Spartina* is threatening *Phragmites*-dominated ecosystems in the eastern coasts of China. One of the possible explanations for the reciprocal invasions is that the environmental conditions in North America favor *Phragmites*, whereas those in China allow *Spartina* to express its competitiveness.

Numerous studies have been carried out on morphology and physiology of *Spartina* and *Phragmites* individually (Gries et al. 1990; Hellings and Gallagher 1992; Naidoo et al. 1992; Hwang and Morris 1994; Armstrong et al. 1996; Colmer et al. 1996; Wijte and Gallagher 1996; Lissner and Schierup 1997; Chambers et al. 1998). Few studies, however, have been carried out to examine whether and how the competitive outcome between *Phragmites* and *Spartina* is affected by the growing conditions. Here, an experimental attempt was made to reveal the effects of the environmental factors on plant intra- and interspecific interactions, and it is hoped that the information obtained would be of help in the understanding of why the two marsh plants can be successful invaders in different habitats, and in their management.

By constructing artificial environmental gradients, we studied the effects of the three abiotic factors (salinity, sediment type and waterlogging) on the performance and interactions between the two marsh species, *Phragmites* and *Spartina*, aiming to (1) reveal the possible shifts of competitive balance between the two species across specific abiotic gradients; (2) interpret the zonation of plant community on coastal marshes from a viewpoint of competitive interaction; (3) provide basic information on the management of *Spartina alterniflora* in the coastal ecosystems.

## Materials and methods

### *Plant materials*

The source materials of *Spartina* and *Phragmites* were collected from the same area of the middle marsh zone at Dongtan, Chongming Island, located at the Yangtze River estuary (31°25′–31°38′N, 121°50′–122°05′E) in April 2003. Their belowground parts were unearthed from the marsh, and then transported to the laboratory in humid plastic bags to prevent desiccation of roots. These collected plant materials were cut into similar-sized plantlets (about 25 cm in length) with a single ramet and attached roots, which were then planted into big quadrate containers containing sand and plenty of water. The plants were grown in an unheated glasshouse for 6 weeks. One week before transplanting, the plants were transported to a polytunnel where the experiments were conducted, so as to allow their acclimatization to the polytunnel conditions.

### *Experimental design*

At the end of May 2003, three separate experiments were set up at the same time in a large polytunnel, in which three environmental variables (i.e. salinity, sediment and waterlogging) were considered singly. We selected these environmental variables and designed three treatments to simulate the environmental variation in wetlands in the Yangtze River estuary.

In each experiment, only one environmental factor was manipulated to produce three levels whereas other two factors were kept constant

*Table 1.* Manipulation of the environmental factors in the three experiments.

| | Salinity % | Sediment | Waterlogging |
|---|---|---|---|
| Salinity experiments | 0‰ | Sand–clay mix | Half-immersion |
| | 15‰ | Sand–clay mix | Half-immersion |
| | 30‰ | Sand–clay mix | Half-immersion |
| Sediment experiments | 15‰ | Sand | Half-immersion |
| | 15‰ | Mix | Half-immersion |
| | 15‰ | Clay | Half-immersion |
| Waterlogging experiments | 15‰ | Sand–clay mix | Non-immersion |
| | 15‰ | Sand–clay mix | Half-immersion |
| | 15‰ | Sand–clay mix | Full-immersion |

Only one factor was manipulated in each experiment while the other two were held constant.

(see Table 1 for more details). The three salinity treatments were 30 g NaCl $l^{-1}$ (30‰), 15 g NaCl $l^{-1}$ (15‰), and freshwater (0‰). The sediment types included pure sand, 1:1 mixture of sand and clay, and 100% clay; and the three levels of waterlogging were maintained, i.e. at 10 cm below the soil surface (non-immersion), at the level of the soil surface (half-immersion), 10 cm above the soil surface (full-immersion).

A randomized block split-plot design was used with six replicate blocks in each experiment. Each of the 18 main-plots (3 treatments × 6 replicates) consisted of six subplot treatments, which represented a series of pairwise combinations of the two species (Table 2). The plants were transplanted into plastic pots with a volume of about 10 l (i.e. 28 cm in diameter and 20 cm in height) at a density of three or six plants per pot. For each species, the plants were selected randomly from the stock in order to reduce the possible influence of clonal variation and plant history. To maintain the environmental conditions at the initial levels throughout the experiments, salinity was re-adjusted once a week experientially, and the water levels were re-adjusted every two days by adding water or saline so that salinity concentrations were kept basically constant. Additionally, the pots were kept weed-free all through the experiments.

In the mid-October, 2003, an end-of-season harvest was conducted. Morphological measurements for *Spartina* were made of the number of vegetative and reproductive ramets, the height of the tallest flowering ramet, and the spica length of reproductive ramets before harvest. Each *Spartina* individual was then cut at ground level. The belowground parts of *Spartina* in each pot were removed by thorough washing. Similar measurements were also made for *Phragmites*. However, *Phragmites* failed to flower by harvesting time, so no data were obtained for the parameters of its sexual reproduction. The plant materials for both species were dried to constant weight at 80°C, and the weights of different parts were combined to give the total biomass per pot.

*Table 2*. Planting densities for each of species combination treatments grown in the salinity, sediment and waterlogging experiments.

| Species combination code* | Number of plants of each species | |
|---|---|---|
| | *Spartina* | *Phragmites* |
| Control (0) | – | – |
| S | 3 | – |
| P | – | 3 |
| S + S | 6 | – |
| P + P | – | 6 |
| S + P | 3 | 3 |

*P = *Phragmites*, S = *Spartina*.

### *Data analysis*

The biomass and morphological data for each species were subject to analysis of variance according to a split-plot randomized block design. Biomass data for *Spartina* and *Phragmites* were log transformed for generating homoscedasticity before ANOVAs were performed. Morphological data for *Spartina* were transformed using either log (height of tallest ramet, length of spica) or square root (number of ramets).

The intensity of intra- and interspecific interactions between the two species was quantified using the Relative Neighbor Effect (RNE) index (Markham and Chanway 1996), as done by Huckle et al. (2000):

$$\mathrm{RNE} = \frac{P_{-N} - P_{+N}}{x}$$

where $P$ is the performance of plants in the presence (+N) and absence (−N) of the neighbors, and $x$ is $P_{-N}$ when $P_{-N}$ is greater than $P_{+N}$ and $x$ is $P_{+N}$ when $P_{-N}$ is greater than $P_{+N}$. This method is a modified version of the Relative Competitive Intensity (RCI) index, a method that has been used to examine competition over a productivity gradient (Wilson and Keddy 1986). The RNE values range from −1 (maximum facilitation) to +1 (maximum competition). It is 0 when no interaction is occurring, negative when the interaction is actually facilitative, and positive when the interaction is competitive.

In this study, the combination of planting treatments represented the presence or absence of neighbors: treatments with standard planting density (three plants per pot) represented the absence of neighbors, while those with the total density of six plants per pot represented the presence of neighbors of the same or different species.

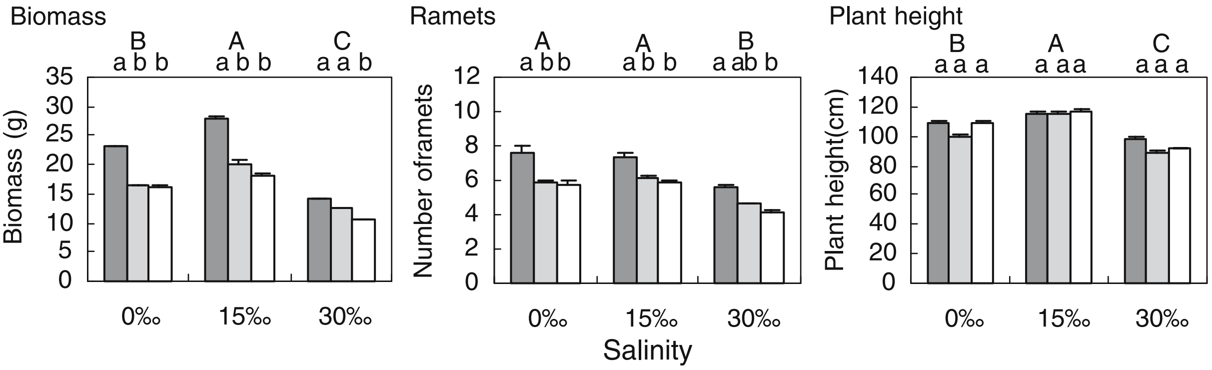
For each experiment, the intensity of intra- and interspecific interactions, quantified by RNE index, was determined using the total biomass as indicators of performance and relative competitive ability of plants. The RNE values were transformed (arcsine) prior to statistical analysis. Relative neighbor effects were defined as competitive or facilitative when the mean value of the index was significantly greater or less than zero (no interaction). Tukey HSD test using RNE values was conducted to examine the difference of intra- and interspecific interactions among the treatments used.

## Results

### *Effects of environmental factors on plant performance*

Under our experimental conditions, *Spartina* flowered and set seeds in all the treatments while *Phragmites* failed to flower. *Spartina* produced generally greater biomass than did *Phragmites* (Figures 1–3). Split-plot analyses of variance showed that salinity level and waterlogging had significant effects on the growth of *Spartina* and *Phragmites* whereas sediment type

**(a)** *Spartina alterniflora*



**(b)** *Phragmites australis*

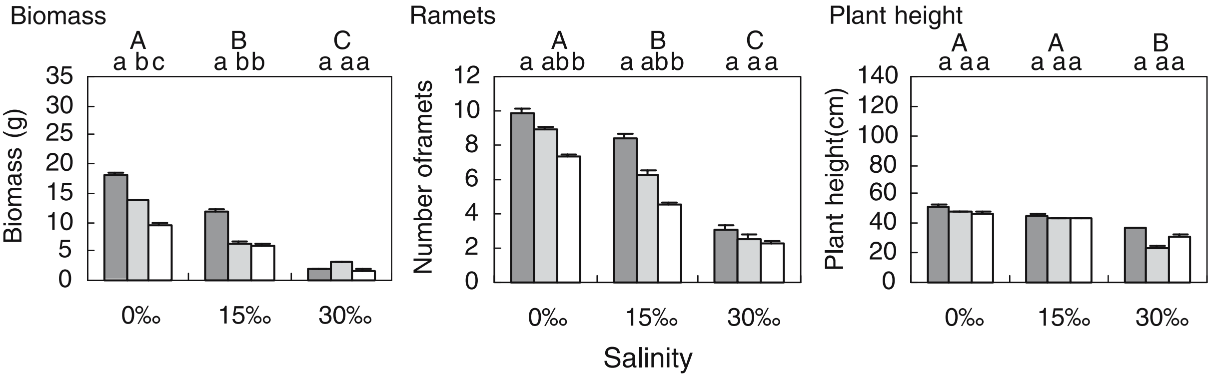
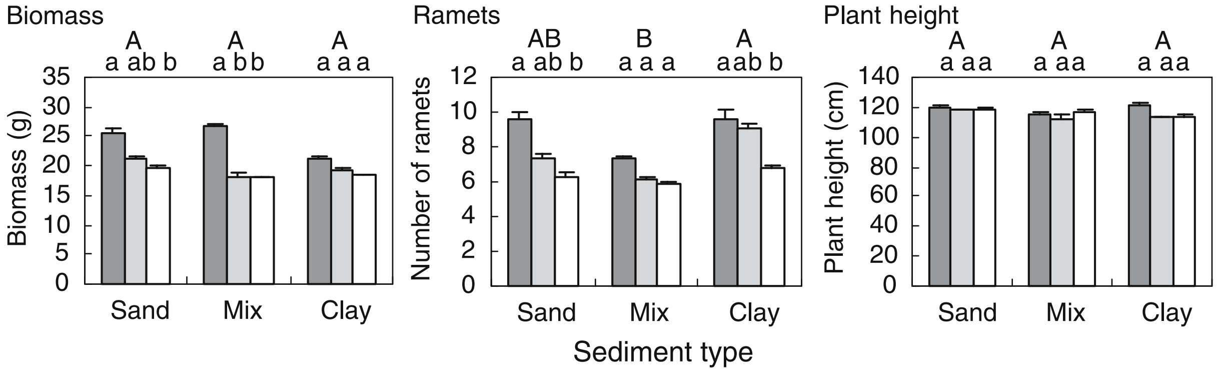


*Figure 1.* Effects of salinity treatment on the performance of study species. Data shown are the mean values using pooled block data for effect of salinity level and species combination on (a) *Spartina alterniflora*, (■: S, ■: S+P, □: S+S), and (b) *Phragmites australis*, (■: P, ■: S+P, □: P + P). Treatments with different code letters are significantly different at the significance level of 5% (Tukey HSD test): uppercase letters denote differences between salinity levels; lowercase letters denote differences between species combinations.

**(a)** *Spartina alterniflora*



**(b)** *Phragmites australis*

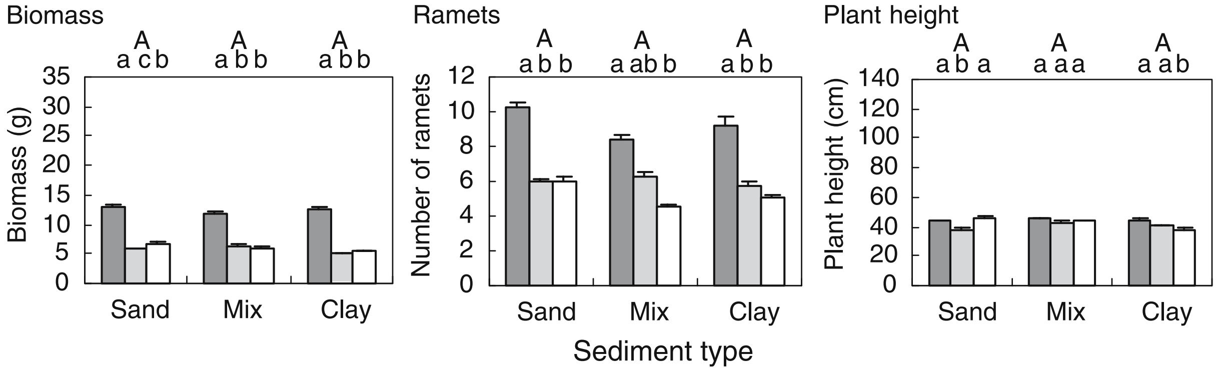


*Figure 2.* Effects of sediment type treatment on the performance of study species. Data shown are the mean values using pooled block data for effect of sediment type and species combination on *Spartina alterniflora* (a) (■: S, ■: S + P, □: S + S), and *Phragmites australis* (b): (■: P, ■: S + P, □: P + P). Treatments with different code letters are significantly different at the significance level of 5% (Tukey HSD test): uppercase letters denote differences between sediment type; lowercase letters denote differences between species combinations.

had no significant effects (Table 3). No block effects were detected in this study (Table 3).

The salinity level had significant effects on all the variables of the two species considered here (Table 3, Figure 1). High salinity (30‰) had significantly inhibitory effects on the growth of both *Spartina* and *Phragmites* (Figure 1). *Spartina* was obviously more tolerant of salinity stress than *Phragmites*, and the optimum salinity level for *Spartina* was found to be 15‰ (Figure 1(a)). In contrast, *Phragmites* performed better than did *Spartina* under the freshwater condition, and its performance declined with increasing salinity (Figure 1(b)).

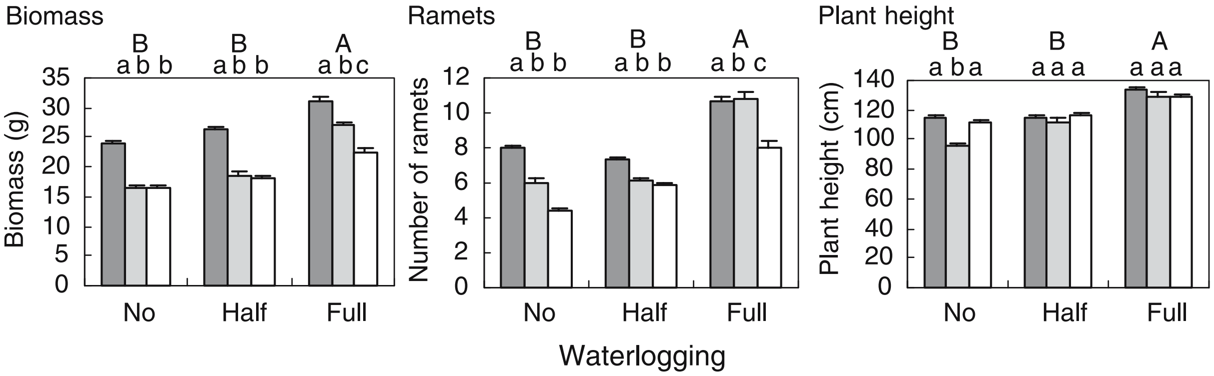
In sediment experiments, the sediment type had no significant effects on the growth of *Spartina* and *Phragmites*, but it did affect the number of flowering ramets and the total number of ramets of *Spartina* (Table 3, Figure 2).

Waterlogging had significant effects on the performance of both *Spartina* and *Phragmites* (Table 3, Figure 3). Biomass and ramet number of *Spartina* and *Phragmites* were significantly reduced in pots where there was no immersion. Other measured variables were also affected by waterlogging (Table 3, Figure 3).

### *Effects of environmental factors on plant interactions*

In all of our treatments, significant effects of species combinations on the biomass and ramet

