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PRIMARY RESEARCH PAPER

Phenotypic plasticity of *Spartina alterniflora* and *Phragmites australis* in response to nitrogen addition and intraspecific competition

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Abstract Phenotypic plasticity of the two salt marsh grasses *Spartina alterniflora* and *Phragmites australis* in salt marshes is crucial to their invasive ability, but the importance of phenotypic plasticity, nitrogen levels, and intraspecific competition to the success of the two species is unclear at present. *Spartina alterniflora* Loisel. is an extensively invasive species that has increased dramatically in distribution and abundance on the Chinese and European coasts, and has had considerable ecological impacts in the regions where it has established. Meanwhile, *Phragmites australis* Cav., a native salt marsh species on the east coast of China, has replaced the native *S. alterniflora* in many marshes along the Atlantic Coast of the US. This study determined the effects of nitrogen availability and culm density on the morphology, growth, and biomass allocation traits of *Spartina alterniflora* and *Phragmites australis*. A large number of morphological, growth, and biomass parameters were measured, and various derived values (culm: root ratio, specific leaf area, etc.) were calculated, along with an index of phenotypic plasticity. Nitrogen addition significantly affected growth performance and biomass allocation traits of *Spartina alterniflora*, and culm density significantly affected morphological characteristics in a negative way, especially for *Spartina alterniflora*. However, there were no significant interactions between nitrogen levels and culm density on the morphological parameters, growth performances parameters, and biomass allocation parameters of the two species. *Spartina alterniflora* appears to respond more strongly to nitrogen than to culm density and this pattern of phenotypic plasticity appears to offer an expedition for successful invasion and displacement of *Phramites australias* in China. The implication of this study is that, in response to the environmental changes that are increasing nitrogen levels, the range of *Spartina alterniflora* is expected to continue to expand on the east coast of China.

Keywords Intraspecific relationships · Nitrogen addition · Phenotypic plasticity · *Phragmites australis* · Plant morphology · *Spartina alterniflora*

Introduction

Environmental conditions occupied by plants are highly variable, both spatially and temporally. As a consequence of such environmental heterogeneity, a remarkable phenotypic variation can be observed

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among individuals of the same genotype developing in different habitats (Avramov et al., 2007). Phenotypic plasticity is the ability of a genotype to produce distinct phenotypes when exposed to different environments during its ontogeny and it has been regarded as an important ecological agent in expanding the habitat range of a species (Zhu et al., 2007). It is essential for the survival of most plant species that they show phenotypic plasticity via variations of morphological and ecophysiological traits in heterogeneous and variable environments, especially for invasive plants.

Rapid changes in morphology and growth characteristics often occur in plants in response to variation in resource availability (Maherali & Delucia, 2001; Wang & Feng, 2004). Because there is an intimate relationship between these changes and resource acquisition, the changes often facilitate the tolerance of stress and invasiveness (Tyler et al., 2007). Some researchers suggested that one of the most significant ways in which plants respond to changing environments is to change root morphology (Schlichting, 1986; Ryser & Lambers, 1995; Fransen et al., 1998), leaf shape and area (Perez et al., 1994), and biomass allocation pattern (Idestam-Almquist & Kautsky, 1995).

Coastal ecosystems are highly variable in various ways because they are affected by the processes of marine, terrestrial, and sometimes riverine ecosystems (Wang et al., 2006) and numerous studies have found that environmental factors play important roles in structuring and functioning of coastal salt marshes (Hemminga & Buth, 1991; Grace & Pugesek, 1997). Nitrogen is the primary factor limiting plant production in many coastal ecosystems. However, as a result of human development, eutrophication of coastal zones caused by nutrient input from watersheds has been one of the most pressing environmental concerns worldwide (Cloern, 2001). One consequence of excessive nutrient loading is the facilitation of species invasions (Dukes & Mooney, 1999). The way in which plant species adapt to changed nutrient conditions may be determined by analyzing their phenotypic response to different nitrogen levels (Elberse & Damme, 2003). In addition, alterations in culm density may crucially affect phenotypic plasticity (Chen, 2000; Cipollini & Bergelson, 2001). In plant populations, sizes of individuals are generally far from uniform. The inequality in plant size, or size hierarchy, has been well documented in even-aged monocultures (Nagashima & Terashima, 1995). Most of the skewed distributions reported are considered to be consequences of competition, because skewness of distribution increases with increase in initial plant density.

Another important factor in structuring salt marshes is plant invasion. Phenotypic plasticity is often cited as an important mechanism of plant invasion (Funk, 2008). However, few studies have evaluated the plasticity of a diverse set of traits among invasive and native species, particularly in different nitrogen resource and culm density habitats, and none have examined the functional significance of these traits.

Spartina alterniflora and *Phragmites australis* (hereafter referred to as *Spartina* and *Phragmites*) are rhizomatous perennial graminoid grasses that grow in the coastal marshes in dense monocultures. As invasive species, both *Spartina* and *Phragmites* present serious threats to the ecosystems they invade. *Spartina*, native to the East and Gulf coasts of North America, has become a highly invasive weed throughout coastal marshes of the Pacific (Poulin et al., 2002; Vasquez et al., 2006; Wang et al., 2006). In China, *Spartina* was first introduced in 1979 to stabilize shorelines, and now flourishes in coastal intertidal zones from Guangxi northward to Tianjin. *Phragmites*, a dominant salt marsh species in the east coast of China, also has replaced the native species, such as *Spartina*, in many marshes along the Atlantic coast of the US (Marks et al., 1994; Windham & