The influence of nutrient addition on the invasion of *Spartina alterniflora* towards the non-tidal wetlands in the Chinese Yellow River delta

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Abstract
Spartina alterniflora is a notoriously invasive species in the low marsh of China, and meanwhile anthropogenic eutrophication is an urgent and prevalent environmental problem in the coastal wetlands. Soils in the coastal wetland are nutrient-poor, nutrient enrichment may enhance the spread of *S. alterniflora* towards the non-tidal marsh of the Yellow River Delta. We conducted a 2-year transplant and nutrient addition field experiment to investigate the influence of nutrient enrichment and interspecific interactions on the performance (growth, survival or inflorescence) of *S. alterniflora*. We found that nutrient addition and species competition did not have significant effects on the variation in performances of *S. alterniflora*. However, vegetative zones (*Suaeda salsa* and *Phragmites australis*), years (2013 and 2014) significantly contributed to the variation. The biomass per stem, survival and inflorescence were much higher in the *P. australis* than the *S. salsa* zone (biomass per stem: 1.86 ± 0.17 g vs. 0.82 ± 0.15 g; survivorship: 79% vs. 36%; inflorescence: 40% vs. 2%), and in 2013 than 2014 (biomass per stem: 1.72 ± 0.19 g vs. 0.91 ± 0.13 g; survivorship: 65% vs. 50%; inflorescence: 36% vs. 6.94%), which may be due to the combination of less flooding frequency and high salinity in the *S. salsa* zone and year 2014. These findings implied that eutrophication may not enhance the spread of *S. alterniflora* towards the non-tidal wetlands in the Chinese Yellow River Delta.

Keywords *Spartina alterniflora* · Nitrogen addition · Phosphorous addition · Yellow River Delta · Invasive species

Introduction

Coastal wetlands provide a diverse range of ecosystem services, for example, the ability to sequester excess nutrients from upland anthropogenic sources and alleviate the effects of eutrophication on marine ecosystems (Brin et al. 2010; Sousa et al. 2008). However, the increased nutrient inputs into coastal wetlands have led to the eutrophication of water and soil (Howarth et al. 2000). This eutrophication influences species interactions,

alters community composition, degrades species diversity (including plant and benthic animals) and deteriorates ecosystem structure and function in coastal wetlands (Crain 2007; Deegan et al. 2012; Fitch et al. 2009; Graham and Mendelssohn 2010, 2016; Hunter et al. 2008; McFarlin et al. 2008).

Nitrogen addition reversed the direction of species competition outcomes, i.e., the superior competitor in low-nutrient condition was out-competed under nitrogen enrichment (Levine et al. 1998a). Species requiring facilitation (the mitigation of environmental stress by neighbour species) were able to survive without facilitation under nitrogen enrichment treatments (Levine et al. 1998b). A study about the effect of nitrogen enrichment and salinity on species distributions in a New England marsh (USA) found that the salt tolerant species that were out-competed by neighbours in the low salinity environment were able to outcompete their neighbours under nitrogen enrichment (Emery et al. 2001). Therefore, the change of competitive outcomes with nutrient enrichment can reduce species richness at the local scale. Furthermore, some studies have reported the influences of nitrogen enrichment on community composition, not just species richness (Graham and Mendelssohn 2010; Traut 2005).

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Several studies have reported eutrophication-related enhancement of the spread of invasive species in coastal wetlands (Thiebaut 2005; Zhao et al. 2015). The enhancement of N inputs caused the acceleration of the spread of *S. alterniflora* in Willapa Bay and San Francisco Bay (USA) (Tyler et al. 2007). Nitrogen enrichment through human activities had facilitated the spread of the invasive species *Phragmites australis* from the high marsh (low salinity) to the low marsh (high salinity) of New England salt marshes, USA (Minchinton and Bertness 2003; Silliman and Bertness 2004). Because eutrophication may enhance the salinity tolerance of invasive species or alleviate competition for nutrients between invasive species and native species, and thus promote the spread of invasive species.

The Yellow River Delta is one of the three most famous and ecologically important river deltas (the Yellow River Delta, the Yangzi River Delta, and the Pearl River Delta) in China. Its coastal wetlands are located at the intersection of the Yellow River and the Bohai Gulf. Coastal wetlands of the Yellow River Delta include plenty of freshwater and marine biological resources, such as the luxuriant vegetation and a large number of fish, which make the delta an important winter habitat for water birds (Li et al. 2006). Thus, the health of coastal wetlands is very important to economic and social development, and the biodiversity conservation of this region.

S. alterniflora is a native species in the coastal wetlands of western Atlantic, and it was introduced into China in 1970s. It was the only salt marsh plant species identified in the first list of invasive species announced by the Ministry of Environmental Protection of the People's Republic of China in 2003. This species has spread from south to north China and occupies large area of China's coastal wetland. The intrusion of *S. alterniflora* has changed the physical and chemical properties of the soil, degraded habitats, reduced biodiversity, and destroyed aquaculture sites within the coastal wetlands in China (Wang et al. 2016; Zhao et al. 2014). *S. alterniflora* was introduced into the Yellow River Delta in 1990 to protect the shoreline from erosion. In 2007, the *Spartina* distribution area was only 614.59 ha (Yu et al. 2009), which increased to 1000 ha in 2012 (Ren et al. 2014), and 3692.07 ha in 2016 (Lu and Yang 2018).

The soil of the Yellow River Delta coastal wetlands was nutrient-poor, and the average of total N, NH_4-N, NO_3-N and total P concentration were 419.37 mg/kg, 3.274 mg/kg, 0.87 mg/kg and 500.86 mg/kg, respectively (Yu et al. 2010), and thus N and P are likely to limit the growth of plant in this region. On the other hand, the eutrophication process is ongoing in the region of Yellow River Delta, because the nutrient input in agriculture is very heavy, for example, the amount of N application is about 20 g/m^2/yr. These nutrients are discharged into wetlands along with farmland wastewater. However, few studies have investigated whether *S. alterniflora* could invade towards non-tidal wetlands in the Yellow River Delta under the background of nutrient enrichment. Therefore, the objective of this study is to find out whether the eutrophication will favor

the invasion of *S. alternifora* in the non-tidal zones of Yellow River Delta. Based on the previous studies, we predict that nutrient addition will promote the performances and spread of *S. alterniflora* in the non-tidal wetlands. To evaluate the prediction, *S. alterniflora* seedlings were transplanted from the low marsh into non-tidal wetlands, and field experiments were conducted to test influences of four manipulated variables: N addition, P addition, with/without neighbours and vegetative zones on the performances of *S. alterniflora*.

Methods

The field experiment was conducted in the Yellow River Delta National Reserve (37°40′N~38°10′N, 118°41′E~119°16′E), which is located in Shandong province, northeast China, and the location of the study site is shown in Fig. 1a. The climate of this region was warm-temperate, with an average annual temperature of 12.2 °C. The average annual precipitation was

(a) The location of the study site
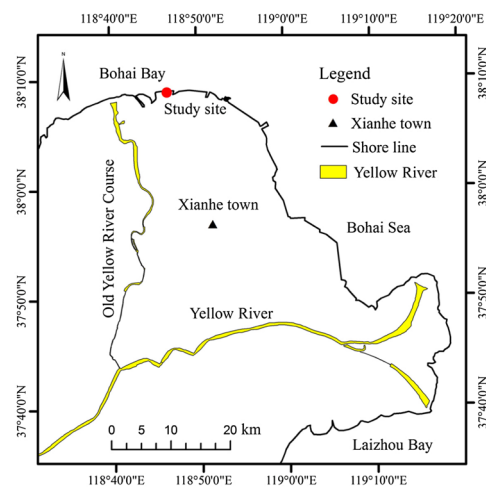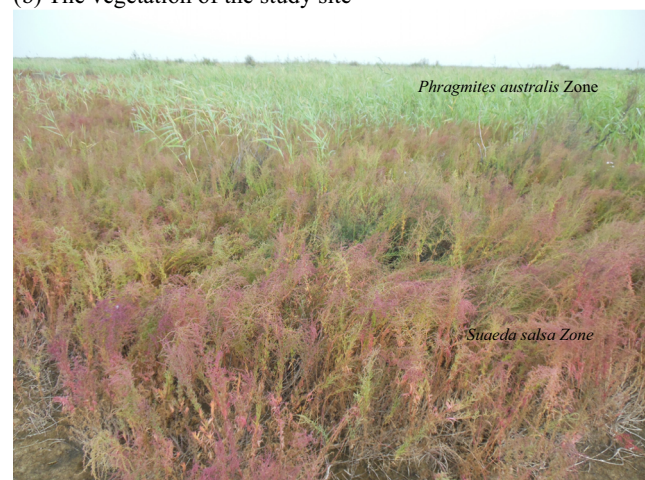

(b) The vegetation of the study site

Fig. 1 The location (**a**) and vegetative zones (**b**) of the study size (Photo credit: Liwen Zhang)

609.5 mm, and precipitation falling was mainly in the summer (Song et al. 2016). The invasive species *S. alterniflora* was found in the low marsh of the Yellow River Delta coastal wetlands. The dominant plant species, *Suaeda salsa* and *P. australis*, form distinct plant zones in the non-tidal wetland (Fig. 1b), and this area has not invaded by *S. alterniflora* currently. The elevation of the *P. australis* zone is higher than the *S. salsa* zone, and the *S. salsa* zone is near the sea, but not inundated by tides because the tides are inhibited by the road (Fig. 2a). This kind of non-tidal wetland was very common in the Yellow River delta because of road construction. The soil salinity within the *S. salsa* zone was higher than the

P. australis zone, and precipitation-induced water logging occurred yearly in the *P. australis* zone from late July to August, but not in the *S. salsa* zone.

Field Experiment

A split-plot experiment was employed in this study (Fig. 2a). Seedlings of *S. alterniflora* were transplanted, and N addition, P addition, and neighbour manipulations were performed in the *P. australis* and *S. salsa* zone (3 blocks were in each zone, Fig. 2b) for two years (2013 and 2014). The N and P addition treatments included three levels each: 0 g/m^2/yr. (i.e., the control,

(a) Field experiment design
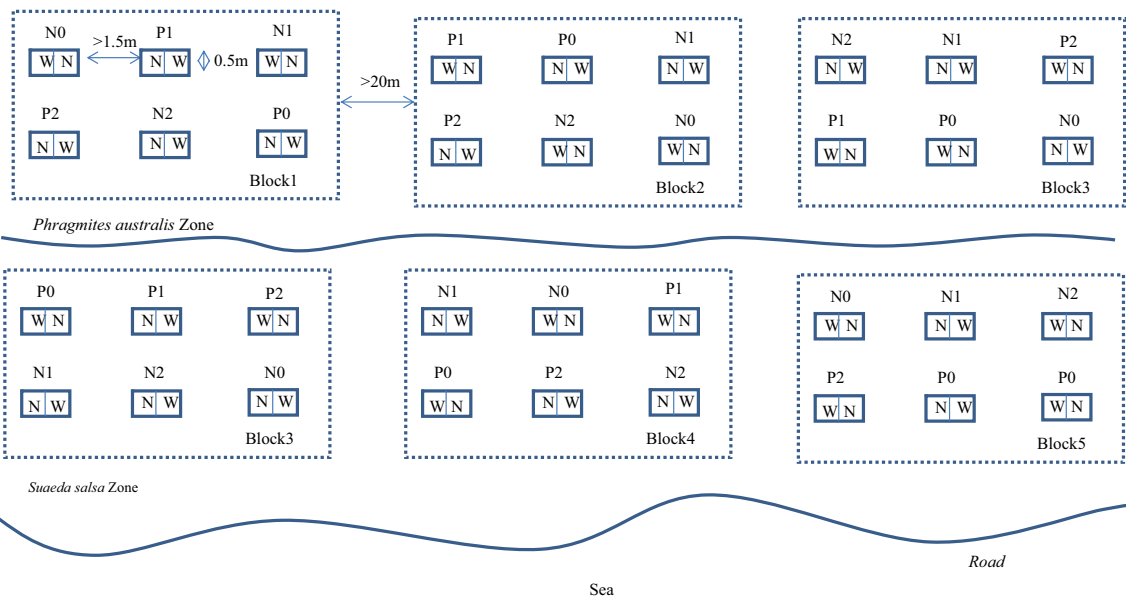
(b) Photographs of the field experiment

Fig. 2 Field experiment design (**a**) and photographs of the field experiment (**b**): *S. alterniflora* transplanted in *Phragmites australis* zone and *Suaeda salsa* zone. "N1", "N1", "N2" and "N3" mean nitrogen addition of 0, 5 g/m^2/yr. and 15 g/m^2/yr. in the plot respectively, and "P1", "P2" and "P3" denote phosphorous addition of 0, 5 g/m^2/yr. and 15 g/m^2/yr. in the plot respectively. "W" is with-neighbour treatment and "N" is without-neighbour treatment. Photo credit: Liwen Zhang

Table 1 The linear mixed effects model predicting influences on average biomass per stem of *Spartina alterflora*