**(a)** *Spartina alterniflora*



**(b)** *Phragmites australis*

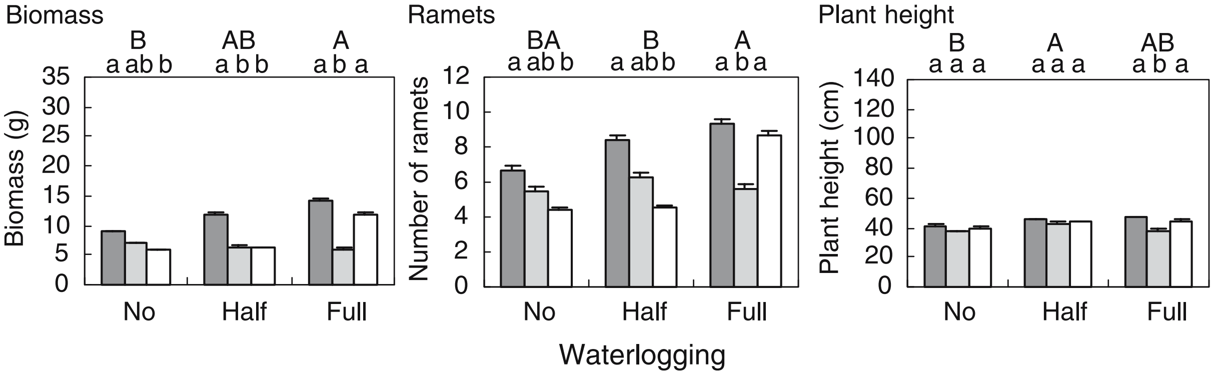


*Figure 3.* Effects of waterlogging treatment on the performance of study species. Data shown are the mean values using pooled block data for effect of waterlogging and species combination on *Spartina alterniflora* (a) (■: S, ■: S + P, □: S + S), and *Phragmites australis* (b) (■: P, ■ S + P, □: P + P). Treatments with different code letters are significantly different at the significance level of 5% (Tukey HSD test): uppercase letters denote differences between waterlogging; lowercase letters denote differences between species combinations.

production were detected (Table 3). There was a general trend that mean biomass and ramet production of the individual plant when it was grown at the standard density (i.e. S or P treatment, 3 plants per pot) were significantly greater, compared with pots where it was grown at double the standard density (S + S or P + P) and with competitors of different species present (S + P) (Figures 1–3). Therefore, both intraspecific and interspecific competition did occur under our experimental conditions.

In salinity treatments, the RNE analysis shows that competitive interactions between *Spartina* and *Phragmites* varied significantly among different salinity levels (Figure 4). It is notable that *Spartina* had a facilitative effect on *Phragmites* at the salinity level of 30‰, which is very close to lethal concentration of *Phragmites* (Figure 4(a)). Based on the results of the RNE analysis, salinity stress altered the competitive balance between *Spartina* and *Phragmites*. *Spartina* had the competitive dominance at the highest salinity level whereas *Phragmites* tended to dominate over *Spartina* at the lowest salinity level although *Phragmites*' performance was reduced at this salinity level. Coexistence of the two species might occur at the salinity of 15‰ (Table 4).

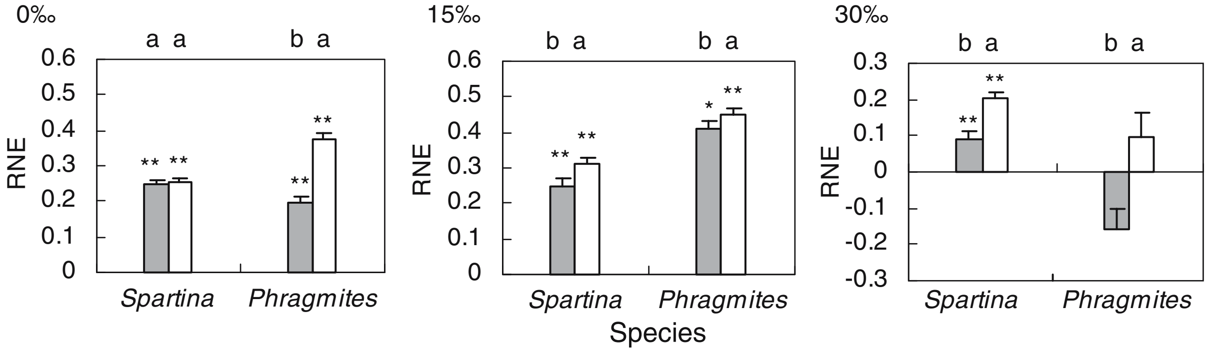
RNE values indicate that significant competitive effects on each other occurred in the sediment experiments (Figure 4(b)). The results of RNE analysis demonstrate that *Spartina* had the competitive dominance over *Phragmites* in sandy

*Table 3*. Summary pf split-plot analyses of variance showing the significance of the effects of block, environmental treatment, and species combination on performance of *Spartina* and *Phragmites*.

