Spartina alterniflora with high tolerance to salt stress changes vegetation pattern by outcompeting native species

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Abstract.   Although many studies have been conducted on the interspecific competition between new arrivals and native plants, few of them have demonstrated how these processes interact with non-resource factors to determine vegetation pattern. This study investigated how salt stress mediates competition between native *Phragmites australis* and invasive *Spartina alterniflora* and thus changes plant communities in Dongtan, a Chinese coast salt marsh. The experiments revealed that the growth and reproduction of the native species declined with increasing salinity but that the invasive species performed well in the salinity range of 0–20‰, illustrating why the invader could proliferate in the high salinity mudflats in Dongtan. Moreover, the native had a high growth rate and therefore exhibited a competitive dominance over the invader at low salinity of ca. 7‰. Thus, the invader could not displace the native, and the native communities were stable in the low salinity zones. In contrast, the growth rate of the invader became higher when salinity increased; correspondingly, it gained the competitive dominance at high salinity of ca. 11‰. As a result, the invader colonising the native communities in high salinity zones performed better and could displace the natives over time. Consequently, after invasive *S. alterniflora* colonisation, the vegetation pattern of Dongtan marsh gradually changed from "mudflat–sedge–*P. australis*" to "mudflat–*S. alterniflora*" and "mudflat–*S. alterniflora* and natives" along the elevation gradients. The findings of the case study demonstrated that if a new arrival has a wide tolerance range to major non-resource stress in an ecosystem, it can not only displace natives by interspecific competition in high stress zones but can also spread into the zones without natives; on the other hand, natives with a narrow ecological amplitude in relation to the non-resource stress can only persist in low stress zones. Therefore, the distribution area of new arrivals increases as the distribution area of natives decreases. Because some non-resource stresses have substantial positive effects on native community invasibility, the practices that change the level of non-resource stress and create favorable conditions for invasive species should be stopped.

Key words: biological invasions; Chongming Dongtan; community succession; ecological amplitude; interspecific competition; non-resource stress; *Phragmites australis*; salt marsh; *Spartina alterniflora*.

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INTRODUCTION

Chance biogeographical events have been enhanced by anthropogenic transport and a decrease in the effects of natural biogeographical barriers as a result of artificial passages created during globalisation (Wang et al. 2006a, Liu et al. 2013). Thus, an important role of plant ecologists is to illustrate the influences of new arrivals on community patterns along environmental gradients to explain plant distribution. Integrated community theory predicts that local environments are biological filters that determine the survival of new arrivals and thus structure a pool of plant species based on physiological tolerances (Christopher et al. 2004). Afterwards, interspecific competition among the plants determines the community patterns. This theory suggests that the physiological tolerance and competitive ability of new arrivals are important influences on community patterns. More broadly, plants often suffer from harsh environmental conditions within their current and potential distribution ranges. However, while many studies have focused on the tolerance to low resource availability and competition under different levels of resource availability (Grime 1977, Tilman 1985, Tilman 1990, Grace 1991, Li et al. 2011, Zhou et al. 2012), the effects of the tolerance of new arrivals to non-resource factors on their performance and competitiveness have been relatively ignored.

The competitor-stress tolerator-ruderal theory and habitat partitioning theory account for stress and competition (Grime 1977, Grace 1991, Wisheu 1998). The competitor-stress tolerate-ruderal theory predicts that the gradients in physical stress and resource availability will show similar patterns of segregation in stress tolerators and excellent competitors (Grime 1977, Grace 1991). Excellent competitors that can grow rapidly and that have high capture rates for all resources dominate highly productive habitats, but the slow growth rates and low resource requirements of stress tolerators allow them to persist in unproductive habitats. Moreover, the habitat partitioning theory predicts that when plant species exhibit distinct preference for habitats, the physiological or morphological characters and not competition determine the performance of plants along an environmental gradient; when

plants have shared preferences for their most preferred habitat type, competitive ability determines their performance (Rosenzweig 1991, Wisheu 1998). These two theories do not distinguish between resource and non-resource stress when predicting the nature of plant interactions along an environmental gradient.

Here, we predict, based on the integrated community theory, the competitor-stress tolerate-ruderal theory and the habitat partitioning theory, that under conditions of stable abundant resources, if a new arrival has a wider ecological amplitude with respect to non-resource stress, it will occupy the harsh habitats where natives do not exist and will compete with native plants in the habitats within the ecological amplitude of the natives. Moreover, the succession of a native community will be initiated if the new arrival has competitive dominance, in which case, the new arrival with high tolerance to non-resource stress can substantially change vegetation pattern.

Rapidly spreading invasive plants in salt marshes are ideal subjects for studying the effects of non-resource stress on plant distribution. The impact of invasive plants that displace native plants is readily apparent and result in adverse effects on the invaded habitats (Burghardt et al. 2010, Corbin and D'Antonio 2011). Salt marshes often have a strong gradient of non-resource stress, such as salinity and inundation, and a small number of plant species distributed in distinct zones. At present, many estuaries and coastal regions are threatened with plant invasions by plants such as *Spartina* and *Phragmites* (Vasquez et al. 2006, Wang et al. 2006a, Medeiros et al. 2013). Dramatically, they can reciprocally invade. For example, Dongtan salt marsh, located in the Yangtze River estuary, Chongming Island, Shanghai, China (31°250′ ∼ 31°380′ N; 121°500′ ∼ 122°050′ E), has two formations that include native *Phragmites australis* (Cav.) Trin and invasive *Spartina alterniflora* Loisel (Li et al. 2009, Wang et al. 2010). This vegetation pattern is typical in the coastal salt marshes of eastern China that favor invasive *S. alterniflora*. Meanwhile, *Phragmites* has competitively displaced native *Spartina* in the marshes along the east Pacific coast (Silliman and Bertness 2004, Vasquez et al. 2006). These examples suggest the importance of environmental conditions on interspecific competition between new arrivals

and native plants.

Inundation and salinity are two major non-resource conditions in salt marshes (Emery et al. 2001, Pennings et al. 2005, Silvestri et al. 2005). Many studies have shown that *P. australis* and *S. alterniflora* have a high tolerance to the anoxia caused by inundation (Maricle and Lee 2002, Wang et al. 2006*a*, *b*, Engloner 2009). The tide in Dongtan marsh is low and infrequent (half-immersion type), and such low-intensity inundation stress does not inhibit the growth of *P. australis* and *S. alterniflora* or change the outcome of their competition (Maricle and Lee 2002, Wang et al. 2006*b*, Wang et al. 2010). Hence, salt stress may be a key factor determining the performance of the two plants, and successful invasions could be explained by the differences in tolerance to salinity between the two plants. We predicted that invasive *S. alterniflora* would be favored by the salinity in the salt marshes along the eastern coast of China and, therefore, would successfully invade.

In this study, several types of experiments have been conducted: pot experiments have been conducted to test the two plants' ecological amplitude with respect to salinity; competitive experiments in the field have been used to test the effects of salinity on competitiveness of two plants; and transplant experiments in the field have further been used to illustrate the differences in the performance of native *P. australis* between the presence and absence of invasive *S. alterniflora*, which represented the competition influence of new arrivals on the stability of native communities along the salinity gradient. In Dongtan salt marsh, methods including long-term remote sensing and ground surveys have been performed to examine vegetation dynamics and the relationship between the performance of plants and soil pore water salinity.

METHODS

Pot experiment

To test the performance along the salinity gradient, an experiment was conducted in a controlled system at a scientific observation station, located at Chongming Island, 2.5 km west of Dongtan marsh. The controlled system consists of 100 cement pools (length 1.5 m × width 1.5 m × height 0.6 m).

The *S. alterniflora* and *P. australis* samples were collected from the middle marsh zone of Dongtan marsh in mid-April. The collected plant materials were cut into similar-sized plantlets ca. 25 cm in length, with a single ramet and attached roots (the materials used in other experiments were the same). The ramets were planted in circular pots (caliber 25 cm × bottom diameter 20 cm × height 20 cm) containing 4.5 kg of sand that was cleaned with freshwater. A total of 30 pots were provided for the experiment: 15 pots of monoculture *P. australis* with 2 ramets in each pot and 15 pots of monoculture *S. alterniflora* with 2 ramets in each pot. All of the pots were placed in cement pools for four weeks with 5.0 cm of freshwater in each pool, and then the salinity treatment was applied.

Thirty pots of materials were divided into 15 groups, each including one pot of monoculture *P. australis* and one pot of monoculture *S. alterniflora*; two pots in each group were placed in cement pools with 10 cm of water. Water salinity was adjusted with unpurified connate sea salt to 0‰, 5‰, 10‰, 15‰ and 20‰. This range of salinity (0–20‰) was chosen because the literatures have documented that *P. australis* is stenohaline and that its spread is facilitated by decreases of salinity in *Spartina* marshes (Vasquez et al. 2005, Vasquez et al. 2006, Wang et al. 2006*b*, Wang et al. 2010); and because the salinity of soil pore water in our Dongtan marsh study system is ca. 4–18‰ (see *Results: Remote sensing and filed survey...* and Fig. 7). There were three pools per salinity level, and the pools of different salinities were randomly arranged. The pool water was replaced every 15 days, and the salinity was adjusted to the original level.

The plants were harvested after six months. We measured the total number of ramets as well as the number of dead ramets of *P. australis* and *S. alterniflora* in each pot. We then cleaned the underground plant structures with water. Each part of the plant was oven-dried at 80°C until a constant weight was reached to determine the total dry biomass. The indices of performance included the total dry biomass, inflorescence dry biomass and ramet death ratio.

P. australis failed to flower at a salinity of 20‰ and thus the inflorescence dry biomass was 0. GLMs were used to test the difference of
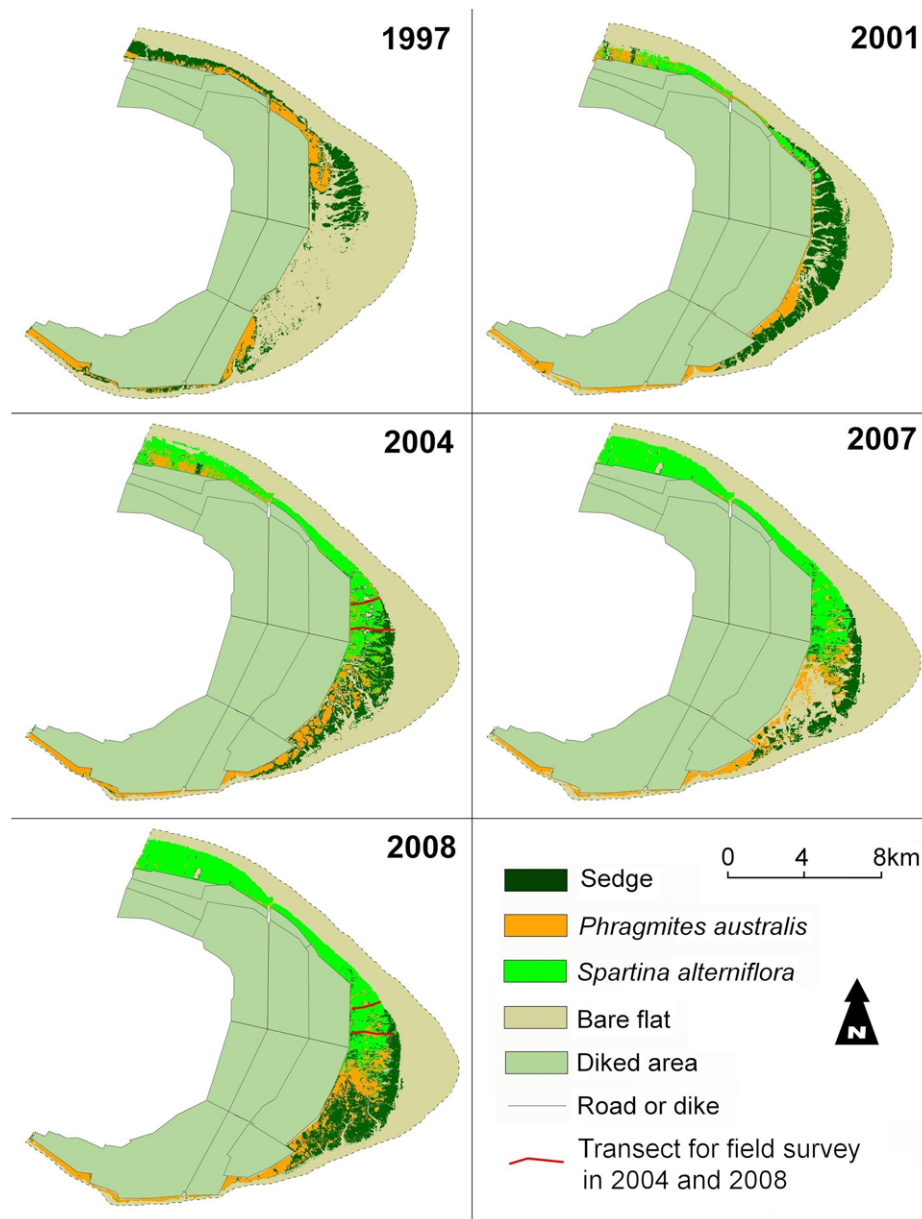
Fig. 1. Dynamics of the vegetation pattern in Dongtan marsh. The shoreline elevation is 100 cm. Sedge includes *Scirpus triqueter*, *Scirpus mariqueter* and *Carex scabrifolia*.

inflorescence dry biomass among salinity groups; a one-way ANOVA was used to test the effects of salinity on the other indices of two plants; Tukey's test was used as a post hoc comparison. A *t*-test was used to analyze the difference of performance between the native and the invader at each salinity level. The significance level was set at 5% (as in the other experiments).

Field competition experiment

The experiment was conducted on the mud-flats of Dongtan marsh within a 60×60 m^2 area containing a tidal creek ca. 2.5 m wide. The salinity in the area adjacent to the tidal creek is lower due to the water from tidal subsidies, and the salinity distal to the tidal creek is higher due to the evaporation of water from the soil. We first
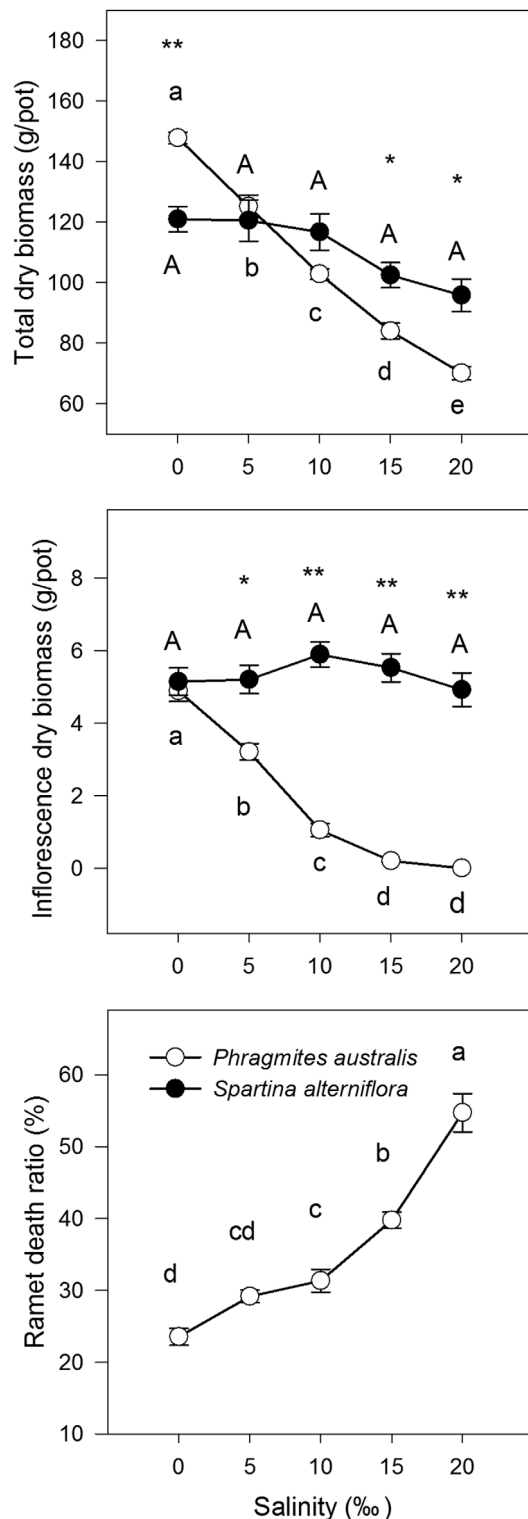
measured the soil pore water salinity. PVC pipes were inserted into the soil (to a depth of 40 cm) and then removed, creating holes. After one hour, soil pore water was extracted from the holes and salinity was measured with a conductivity meter (Metter Toledo Company, Switzerland). The mudflat was then divided into a high-salinity zone and a low-salinity zone, with salinities of 11.83‰ ± 0.21‰ and 7.03‰ ± 0.19‰ (mean ± SE), respectively (t-test, $P < 0.05$, $n = 10$).

Eight plots were established in each zone, and the plots were spaced 5.0 m apart. Three quadrats were established in each plot, and the quadrats were spaced 2.0 m apart. In mid-April, the collected ramets were planted. In each plot, one quadrat was planted with 16 ramets of *P. australis* spaced at 0.3-m intervals, the second quadrat was planted with 16 ramets of *S. alterniflora* spaced at 0.3-m intervals, and the third quadrat was planted with 16 ramets of *P. australis* and 16 ramets of *S. alterniflora* spaced 0.15 m apart. There were four rows in each monoculture quadrat and four ramets in each row. Similarly, there were four rows in each mixture quadrat and eight ramets in each row. The ramets of one plant was surrounded by those of another plant species, with the exception of the ramets in the mixture quadrat edge row. As some planted *P. australis* died, we replaced the dead ramets with additional ramets; in late May, we found that all of the replacement plants of *P. australis* had survived.

Seven months later, we randomly selected four plots in each zone, collected all the plants in the center of the quadrat (0.25 m²), and measured the

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Fig. 2. Effects of salinity on the performance of *Phragmites australis* and *Spartina alterniflora* in the pot experiment. *S. alterniflora* had no dead ramets and, thus, had no ramet death ratio. Capital letters indicate significant differences of *S. alterniflora* performance along the salinity gradient; lowercase letters indicate significant differences of *P. australis* performance along the salinity gradient. Asterisks (*) indicate significant differences between *S. alterniflora* and *P. australis* (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Standard errors of 3 replicate pots are shown.
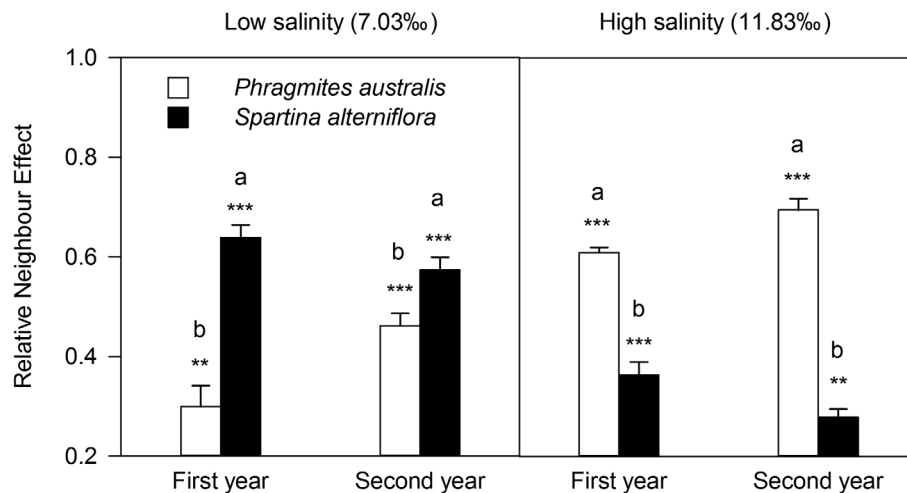
Fig. 3. Effects of salinity on the interactions between *Phragmites australis* and *Spartina alterniflora* in the field competition experiment. Data shown are the mean interspecific relative neighbor effects (RNE) in the aboveground dry biomass in the treatment of salinity level in two years. Lowercase letters indicate significant differences of RNE between two plants. Asterisks (*) indicate that the RNE is greater than zero (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Standard errors of 4 replicate plots are shown.

aboveground dry biomass, density and flower ratio. The same measurements were taken in the remaining four plots in mid-November of the following year. The competition intensity was measured using the relative neighbor effect (RNE) (Williams and McCarthy 2001),

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

where P is the performance of plants in the presence (+N) and absence (−N) of neighbors, 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}. The RNE value is 0 when no interaction occurs, negative when the interaction is facilitative, and positive when the interaction is competitive.

A repeated measures ANOVA was used to analyze the effects of salinity and plant species on the RNE, Tukey's test was used as a post hoc comparison. A *t*-test was used to analyze the difference between the RNE value and zero. Similarly, a repeated measures ANOVA was used to analyze the effects of salinity and the planting pattern on the performance of the two plants, Tukey's test was used as a post hoc comparison. Because *P. australis* failed to flower in the first year, a two-way ANOVA was used to analyze the effects of salinity and interspecific interactions on

the flower ratio in the second year, Tukey's test was used as a post hoc comparison. A *t* - test was used to analyze the difference of performance of each plant species between mixture and monoculture in a same year.

Field transplant experiment

From the dike to the seaward side of Dongtan marsh, we chose 4 monoculture communities of *P. australis* and randomly set 16 quadrats in each community. Eight quadrats were chosen to transplant *S. alterniflora* in mid-April, and one quadrat was planted with 36 ramets of *S. alterniflora* spaced at 0.4-m intervals. The remaining eight quadrats served as the control.

Six months later, we randomly selected four treated quadrats and four control quadrats and collected the plants in the center (1 m²) of the planting zone and the control. Then, we measured aboveground dry biomass, density and flower ratio. The soil pore water salinity was measured synchronously. The same measurement was conducted in the remaining quadrats in mid-November of the following year.

The performance of transplanted *S. alterniflora* represented the invasiveness of new arrivals. Moreover, the differences of performance of *P. australis* between the presence and absence of

Fig. 4. Effects of salinity and interspecific competition on the performance of *Phragmites australis* in the field competition experiment. Asterisks (*) indicate significant differences between monoculture and mixture (*$p <$ 0.05, **$p <$ 0.01, ***$p <$ 0.001). The planted *P. australis* failed to flower in the first year, and a two-way ANOVA was used to analyze the effects of salinity and interspecific interactions on the flower ratio of this native in the second year, with Tukey's test used as the post hoc comparison (the effect of salinity, $F = 63.90$, $p = 0.005$; the effect of competition, $F = 5.03$, $p = 0.01$; the interaction, $F = 0.94$, $p > 0.05$; all df = 1). Standard errors of 4 replicate plots are shown.
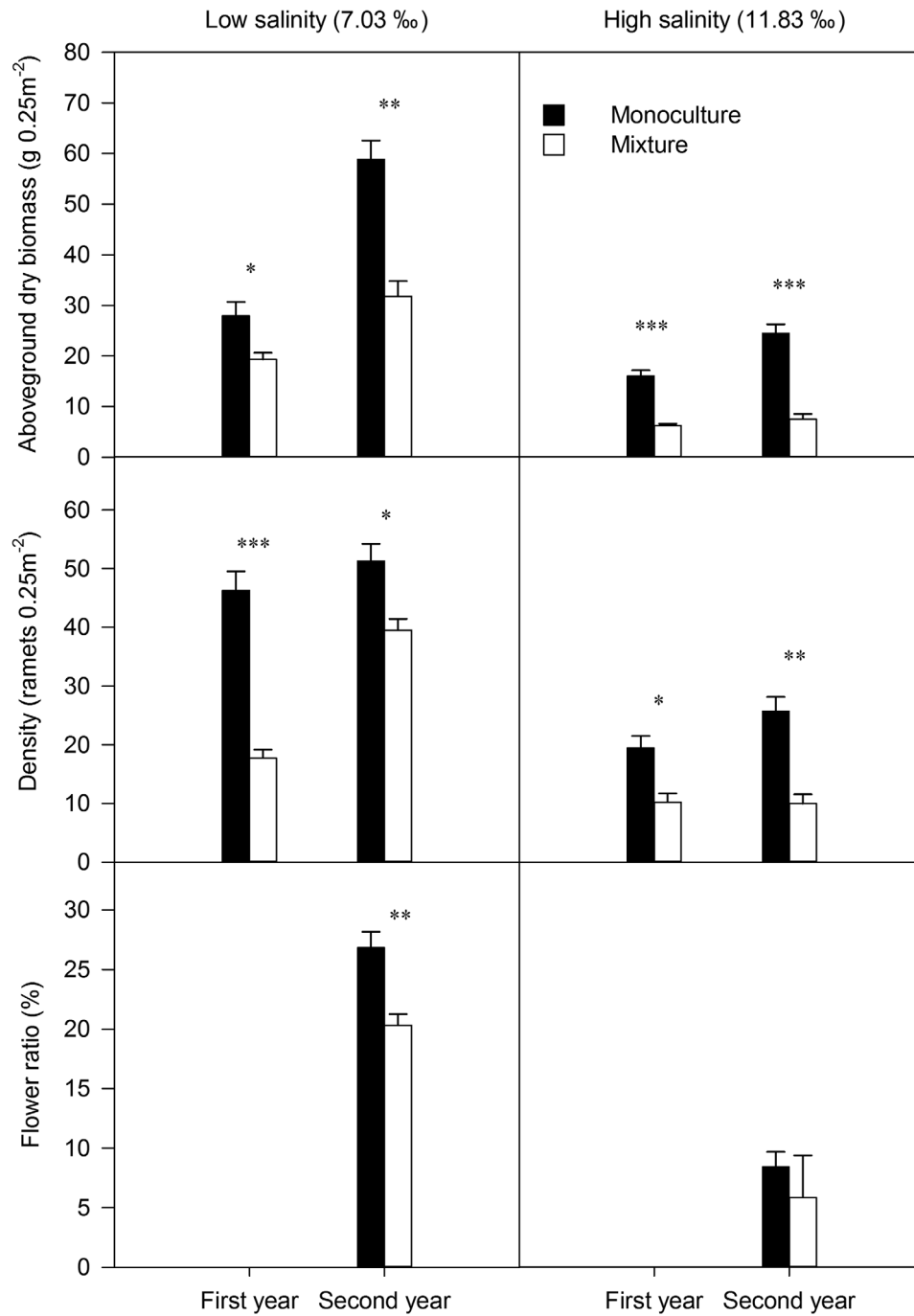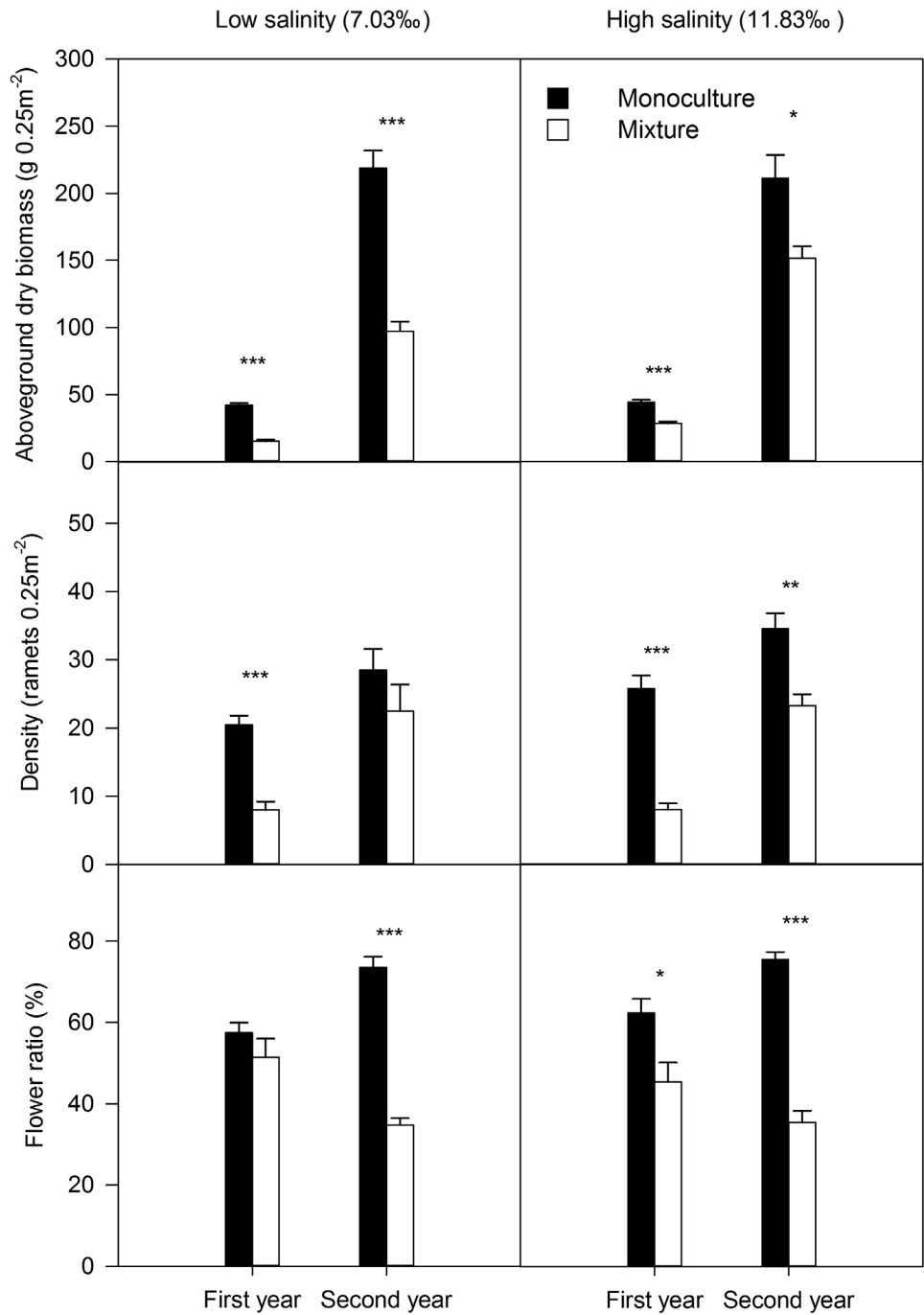
Fig. 5. Effects of salinity and interspecific competition on the performance of *Spartina alterniflora* in the field competition experiment. Symbols are as in Fig. 4. Standard errors of 4 replicate plots are shown.

transplanted *S. alterniflora* represented the influences of new arrivals on the native communities. Here, the new arrival influences (NAI) were measured as the influence of new arrivals on the native communities,

$$\text{NAI} = \frac{P_\text{T}}{P_\text{C}} \times 100\%$$
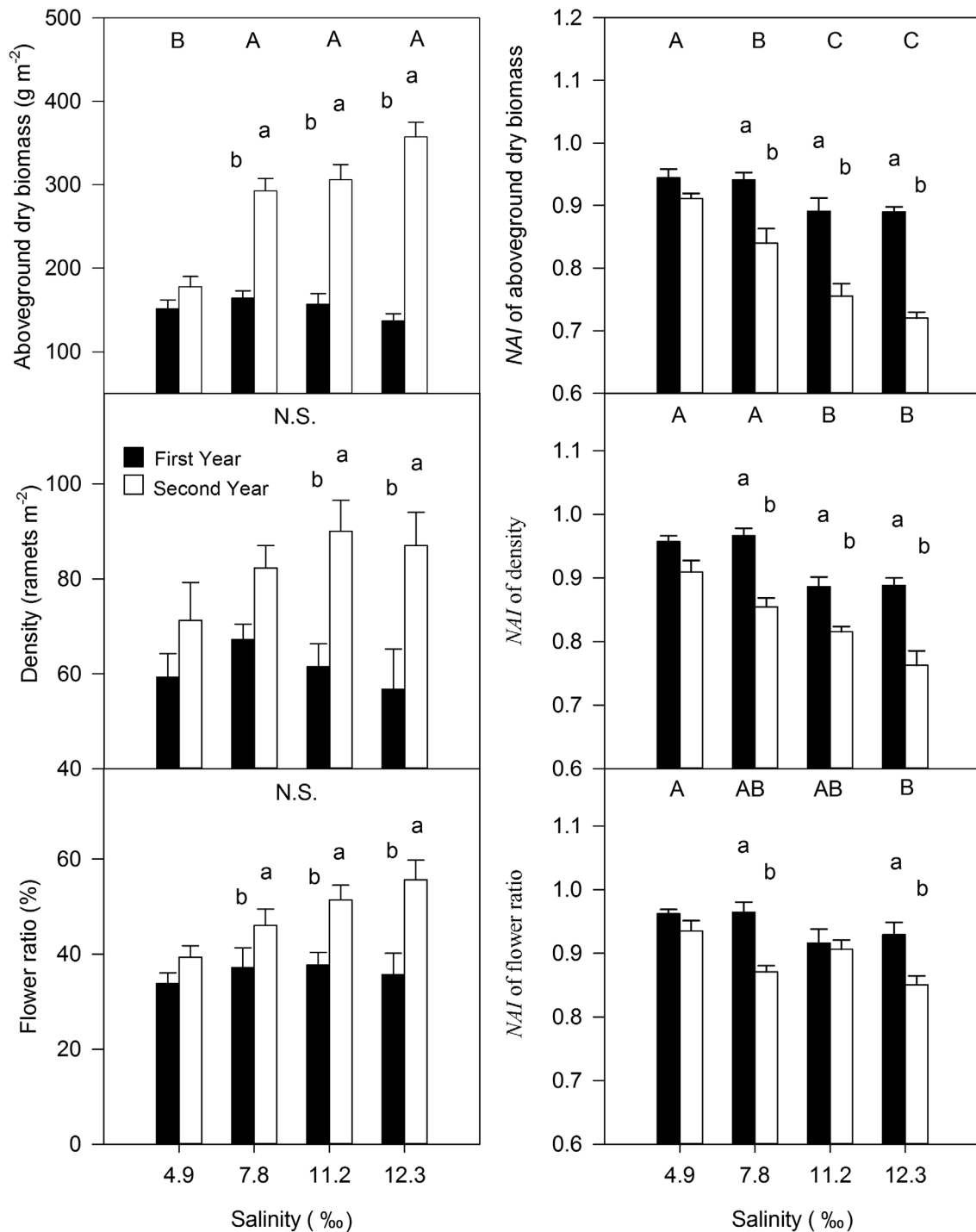
Fig. 6. Effects of salinity on the performance and new arrival influences (NAI) of planted *Spartina alterniflora* in *Phragmites australis* community in the field transplant experiment. NAI is the difference of *P. australis* performances between the presence and absence of transplanted *S. alterniflora*. Capital letters indicate significant differences among salinity groups; lowercase letters indicate significant differences between two years at each salinity level. Standard errors of 4 replicate quadrats are shown.

where P_T and P_C were the performance of matrix *P. australis* in the presence and absence of transplanted *S. alterniflora*, respectively. The greater the NAI, the lower the invasibility and the higher the community stability. Thus, when the NAI decreases over time, the succession of the native community occurs.

A repeated-measures ANOVA was used to analyze the effects of salinity on the performances and NAI of the transplanted *S. alterniflora*, and a Tukey's test was used as the post hoc comparison.

Remote sensing and field survey

Remote sensing has been conducted eight times since 1997, and image formats were uniformly Landsat-5TM (except in 2001 and 2002, when the image format is Landsat 7 ETM+) transformed. Remote-sensing data were obtained in mid-November, when *P. australis* was withered and yellowed and *S. alterniflora* was still green; sedges, including *Scirpus triqueter*, *Scirpus mariqueter* and *Carex scabrifolia*, were relatively short, yellowed and fallen over. Therefore, their respective reflectivity of near-infrared and mid-infrared lights is significantly different. To ensure that the final correction precision is within one pixel, we first conducted a geographical correction for the ASTER data from 2004 using six ground-control points with obvious ground characteristics. There were two points in the monoculture community of *P. australis*, two points in the monoculture community of *S. alterniflora*, and two points in the mixture community of *S. triqueter*, *S. mariqueter* and *C. scabrifolia*. Moreover, rectification and geometric correction were conducted for all the data based on this image. Because the image is small, the polynomial method was used for all correction models, followed by the acquisition of optimal bands through PCA analysis and false-color processing (used for artificial interpretation). Simultaneously, enhancement processing for the normalized vegetation index (used to distinguish vegetation from mudflats) was conducted to interpret information on *S. alterniflora*, *P. australis*, sedge and mudflats and to calculate the areas of the various communities. To ensure the accuracy of the calculation, stratified random sampling based on an error matrix was applied to the categorized remote-sensing results; all of the categorized

images and corrected, classified results were assessed, and the accuracy of classified results was shown to be above 85%.

The surveys were conducted in mid-October of 2004 and 2008. In each survey, two transects (south/north) with an interval of 1100 m throughout the vegetation were investigated (Fig. 1). Nine sampling plots were set in each transect based on vegetation types, and four quadrats (1 m × 1 m) were randomly established in each sampling plot. We collected the aboveground parts of the plants in each quadrat and measured the soil pore water salinity. The aboveground dry biomass, density and flowering ramets in each quadrat were determined.

Pearson correlation analysis was used to test the relationship between salinity and plant performance at each transect in each year. A repeated ANOVA was used to test the difference of salinity between the year of 2004 and 2008 in the South transect; the same analysis was performed for the North transect.

RESULTS

Pot experiment: salinity tolerance range of two plants

The performance of *P. australis* significantly decreased along the salinity gradient (Fig. 2). At a salinity of 10 ‰, the inflorescence dry biomass of *P. australis* was ca. 0.8 g, which was one sixth of that in freshwater, and thus, *P. australis* failed to sexually reproduce; at a salinity of 15‰, the death rate of *P. australis* ramets was ca. 40% (Fig. 2). *P. australis* could survive in the highest salinity of 20‰ in this study (Fig. 2). In contrast, the total dry biomass and inflorescence dry biomass of *S. alterniflora* did not substantially change along the salinity gradient (Fig. 2). Moreover, the invader had no dead ramet. Thus, *S. alterniflora* could normally grow and sexually reproduce in the salinity of 0–20‰ (Fig. 2).

In treatment salinities of 0 and 5‰, *P. australis* produced more biomass than *S. alterniflora* (Fig. 2), and thus had a higher growth rate. Moreover, the biomass of *P. australis* declined with increasing salinity but that of *S. alterniflora* did not (Fig. 2). Consequently, *S. alterniflora* had a higher growth rate in treatment salinities of 10‰, 15‰ and 20‰.

Table 1. Summary of repeated-measures ANOVA of the effects of salinity and plant species on the relative neighbor effect (RNE) in the field competition experiment.

Source	df	F	p
Between subjects			
Salinity	1	0.13	0.729
Species	1	6.66	0.024
Salinity × species	1	187.99	<0.001
Within subjects			
Time	1	2.44	0.144
Time × salinity	1	2.42	0.146
Time × species	1	40.42	<0.001
Time × salinity × species	1	0.84	0.377

Note: $p < 0.05$ is taken to be significant.

Competition experiment: effect of salinity on plant interactions

The differences of relative neighbor effect (RNE) showed that P. australis exhibited a competitive dominance over S. alterniflora at a low salinity of 7.03‰ (Table 1; Fig. 3), but S. alterniflora gained competitive dominance at a high salinity of 11.8‰ (Table 1; Fig. 3). Both at low and high salinity, the RNEs of P. australis and S. alterniflora were significantly greater than zero (Fig. 3). Thus, the strong interspecific competition substantially inhibited the performance of two plants (Tables 2 and 3; Figs. 4 and 5). The competitive inhibition of P. australis by S. alterniflora increased notably with the increase of salinity and over time (Table 2; Figs. 3 and 4); in contrast, the competitive inhibition of S. alterniflora by P. australis insignificantly increased with the decrease of salinity (Table 3; Figs. 3 and 5).

Transplant experiment: effect of salinity on performance and influence of invader

The performance of S. alterniflora transplanted in the native communities where the salinities were higher than 7.8‰ improved rapidly over time, but S. alterniflora transplanted at the salinity of 4.9‰ did not significantly change (Table 4; Fig. 6). Moreover, the new arrival influences (NAI) at salinity of 4.9‰ did not substantially change over time, but those in salinities higher than 7.8‰ declined significantly over time (Table 4; Fig. 6). This indicated that the community stability of native P. australis could be maintained in low salinity zones and that the rate of community succession from the native to the invader was improved with the increase of salinity.

Remote sensing and filed survey: dynamic of vegetation pattern

Moving from the dike to the seaward side of Dongtan salt marsh, the soil pore water salinity gradually increased from ca. 4.5‰ to 15.5‰ and then decreased to ca. 8.5‰ (Fig. 7). Moreover, in the same transect, salinity did not change significantly over time (North transect: $F = 0.143$, $p = 0.708$; South transect, $F = 0.012$, $p = 0.915$; one-way repeated-measures ANOVA).

The vegetation pattern in Dongtan marsh in 1997, when S. alterniflora had not colonized, included two formations, P. australis and sedges including S. mariqueter, S. triqueter and C. scabrifolia (Fig. 1). The sedges occupied the low and middle marshes, and P. australis spread into the high marsh closest to the dike (Fig. 1).

After S. alterniflora colonized the north zone of

Table 2. Summary of repeated-measures ANOVA of the effects of salinity and interspecific competition on the performances of *Phragmites australis* in the field competition experiment.

Source	Aboveground dry biomass			Density		
	df	F	p	df	F	p
Between subjects						
Salinity	1	223.71	<0.001	1	200.00	<0.001
Planting pattern	1	125.26	<0.001	1	101.23	< 0.001
Salinity × planting pattern	1	2.50	0.140	1	4.97	0.046
Within subjects						
Time	1	63.23	<0.001	1	24.35	<0.001
Time × salinity	1	25.37	<0.001	1	9.41	0.010
Time × planting pattern	1	14.69	0.002	1	2.06	0.177
Time × salinity × planting pattern	1	2.86	0.116	1	11.95	0.005

Notes: $p < 0.05$ is taken to be significant. *Phragmites australis* failed to flower in the first year. A two-way ANOVA was used to analyze the effects of salinity and interspecific interactions on the flower ratio of this plant in the second year, with Tukey's test used as the post hoc comparison.

Table 3. Summary of repeated-measures ANOVA of the effects of salinity and interspecific competition on the performances of *Spartina alterniflora* in the field competition experiment.

Source	Aboveground dry biomass			Density			Flower ratio		
	df	F	p	df	F	p	df	F	p
Between subjects									
Salinity	1	6.33	0.027	1	3.09	0.104	1	0.03	0.859
Planting pattern	1	81.10	<0.001	1	48.48	<0.001	1	112.55	<0.001
Salinity × planting pattern	1	8.54	0.013	1	2.37	0.150	1	1.49	0.246
Within subjects									
Time	1	487.78	<0.001	1	64.79	<0.001	1	0.10	0.760
Time × salinity	1	1.58	0.232	1	0.07	0.800	1	0.136	0.719
Time × planting pattern	1	30.98	<0.001	1	5.06	0.044	1	40.03	<0.001
Time × salinity × planting pattern	1	4.29	0.060	1	<0.001	1.000	1	1.22	0.290

Note: $p < 0.05$ is taken to be significant.

Dongtan marsh, this invader not only spread into mudflats without the natives but also displaced native plants in the high salinity zones (Figs. 1 and 7). Thus, the vegetation pattern in Dongtan marsh changed from "mudflat–sedge–*P. australis*" to "mudflat–*S. alterniflora*" in the northern zone, "mudflat–*S. alterniflora* and natives" in the middle zone, and the original "mudflat–sedge–*P. australis*" zonation in the southern zone (Fig. 1). Moreover, the total vegetation area in Dongtan marsh increased overtime while the distribution areas of natives decreased. *S. alterniflora* has become the largest plant community as of 2004 (Fig. 8).

The aboveground dry biomass, density and number of flowering ramet of natives including *P. australis* and *S. mariqueter* were negatively correlated with soil pore water salinity in the field, but the growth and sexual reproduction of invasive *S. alterniflora* were not correlated with salinity (Table 5; Fig. 7).

DISCUSSION

In this case study, the results obtained by the pot and field experiments demonstrate that (1) excellent competitors and non-resource stress tolerators can share preferences for their most preferred habitat type, and their interspecific competition can occur in both favorable and unfavorable non-resource conditions; (2) at any level of a non-resource stress, if a plant can grow rapidly, it has a competitive advantage and the non-resource stress can change plant growth rate and thus affect its competitiveness; and therefore (3) a new arrival with a high tolerance to major non-resource stress factors can outcompete the natives and consequently change vegetation pattern in physiologically stressful ecosystems.

Table 4. Summary of repeated-measures ANOVA of the effects of salinity on performances and new arrival influences (NAI) of *Spartina alterniflora* in the field transplant experiment.

Source	Aboveground dry biomass			Density			Flower ratio		
	df	F	p	df	F	p	df	F	p
Performance									
Between subjects									
Salinity	3	6.23	0.009	3	0.67	0.589	3	1.67	0.22
Within subjects									
Time	1	1050.99	<0.001	1	92.32	<0.001	1	77.22	<0.001
Time × salinity	3	59.84	<0.001	3	4.32	0.028	3	5.28	0.015
NAI									
Between subjects									
Salinity	3	42.38	<0.001	3	20.07	<0.001	3	4.75	0.021
Within subjects									
Time	1	73.26	<0.001	1	91.19	<0.001	1	23.28	<0.001
Time × salinity	3	5.17	0.016	3	3.75	0.041	3	3.50	0.050

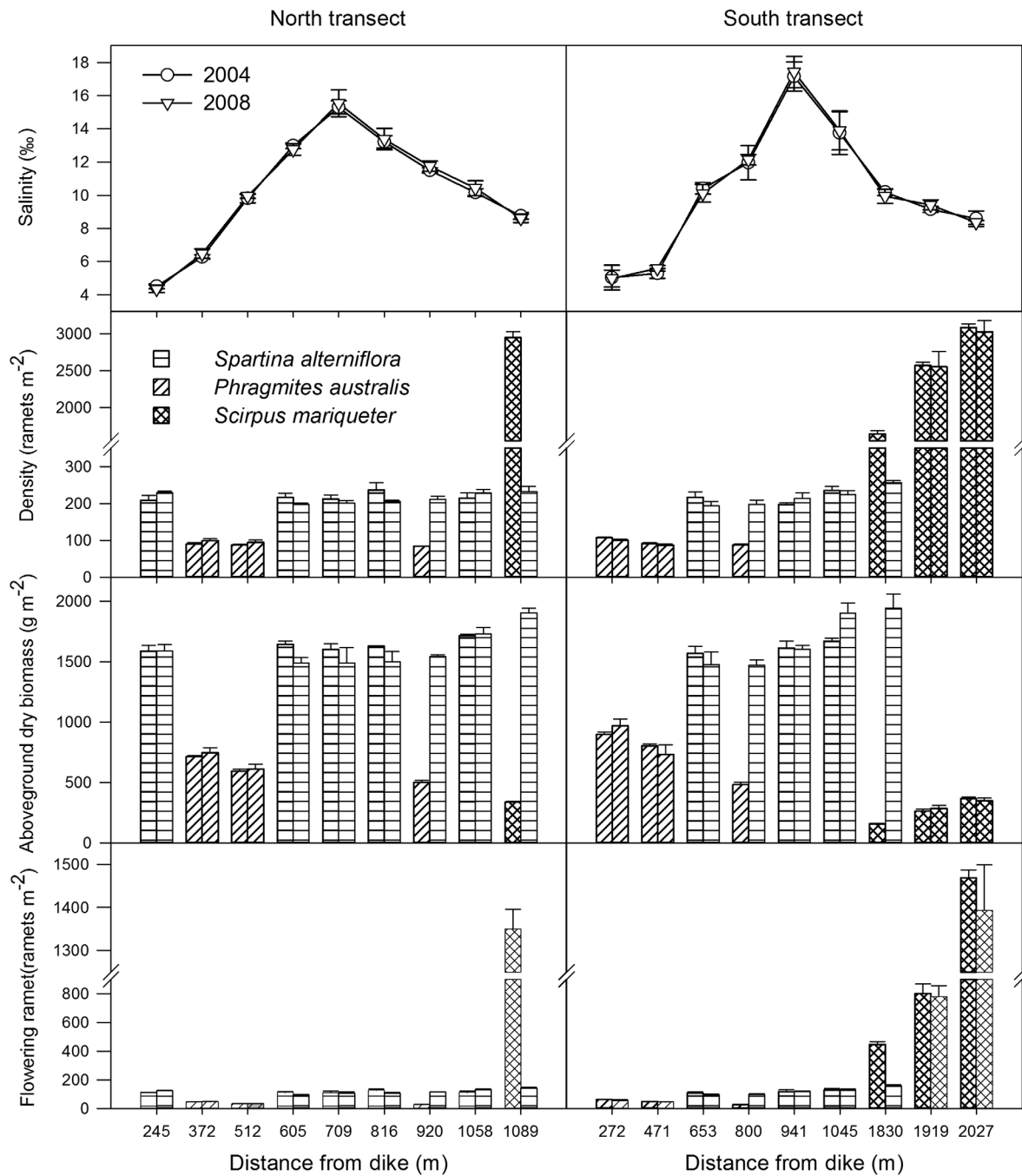*Note: $p < 0.05$ is taken to be significant.*