Effects	Sum square	Mean square	Df	F-value	P value
Fixed effects					
Zone	12.536	12.536	1	7.991	0.047[*]
NP	10.769	2.154	5	1.373	0.240
NB	2.195	2.195	1	1.399	0.239
Zone:NP	7.833	1.567	5	0.999	0.422
Zone:NB	1.988	1.988	1	1.267	0.263
NP:NB	4.539	0.908	5	0.579	0.716
Zone:NP:NB	10.997	2.199	5	1.402	0.229
	Chi squre	Chi Df	P value		
Random effects					
Block	3.675	1	0.055		
Year	8.794	1	0.003[*]		

Plant vegetative zones (Zone), N and P enhancements (NP), the neighbour treatments (NB) and their interactions were set as fixed-effect factors, and Block and Year were set as random-effect factors. "Vegetative zones" includes the *Phragmites australis* and *Suaeda salsa* zone. "Year" includes 2013 and 2014. "Neighbour" includes treatments with and without neighbours

'[*]' indicates *p* value<0.05

N0, or P0), 5 g/m^2/yr. (N1 or P1) and 15 g/m^2/yr. (N2 or P2). The neighbour treatment included two levels: with/without neighbours. For without-neighbours treatment, the surrounding plants (native species: *P. australis* or *S. salsa*) were removed. In total, there were 72 0.5 m × 0.5 m plots (Fig. 2a).

In May 2013, seventy-two 0.16 m × 0.16 m × 0.16 m *S. alterniflora* seedling blocks were excavated and transplanted to the center of each experimental plots. After transplantation, seedling blocks were watered daily with fresh water for one week to avoid transplant shock (Crain et al. 2004) and ensured transplant survival for the experiment. Surrounding plants were removed every two weeks for the without-neighbours level of the neighbour treatment. N (urea, $H_2NCONH_2(CO(NH_2)_2)$, for urea was the main fertilizer used in the agriculture in this region) and P $(Ca(H_2PO_4)_2 \cdot H_2O)$ were hand-casted to the plots in June 2013. In June, the electric conductivity (EC), as well as the maximum height and number of living stems for each *S. alterniflora* within each plot were measured. In September 2013, the status (i.e., alive, inflorescent, or dead) were recorded and harvested the live stems of each *S. alterniflora* within each plot. The stems were oven-dried for 72 h at 70 °C to obtain the dry biomass. The dead *S. alterniflora* individuals were removed and replaced them with living individuals in May 2014, and then repeated the 2013 experiments.

Data analysis

According to the experiment design, linear mixed-effects models were used to analyze the effects of vegetative zones, N and P enhancements, the neighbour treatments, years and blocks and the interaction of blocks and nutrient addition on the growth (biomass per stem, change in number of plant stems, change in maximum plant height) of *S. alterniflora*, and the best-fit model was selected. Vegetative zones, N and P enhancements, the neighbour treatments and their interactions were set as fixed-effects factors. Years, blocks and the interaction of blocks and nutrient addition were set as random-effects factors. The post-hoc Tukey HSD multiple comparisons method was employed to compare means of significant treatment levels. Generalized linear mixed-effects models were employed to analyze the effects of vegetative zones, N

Table 2 The linear mixed effects model predicting influences on change in number of plant stems of *Spartina alterflora*

Effects	Sum square	Mean square	Df	F-value	P value
Fixed effects					
Zone	109.428	109.428	1	3.943	0.116
NP	226.692	45.338	5	1.634	0.158
NB	20.984	20.984	1	0.756	0.387
Zone:NP	156.033	31.207	5	1.125	0.353
Zone:NB	12.206	12.206	1	0.440	0.509
NP:NB	159.176	31.835	5	1.147	0.341
Zone:NP:NB	85.785	17.157	5	0.618	0.686
	Chi square	Chi Df	P value		
Random effects					
Block	19.677	1	<0.001[***]		
Year	23.537	1	<0.001[***]		

Plant vegetative zones (Zone), N and P enhancements (NP), the neighbour treatments (NB) and their interactions were set as fixed-effect factors, and Block and Year were set as random-effect factors. "Vegetative zones" includes the *Phragmites australis* and *Suaeda salsa* zone. "Year" includes 2013 and 2014. "Neighbour" includes treatments with and without neighbours

'[***]' denotes p value<0.001

Table 3 The linear mixed effects model predicting influences on change in maximum plant height of *Spartina alterflora*