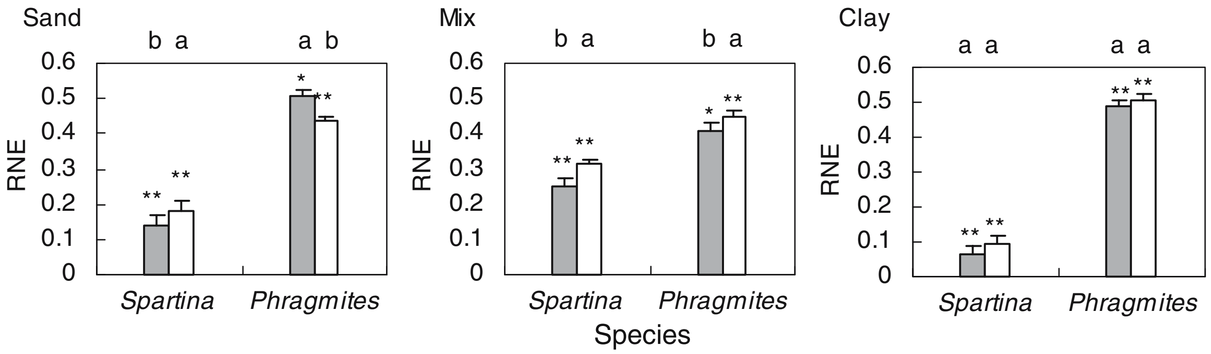
| | | *Spartina alterniflora* | | | | | | *Phragmites australis* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Experiments | Sources of variation | Total biomass | Total (?) | Flowering Ramets biomass | Ramets biomass | Tallest ramets | Spica length | Total biomass | Total # ramets | Tallest ramets |
| (a) Salinity | Block | | | | | | | | | |
| | Treatment | ** | ** | * | * | ** | ** | ** | ** | ** |
| | Species | ** | ** | ** | ** | | | ** | ** | ** |
| | Treatment × Species | * | ** | ** | | | | ** | | ** |
| (b) Sediment | Block | | | | | | | | | |
| | Treatment | | | ** | * | | | | | |
| | Species | ** | ** | ** | ** | | | ** | ** | * |
| | Treatment × Species | | | | | | ** | | | |
| (c) Water-logging | Block | | | | | | | | | |
| | Treatment | ** | ** | ** | ** | ** | | ** | ** | ** |
| | Species | ** | ** | ** | ** | | | ** | ** | ** |
| | Treatment × Species | | ** | * | * | | | ** | ** | |

*$P < 0.05$, **$P < 0.01$.

**(a)** Salinity



**(b)** Sediment type



**(c)** Waterlogging

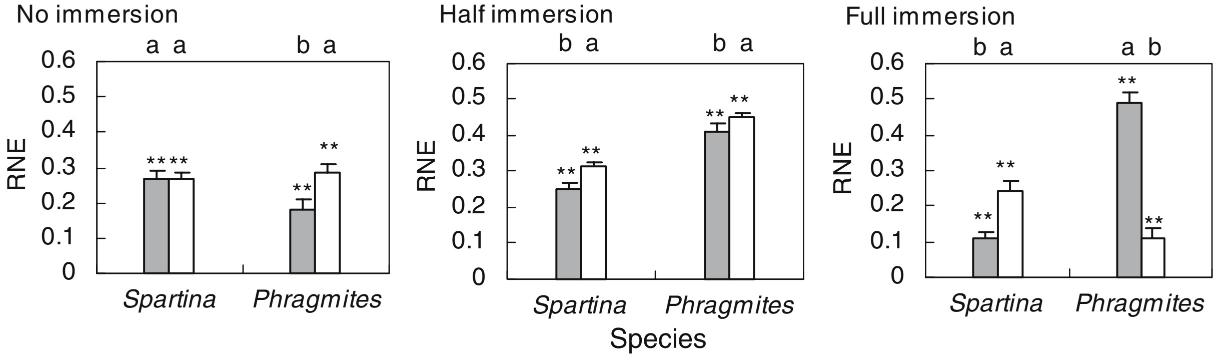


*Figure 4.* Effects of three environmental factors on plant interactions. Data shown are the mean interspecific and intraspecific RNE (Relative Neighbor Effects) index in each treatment using pooled block data for the total biomass in the treatment of salinity level (a), sediment type (b) and waterlogging (c) (■: interspecific, □: intraspecific). * indicates that the RNE value is greater than zero (*$P < 0.05$; **$P < 0.01$). Treatments with different code letters are significantly different at the significance level of 5% (Tukey HSD test).

sediment, and the two species might co-exist in both sand–clay mix and clay (Table 4).

Significant competitive effects on each other were detected in waterlogging treatment (Table 3). RNE analyses show that the intensity of intra- and interspecific competition varied among the water treatments (Figure 4(c)). ANOVA of the RNE values indicates that *Spartina* had the competitive dominance over *Phragmites* when grown in the full-immersion treatment, and that *Phragmites*

*Table 4.* Summary of competitive balance between *Spartina* and *Phragmites* based on the values of RNE, as affected by the growing conditions.

| Factors manipulated | Treatments used | Relative intensity of intra- and interspecific competition | | Competitive outcome |
|---|---|---|---|---|
| | | *Spartina* | *Phragmites* | |
| Salinity | 0‰ | Inter- = Intra- | Inter- < Intra- | *Phragmites* dominant |
| | 15‰ | Inter- < Intra- | Inter- < Intra- | Co-existence |
| | 30‰ | Inter- < Intra- | Inter- < Intra- | *Spartina* dominant |
| Sediment type | Sand | Inter- < Intra- | Inter- > Intra- | *Spartina* dominant |
| | Sand–clay mix | Inter- < Intra- | Inter- < Intra- | Co-existence |
| | Clay | Inter- = Intra- | Inter- = Intra- | Co-existence |
| Waterlogging | Non-immersion | Inter- = Intra- | Inter- < Intra- | *Phragmites* dominant |
| | Half-immersion | Inter- < Intra- | Inter- < Intra- | Co-existence |
| | Full-immersion | Inter- < Intra- | Inter- > Intra- | *Spartina* dominant |

gained the competitive superiority in the treatments without immersion. Coexistence of the two species was possible in the half-immersion treatment (Table 4).