Fig. 7. Salinity and performances of plants in 2004 and 2008 in Dongtan marsh. Left columns represent the performances of plants in 2004; right columns represent the performances of plants in 2008. Changes of plant species in an investigated plot are indicated by different hatching patterns in the left and right columns. Standard errors of 4 replicate quadrats are shown.

Table 5. Pearson correlations between salinity and the performance of the plants in Dongtan salt marsh.

Index	2004			2008		
	n	Pearson correlation	p	n	Pearson correlation	p
Phragmites australis						
Aboveground dry biomass	24	−0.896	<0.001	16	−0.592	0.016
Density	24	−0.577	0.003	16	−0.001	0.997
No. flowering ramet	24	−0.890	<0.001	16	−0.901	<0.001
Spartina alterniflora						
Aboveground dry biomass	32	0.071	0.701	48	−0.154	0.296
Density	32	0.080	0.662	48	−0.324	0.025
Flower ratio	32	0.193	0.389	48	−0.151	0.307
Scirpus mariqueter						
Aboveground dry biomass	16	−0.772	<0.001	8	−0.788	0.020
Density	16	−0.757	0.001	8	−0.876	0.004
No. flowering ramet	16	−0.657	0.006	8	−0.525	0.182

Note: $p < 0.05$ is taken to be significant.

Effects of tolerance to non-resource stress on plant competitiveness

The competitor-stress tolerator-ruderal theory predicts that competitors exist in highly productive habitats and that stress tolerators persist in unproductive habitats (Grime 1977, Grace 1991). However, our results demonstrated that *S. alterniflora*, as a stress tolerator, could not only flourish in high salinity habitats but also perform well in freshwater and low salinity habitats (Figs. 1, 2, 5, 6 and 7). Moreover, as a competitor, *P. australis* could dominate low salinity habitats and persist in high salinity habitats (Figs. 1, 2, 4, 6 and 7). On the other hand, the habitat partitioning theory predicts that interspecific competition often occurs in a favorable habitat for both competitors (Rosenzweig 1991, Wisheu 1998). Nevertheless, our experiments showed that although both freshwater and low salinity were favorable to the growth of *P. australis* and *S. alterniflora* and high salinity was unfavorable to *P. australis* growth (Fig. 2), the interspecific competition between two the plant species did not arise in only low salinity habitats but also occurred in high salinity habitats (Fig. 3). Similarly, Vasquez et al. (2006) and Wang et al. (2006b) have shown that the interspecific competition between *P. australis* and *S. alterniflora* can arise in a very
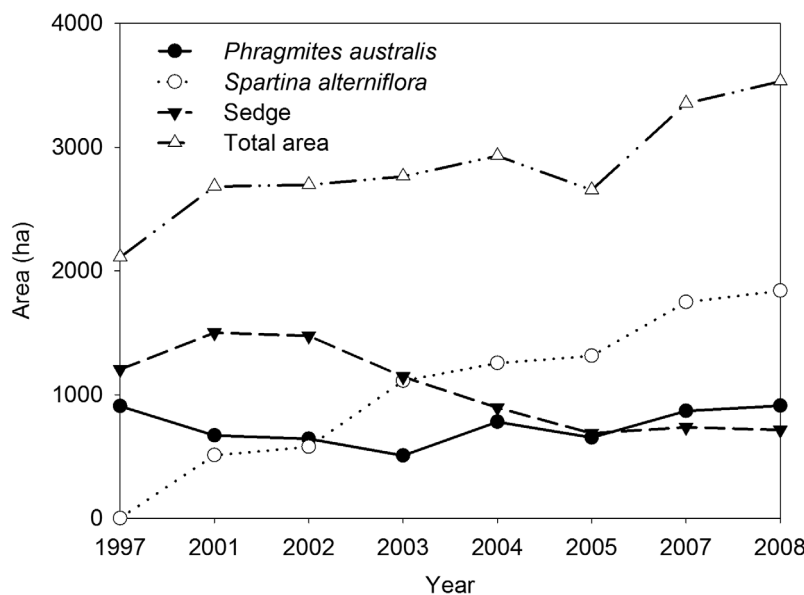

Fig. 8. Changes in the vegetation area and distribution area of the plants in Dongtan marsh since 1997.

wide salinity range of 0–30‰.

Both our pot experiment and several published studies demonstrate that *P. australis* produces more aboveground biomass than *S. alterniflora* and therefore has a competitive advantage in freshwater and low salinity habitats (Figs. 2 and 3) (Vasquez et al. 2006, Wang et al. 2006*b*). This type of growth response has been described as a phalanx life strategy, which allows the plant to exclude other plants from invading by increasing the size of aboveground tissues and root per unit time, resulting in high capture rate for all resources due to a high growth rate (Grime 1977, Grace 1991, Vasquez et al. 2006). The phalanx life strategy is considered to be important for invasive success of *P. australis* in *Spartina* marshes (Vasquez et al. 2006).

Because it is not a salt stress tolerator, *P. australis* loses the competitive advantage in high salinity conditions (Figs. 2 and 3). Vasquez et al. (2005) have shown that the increase of salinity can strongly inhibit the growth of three haplotypes (viz. F, M and AC) of *P. australis*, which are often attributed to the ecophysiological features of this plant. For example, the osmotic potential of *P. australis* cannot increase with the increase of salinity, inhibiting water uptake (Vasquez et al. 2006). Touchette (2007) has suggested that salt may prevent absorption and transportation of nutrition in plants. Furthermore, the transpiration and photosynthesis of *P. australis* is very sensitive to salt stress (Jiang et al. 2009). Thus, *P. australis* has a narrow ecological amplitude with respect to salinity, which will lead to a decrease in the growth rate along the salinity gradient (Fig. 2) (Vasquez et al. 2006, Engloner 2009). Consequently, this competitor loses its competitive advantages in high salinity conditions (Fig. 3) (Vasquez et al. 2006, Wang et al. 2006*b*). Other ecologists have also shown that some nonresource stress can substantially influence plant competitiveness (Emery et al. 2001, Wang et al. 2006*b*, He et al. 2013).