Effects	Sum square	Mean square	Df	F-value	P value
Fixed effects					
Zone	3551.3	3551.3	1	5.162	0.085
NP	1372.7	274.5	5	0.399	0.848
NB	0.5	0.5	1	0.001	0.978
Zone:NP	3082.4	616.5	5	0.896	0.487
Zone:NB	1266.9	1266.9	1	1.841	0.178
NP:NB	4825.4	965.1	5	1.403	0.230
Zone:NP:NB	1610.6	322.1	5	0.468	0.799
	Chi square	Chi Df	P value		
Random effects					
Block	39.797	1	<0.001***		
Year	66.037	1	<0.001***		

Plant vegetative zones (Zone), N and P enhancements (NP), the neighbour treatments (NB) and their interactions were set as fixed-effect factors, and Block and Year were set as random-effect factors. "Vegetative zones" includes the *Phragmites australis* and *Suaeda salsa* zone. "Year" includes 2013 and 2014. "Neighbour" includes treatments with and without neighbours

'***' denotes p value<0.001

and P enhancement, the neighbour treatments, years and blocks on the survival and inflorescence of *S. alterniflora*, because of the binomial distribution of the dependent variables (survival and inflorescence). Multiple models were compared and the best-fit model was selected according to AIC values. One-way ANOVA was used to analyze the difference of electric conductivity between vegetative zones or years. All the above analyses were conducted in R i386 3.5.2, and the package "lmerTest" was used to perform the linear mixed-effects models (R Development Core Team 2017).

Results

No significant effects of N and P enhancement were found on the average biomass per stem (F-value = 1.373, *P* value = 0.240, Table 1), change in number of plant stems (F-value = 1.634, *P* value = 0.158, Table 2), change in maximum plant height (F-value = 0.399, *P* value = 0.848, Table 3), survival (Chi-square = 15.180, P value = 0.126, Table 4), and

inflorescences (Chi-square = 6.907, *P* value = 0.734, Table 5) of *S. alterniflora*. Neighbour treatments also had no significant effect on the average biomass per stem (F-value = 1.399, P value = 0.239, Table 1), change in number of plant stems (F-value = 0.756, *P* value = 0.387, Table 2), change in maximum plant height (F-value = 0.001, *P* value = 0.978, Table 3), survival (Chi-square = 10.325, P value = 0.587, Table 4), and inflorescences (Chi-square = 6.110, *P* value = 0.910, Table 5) of *S. alterniflora* (Appendices Fig. S1). Additionally, the interaction of nutrient addition and neighbour treatments also had no significant effect on the performances of *S. alterniflora*, thus nutrient addition may not change the species interactions between *S. alterniflora* and native species.

However, the variation in biomass per stem was found to be explained best by a fixed-effect factor: vegetative zones and the random-effect factor (i.e. year), with a higher biomass per stem found in the *P. australis* zone than the *S. salsa* zone (1.86 ± 0.17 g vs. 0.82 ± 0.15 g, *P* value<0.05, Table 1 and Fig. 3a) and with a higher biomass per stem found in 2013 than 2014 (1.72 ± 0.19 g

Table 4 Comparison and selection of the general linear mixed effects models predicting influences on survival of *Spartina alterflora*

Models	AIC	Chi-square	Chi-df	P value
Model1:Survival~ (1 | Block) + (1 | Year)	186.11			
Model2:Survival ~ Zone + (1 | Block) + (1 | Year)	175.12	12.992	1	<0.001***
Model3:Survival ~ Zone * NP + (1 | Block) + (1 | Year)	179.94	15.180	10	0.126
Model4:Survival ~ Zone * NP * NB + (1 | Block) + (1 | Year)	193.61	10.325	12	0.587

Plant vegetative zones (Zone), N and P enhancements (NP), the neighbour treatments (NB) and their interactions were set as fixed-effect factors, and Block and Year were set as random-effect factors. "Vegetative zones" includes the *Phragmites australis* and *Suaeda salsa* zone. "Year" includes 2013 and 2014. "Neighbour" includes treatments with and without neighbours

'***' denotes p value<0.001

Table 5 Comparison and selection of the general linear mixed effects models predicting influences on the inflorescences of *Spartina alterflora*

Models	AIC	Chi-square	Chi-df	P value
Model1:Inflorescences ~ (1 | Block) + (1 | Year)	95.971			
Model2:Inflorescences ~ Zone + (1 | Block) + (1 | Year)	92.037	5.934	1	0.015*
Model3:Inflorescences ~ Zone * NP + (1 | Block) + (1 | Year)	105.130	6.907	10	0.734
Model4:Inflorescences ~ Zone * NP * NB + (1 | Block) + (1 | Year)	123.020	6.110	12	0.910