## Discussion

In this study, we examined the effects of three environmental factors (salinity, sediment and waterlogging) on the performance of *Spartina* and *Phragmites* and competitive interactions between the two marsh species, two of which (salinity and waterlogging) were found to have significant effects. In all the experiments, the treatments of species combination also had significant effects on the performance of the two species. The results obtained here show that there were significant intra- and interspecific interactions at all the levels of environmental factors in our experiments, and it was revealed by RNE analysis that the competitive interactions between *Spartina* and *Phragmites* varied significantly among different growing conditions. As a result of the varying intra- and interspecific interactions, the competitive balance between *Spartina* and *Phragmites* varied with the environmental factors.

### *Effects of individual environmental factors*

#### *Salinity*

The results obtained here show that *Spartina* and *Phragmites* responded differently to the variation in salinity (Figure 1). Obviously, *Spartina* was more tolerant of salt stress than *Phragmites*, and the differences of their responses to the stress of salinity between the two species resulted in the shift of competitive interaction. Numerous studies have investigated the growth responses of *Spartina* to the variation in salinity, but the results are mixed. Some studies have shown that salt inhibition of *Spartina* growth increases with increasing salinity (Gosselink 1970; Phleges 1971; Smart and Barko 1980), while others have shown that the optimum growth occurs at medium salinity of 10‰–20‰, over which its growth is inhibited (Haines and Dunn 1976; Landin 1991; Lewis and Weber 2002). In our salinity experiment, the greatest biomass production of *Spartina* occurred at the middle salinity (i.e. 15‰), suggesting that the moderate level of salinity promote the growth of *Spartina* under our experimental conditions.

Our experiment shows that *Spartina* was more tolerant of salt stress than *Phragmites*. The growth of *Phragmites* declined rapidly with increasing salinity, suggesting that *Phragmites* be relatively more sensitive to salinity than *Spartina*. This finding agrees with many previous studies which show that dieback of *Phragmites* takes place at higher salinity (e.g. > 15‰), and all plants culture dies at salinity 35‰ (Lissner and Schierup 1997; Hartzendorf and Rolletschek 2001).

In the salinity experiment, it is dramatic that the growth of *Phragmites* was detected to be facilitated by *Spartina* when grown at the sublethal concentration, salinity 30‰. That is, the interactions between *Spartina* and *Phragmites* were changed by salinity level. The possible mechanism is that *Spartina* spp. can absorb salt selectively by roots (Smart and Barko 1980; Bradley and Morris 1991) and the salt absorption of *Spartina* might reduce the interstitial water salinity of rhizosphere soil of *Phragmites*. Therefore, *Spartina* has the competitive superiority over *Phragmites* at high salinity level, but *Phramites* may outcompete *Spartina* in fresh water (Table 4). More generally, the competitive balance between the native and invasive alien plants is shifted by the salt stress.

### *Sediment type*

In the sediment experiment, no significant effects of sediment type on biomass production of the two species were detected, implying that *Spartina* and *Phragmites* are well adapted to different particle size of the substrate.

The invasive alien plant, *Spartina* does not always outcompete *Phragmites* in different sediment types. *Spartina* shows competitive superiority over *Phragmites* in sandy substrate, while their co-existence may be possible in sand–clay mix and clay sediments (Table 4). Generally, the sand sediment has a better condition for gas exchange, compared with clay sediment. Therefore, our results imply that there is a general trend that *Spartina* might gain the competitive dominance over *Phragmites* when the stress of anoxic sediments is reduced.

### *Waterlogging*

Prolonged waterlogging might lead to oxygen deficiencies, even in flood-tolerant plants such as *Spartina* and *Phragmites* (Mendelssohn et al. 1981; Mendelssohn and McKee 1988; McKee et al. 1989; Hellings and Gallagher 1992). However, the significantly greater biomass production, number of ramets and the plant height were observed in fully immersed pots where water level was maintained at 10 cm above the soil surface, attributable to the well-developed aerenchyma systems in the tissue of the two species, which can enhance metabolic efficiency and facilitate internal oxygen transport (Mendelssohn et al. 1981; Mendelssohn and Postek 1982; Gries et al. 1990; Maricle and Lee 2002). As a result, the performance of the two salt marsh plants is improved when water availability increases.