S. alterniflora becomes an excellent competitor in high salinity conditions due to its high tolerance (Figs. 2 and 3). *Spartina* plants have a salt gland and thus can excrete excess salt on the leaf face (Levering and Thomson 1971, Wang et al. 2006*a*). Therefore, *S. alterniflora* suffers relatively little damage from high salinity. Specifically, some scholars have reported that the

photosynthesis of cordgrass does not significantly change in the salinity range of 0–510 mM (Mateos-Naranjo et al. 2010, Redondo-Go'mez et al. 2011). Moreover, *S. alterniflora* can efficiently absorb water at high salinity because it's osmotic potential will increase with increasing salinity (Vasquez et al. 2006). These ecophysiological features help *S. alterniflora* maintain a constant growth rate over a wide salinity range (Fig. 2). Thus, this stress tolerator gains the competitive superiority in high salinity conditions where the growth rate of *P. australis* is low (Figs. 2 and 3) (Vasquez et al. 2006, Wang et al. 2006*a, b*).

Influences of new arrival tolerance to non-resource stress on vegetation pattern

Dongtan marsh, a coastal wetland, is influenced by many factors, such as the tide, evaporation, rainfall and topography (Li et al. 2009, Tang et al. 2013). The zones below the mean neap-tide water level have a medium salinity because of large-scale input of water from tidal subsidies. With increasing elevation, although the input of salt from tidal water gradually reduces, the evaporation of soil water can increase soil salinity. Therefore, salinity was the highest in the middle marsh. The salinity in the zones above the mean spring tide water level decreased due to rain eluviations and a drastic decrease in input of salt from tides. Thus, moving from the dike to the seaward area of Dongtan salt marsh, the high marsh closest to the dike has the lowest salinity of ca. 5‰, the middle marsh has the highest salinity of ca. 15‰, and the low marsh has a sub-high salinity of ca. 8‰ (Fig. 7). On the other hand, our previous study has shown that the inundation time in the low, middle and high tidal zones of Dongtan marsh are ca. 40–80 h/15 d, 40 h/15 d and 15 h/15 d, respectively (Tang et al. 2013). Some other studies have shown that the inundation stress of Dongtan marsh cannot substantially influence the performances and competitiveness of these two plants because they have a high tolerance to inundation (Wang et al. 2006*a, b*, Wang et al. 2010).

Before *S. alterniflora* colonized Dongtan marsh, the zonation of the plant communities along the elevation gradients was mudflat–sedge–*P. australis* (Fig. 1), which was related to the variation in salinity that is associated with the interaction

between soil elevation and tide (Pennings and Callaway 1992, Pennings et al. 2005). Because sedges, including *S. triqueter*, *S. mariqueter* and *C. scabrifolia*, have a higher tolerance to salt than *P. australis* (Wang et al. 2010), they occupied the low and middle marshes (Fig. 1) and *P. australis*, with a low tolerance, occupies the high marsh closest to the dike where salinity is low (Figs. 1 and 7). Due to *S. alterniflora* invasions, the effects of soil elevation and tide became less profound.

After *S. alterniflora* colonizes, the zonation of plant communities in Dongtan marsh can be interpreted as reflecting stages in a succession sequence associated with the salinity. Because the salinity of the mudflats in Dongtan marsh is favorable for *S. alterniflora* growth (Figs. 2 and 5) (Chen et al. 2004), this invader has rapidly spread into the mudflats (Fig. 1). In mudflats, the annual average horizontal expansion rate of *S. alterniflora* has been documented to be 74.3 ± 8.6 cm (Chen et al. 2004), explaining why the vegetation area and the distribution area of the invader in the marsh increased quickly (Figs. 1 and 8).

Moreover, because the majority of Dongtan marsh is characterized by high salinity and *S. alterniflora* becomes more aggressive over time under high salinity conditions (Figs. 3 and 5), the field transplant experiment showed that this invader displayed good performance and a high influence (NAI) on native *P. australis* in high salinity zones (Fig. 6). In addition, Chen et al. (2004) have reported that *S. alterniflora* has an obvious competitive advantage over other natives such as *S. mariqueter* in wide salinity conditions. Thus, *S. alterniflora* can rapidly displace the natives in high salinity conditions and lead the native community to proceed into the invaded stage (Figs. 1 and 7). Consequently, the vegetation pattern has changed over time (Fig. 1).

According to some theories, community succession is induced by decreasing resource abundance, altering resource availability or competition for limiting resources (Tilman 1985, Raevel et al. 2012). Here, *S. alterniflora* rapidly changed the community structure of *P. australis* in the high salinity zones (Figs. 1, 6 and 7). These findings indicate that the differences of tolerance to non-resource stress between new arrivals and natives can profoundly influence the trajectory of community development by influencing the outcomes of interspecific competition, which supports the integrated community theory suggesting that physiological tolerance and competitive ability of new arrivals are the important influences on community patterns (Christopher et al. 2004).

There are similar processes induced by *Spartina townsendii* and *Spartina angelica* in other Pacific coastal marshes, such as in eastern China (Li et al. 2011). For example, in coastal salt marshes in Dafeng, Qidong and Jiuduansha, China, the vegetation pattern was mudflat-sedge or mudflat-*P. australis* before *Spartina* plants colonized; at present, the vegetation pattern is mudflat–*Spartina* spp., mudflat–sedge–*Spartina* spp. and mudflat–*P. australis*–*Spartina* spp. (Li et al. 2009). In contrast, because the inhibitory effects of *P. australis* on *S. alterniflora* were increased by a decrease in salinity (Figs. 3 and 5), the vegetation pattern of many *Spartina* spp. marshes with low salinity in North America has been changed by *P. australis* and its salt-tolerant haplotype (Silliman and Bertness 2004, Vasquez et al. 2006) This implies that differences in responses of plants to non-resource stress can contribute to the maintenance of diversity in heterogeneous environments and explain zonation patterns in physiologically stressful ecosystems.

Implications for management

In this study, the invasive *S. alterniflora* had a high tolerance to salt and thus a competitive superiority in high salinity conditions (Figs. 2 and 3). Therefore, projects that increase soil salinity and subsequently exacerbate invasions should be practiced carefully. In recent years, the sea level has risen ca. 6.5 mm/year at the mouth of the Yangtze River, which is a rate much higher than the annual mean of 1.4 mm/year (Wang et al. 2006*b*). Additionally, the South-to-North Water Transfer and Three-Gorge engineering projects in China have caused decreases in the freshwater flow into the estuaries and an increase of seawater intrusion. Thus, the soil salinity of the estuaries has risen. In response to this increase, the spread of *Spartina* spp. may be accelerated in the marshes of eastern China in the future. In contrast, there are activities such as pasturing, hay harvesting and lumbering in some marshes along the Atlantic coast of the United

States that have reduced the soil salinity by increasing the freshwater influx into the marshes and thus have created favorable conditions for invasive *Phragmites* species (Silliman and Bertness 2004, Vasquez et al. 2006). Here, we recommend that practices that change the soil salinity and thereby create favorable conditions for invasive species should be stopped or, at a minimum, reduced.

Controlled *S. alterniflora* should not be allowed to recover. This species has many propagules, including seeds and underground stems (Wang et al. 2006a). Once colonized, *S. alterniflora* has a guerrilla strategy by which it can avoid stresses, including competition and infertility in microhabitats, and thus can expand rapidly (Vasquez et al. 2006). It is important to note that there is a high possibility of colonisation by *S. alterniflora*. In this study and other studies conducted in the same period, only 7 of the 650 (1.1%) planted *S. alterniflora* died. Hence, even if controlled projects are practiced, *S. alterniflora* may recover. The effective method is a periodic survey after control to remove the recovering invader.

Conclusions

This case study shows that if a new arrival has a wide tolerance range to major non-resource stress factors of physiologically stressful ecosystems, it can not only displace natives by interspecific competition in the high-stress zone and consequently initiate community succession but also rapidly spread into the zones without native plants. In contrast, native species with narrow ecological amplitude with respect to the non-resource stressors can occupy only the low stress zones where they have a high growth rate and subsequent competitive dominance over the new arrival. Consequently, the vegetation area significantly increased after colonisation by the new arrival, and the vegetation pattern changes. These results highlight that the rise of major non-resource stressor levels can substantially increase the invasibility of the native community. Thus, practices that change the non-resource stress level and create favorable conditions for invasions should be avoided.

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