Plant vegetative zones (Zone), N and P enhancements (NP), the neighbour treatments (NB) and their interactions were set as fixed-effect factors, and Block and Year were set as random-effect factors."Vegetative zones" includes the *Phragmites australis* and *Suaeda salsa* zone. "Year" includes 2013 and 2014. "Neighbour" includes treatments with and without neighbours
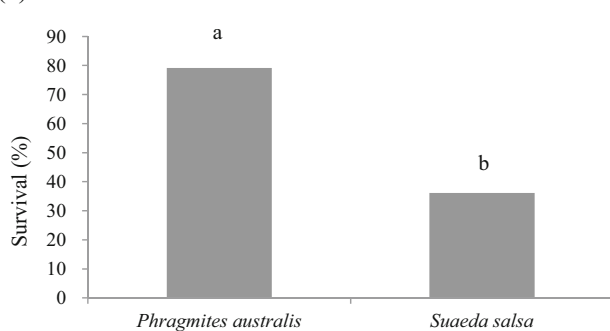
'*' denotes p value<0.05

vs. 0.91 ± 0.13 g, *P* value<0.05, Table 1 and Fig. 4a). Variation of change in individuals of *S. alterniflora* and change in maximum plant height from June to September

(a) Biomass per stem
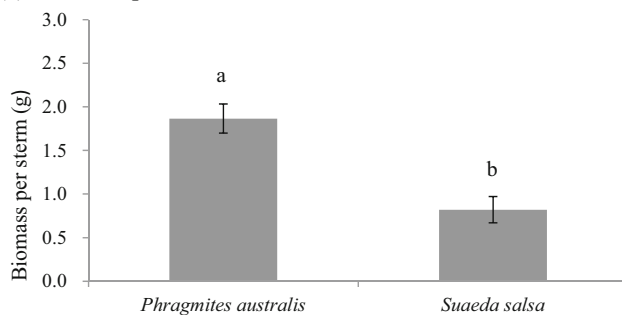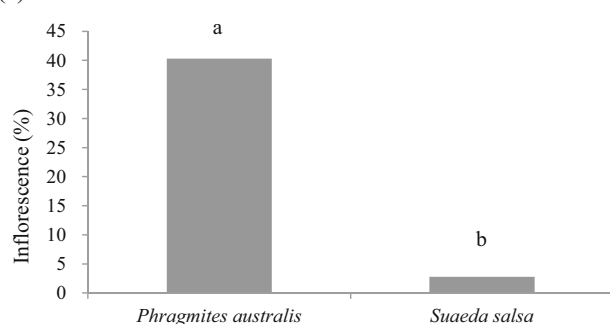

(b) Survival

(c) Inflorescences

Fig. 3 The variation in the performances (biomass per stem, survival and inflorescences) of *S. alterniflora* from different vegetative zones. The error bar is ±SE and *n* = 72

were only significantly influenced by random-effect factors: block and year (with less dead individuals found in 2013 than 2014, -1.17 ± 0.70 stems vs. -7.49 ± 0.91 stems, P value<0.05; with a higher maximum plant height changed found in 2013 than 2014, 39.63 ± 6.59 cm vs. -16.20 ± 3.08 cm, P value<0.05; Tables 2, 3 and Fig. 4b, c).

Vegetative zones also had a significant effect on survival of *S. alterniflora*, with a higher level of survival found in the *P. australis* zone than the *S. salsa* zone(survivorship 79% vs. 36%, P value <0.05; Table 4 and Fig. 3b), also with a higher level of survival found in 2013 than 2014 (survivorship 65% vs. 50%, P value <0.05; Table 4 and Fig. 4d). The inflorescence status of *S. alterniflora* was significantly affected by vegetative zones (with more inflorescence present in the *P. australis* zone than the *S. salsa* zone, 40% vs. 2% plots, P value <0.05; Table 5 and Fig. 3c), and also with a higher level of inflorescence found in 2013 than 2014 (inflorescence: 36% vs. 6.94%, P value <0.05; Table 5 and Fig. 4e).

Moreover, the soil salinity was higher in the *S. salsa* than the *P. australis* zone (10.92 ± 0.32 mS/cm vs. 6.90 ± 0.17 mS/cm, F-value = 9.12, P value<0.001; Appendices Fig. S2), and it was also higher in 2014 than in 2013 (9.59 ± 0.36 mS/cm vs. 8.19 ± 0.32 mS/cm, F-value = 124.95, P value<0.01; Appendices Fig. S2).