The competitive balance was also shifted by waterlogging conditions. There was a trend that *Phragmites* outcompeted *Spartina* in less immersed habitats, while *Spartina* had a competitive superiority over *Phragmites* when the water availability increased. The results from the waterlogging experiment indicate that the competitive superiority can be shifted by water availability.

The effects of environmental factors on the growth of *Spartina* and *Phragmites* in our experiments indicate that the interactions between salinity and waterlogging might be remarkable in relation to competition between the two species. Consequently, an orthogonal designed experiment might be needed to study the effects of salinity and waterlogging on the competitive interactions between *Spartina* and *Phragmites*.

### *Some implications*

Our study offers an explanation for the zonation of plant communities in the tidal salt marshes in the Yangtze River estuary, where the physical environments are significantly affected by tidal water (Yang and Zhu 1993; Chen et al. 2003). Our field experiments (Wang et al. unpublished data) conducted in the salt marshes of the Yangtze River estuary show that with the rapid development of tidal salt marshes, the elevation of the marshes increases and the effects of tidal inundation become less profound. As a result, the succession of plant community is very rapid in the salt marshes in Yangtze River estuary. Previous field studies in the Yangtze River estuary have also demonstrated that *S. alterniflora* can well colonize the lower marshes that are in the early stage of succession, and *P. australis* occupies the middle marshes (Chen et al. 2003; Chen 2004). Sanchez's study (1998) indicates the existence of the gradients of abiotic factors such as electrical conductivity, redox potential and flooding depth perpendicular to the coastline. Our previous survey (Chen et al. 2003) has shown that the lower marshes in the Yangtze River estuary are characterized by higher salinity level, larger soil particle size and high frequency and long duration of tidal inundation, which can all increase the relative competitive ability of *Spartina* in relation to

*Phragmites*. Thus, the alterations of competitive interactions between *Spartina* and *Phragmites* along the elevational gradient in the salt marshes might lead to the successful invasion of *Spartina* in the lower salt marshes which are in the early stage of succession.

Our findings may have important implications for the environmental changes in the Yangtze River estuary although these are somewhat speculative. Several large water projects have been or are being carried out in the Yangtze River Basin, including the Three-Gorge Project and the Project of South-to-North Water Transfer. It has been recognized that dams and diversions in the upper drainage basin could cause the reduction of freshwater and sediment influx to the river estuaries, which leads to increased water salinity as a result of seawater intrusion and decreased sediment accretion in the river mouth (Sharaf el Din 1977; Wang 1998; Lee et al. 2004). In fact, the declining tendency in discharge of the Yangtze River caused by human activities has been detected in recent years (Wang 1998; Zhang and Chen 2002). At the same time, sea-level rise may lead to the environmental changes in the estuary. Over the last 100 years, the sea level has risen at an estimated rate of 6.5–11.0 mm/year in the Shanghai area of the Yangtze River mouth (Wang 1998), which is much higher than the mean annual rate of 1.4 mm/year. Rising sea level is expected to result in greater frequency and duration of inundation, higher salinity and coastal erosions in coastal wetlands (Boesch et al. 1994; Zhang et al. 2004).

As indicated in Table 4, *Spartina* has a competitive superiority over *Phragmites* in the habitats with high salinity and inundation. Therefore, it is speculated that the combined effects of the above two processes may be the creation of more habitats that favor *Spartina* over *Phragmites*. In response to the environmental changes, the range of *Spartina* is expected to expand further in the Yangtze River estuary in the future.

The findings also have important implications for ecological prediction, conservation and restoration of the salt marsh communities. Since the competitive balance can be shifted by environmental stresses, Perry et al. (2004) have proposed that manipulating environmental conditions to give native species a competitive advantage over invasive species could reduce ecosystem vulnerability. The tidal flats and marshes in the Yangtze River estuary are strongly affected by the tidal water flow, so the artificial alterations to environmental factors might be less effective. Based on our field observations that the competitive ability of *Phragmites* increases with the rapid development of the marshes, the establishment of *Phragmites* populations in brackish marshes may be of help for controlling the invasion of *Spartina*.

## Concluding remarks

Our case study indicates that invasive alien species are not necessarily born competitive, but environmental factors are important mediators of the competitive balance between co-occurring native and invasive alien plants, which supports the viewpoint that the outcomes of competition between co-occurring native and invasive alien plants depend on the growing conditions. Understanding how the growing conditions alter the invading ability of invasive species has important implications for the management of plant invasions. However, this study examined only the respective effects of three environmental factors on the competitive interactions of *Spartina* and *Phragmites*, thus further work is needed to study their interactive effects on them.

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