Discussion

It was surprising that nutrients enhancement including N and P had no effect on the survival, growth and inflorescence of *S. alterniflora*. N and P addition also did not influence the species interactions in our study. However, evidences in N enhancement-related spreading of invasive plant species were accumulating from plant communities of a variety of ecosystems (Davis et al. 2000; Fenn et al. 2003). Nitrogen addition had been shown to increase the aboveground biomass of *S. alterniflora* in its native habitat within the United States (Buresh et al. 1980; Darby and Turner 2008; Tyler et al. 2003) and within non-native habitats, such as in the Willapa
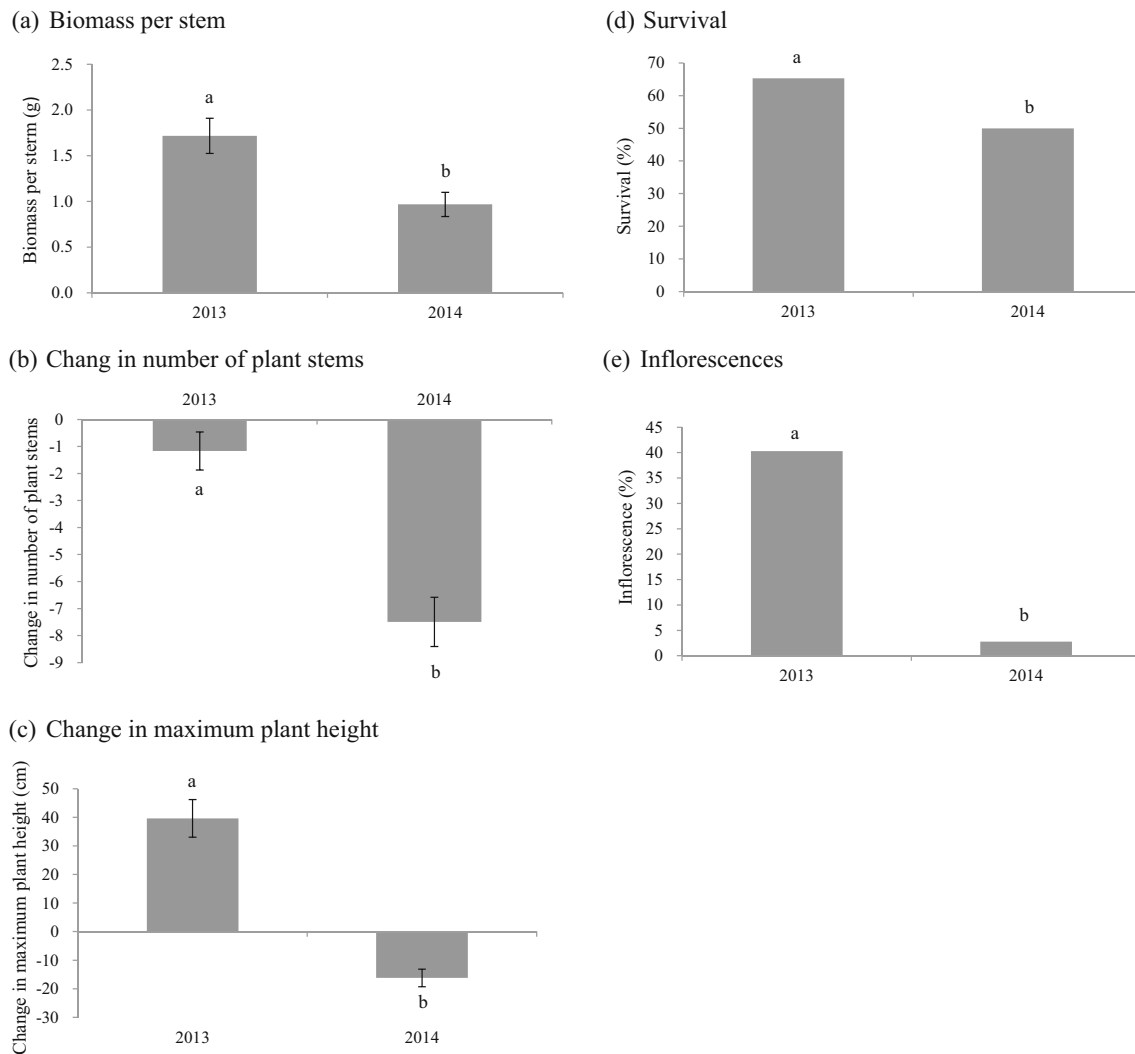
(a) Biomass per stem

(d) Survival

(b) Chang in number of plant stems

(e) Inflorescences

(c) Change in maximum plant height

Fig. 4 The variation in the performances (biomass per stem, survival and inflorescences) of *S. alterniflora* between 2013 and 2014. The error bar is ±SE and n = 72

Bay and San Francisco Bay in the United States (Tyler et al. 2007) and in China (Zhao et al. 2015). Nitrogen enrichment also had the potential to improve competitive ability of invasive species, allowing them to outcompete native species (Allen et al. 2018; Chambers et al. 2007; James et al. 2008; Pennings et al. 2002; Tyler et al. 2007). The disparity may be due to the environmental conditions of the study sites. The experiments in those studies were conducted in the low marsh or mud flat, and the environmental factors were very different between the low marsh and the non-tidal wetland. In the low marsh, the tide flooded every day even twice a day, however, in the non-tidal wetland in the Yellow River Delta, the flooding frequencies was much lower. Direct evidence from a manipulative experiment showed that elevated inundation flooding frequencies can promote the spread of *S. alterniflora* (Xue et al. 2018). Additionally, a study reported that salinity induced by less flooding frequency in high marsh, but not competition was suggested to be the most important

factor suppressing the spread of this smooth cordgrass, although *S. alterniflora* can tolerant high salinity (He et al. 2012). Nutrient enrichment may increase the salinity and drought tolerance of plants by increasing proline levels within plant cells, mediating osmotic equilibrium and increasing water use efficiency (Levine et al. 1998a, b), but this mechanism did not work in our study. Therefore, the environmental condition of the low flooding frequency may overwhelm the effect of nutrient and inhibit the performances of *S. alterniflora* in the non-tidal wetlands.

The presence of neighbours also did not significantly influence the survival and growth of *S. alterniflora* in our study. The limited effect of neighbours may have been due to attenuation of drought or salinity effects on *S. alterniflora* growth in the presence of neighbours. These results were, to some extent, consistent with previous studies, which have argued that nitrogen enrichment can reverse the competitive dominance hierarchy of species (Emery et al. 2001; Levine et al. 1998a, b).

Nevertheless, the performance outcomes of species interactions between invasive and native species were still competitions but not facilitations under the condition of nitrogen addition, however, the intensity of competition reduced.

The results showed that the only fixed-effect factor significantly influenced the survival and growth of *S. alterniflora* in the non-tidal wetland was vegetative zone. The survival, growth and reproduction performances of *S. alterniflora* in the *P. australis* zone were better than the *S. salsa* zone. Especially, most of the *S. alterniflora* could not survive in the *S. salsa* zone in 2014. Soil moisture and salinity may be the reason. The moisture in the soil of the *S. salsa* zone was much lower than the low marsh which was flooded by the tide daily, and water-logging occurred from late July to August in the *P. australis* zone which made the water level in the *P. australis* zone higher than that in the *S. salsa* zone. Salinity in the *S. salsa* zone was higher than in the *P. australis* zone. *S. alterniflora* is sensitive to water content, in *S. alterniflora* native habitat in the the USA, prolonged drought and elevated salinity also could lead to the dieback of *S. alterniflora* (Marsh et al. 2016). Salinity and drought likely restricted the survival and growth of *S. alterniflora* in the *S. salsa* zone.

The random-effect factor: year was also an important factor influencing the survivor and growth of *S. alterniflora* in the non-tidal wetland. Plant performance measurements in 2013 were suggestive of superior overall performance than in 2014. The follow reasons may cause this result. Firstly, the strong effect of year may also be due to variation in salinity, and salinity in 2014 was higher than in 2013 within the same vegetative zone (appendixes Fig. S2 and S3). Secondly, seasonal differences may matter for *S. alterniflora*. The growth in *S. alterniflora* was strongly seasonal, even in places without strong seasonal temperature differences (Hill and Roberts 2017). This may affect their seasonal leaf tissue concentrations and thus their nutrient limitation status and the response to nutrient addition.

Conclusions

After two-year experiment, we found N and P enrichments were unlikely to promote the spread of *S. alterniflora* toward the Yellow River Delta non-tidal wetland. This result may attribute to the combination of the less flooding frequency and high salinity in the non-tidal wetland. Therefore, the control and management of *S. alterniflora* invasion should focus on the spread of *S. alterniflora* in low marsh of tidal wetlands.

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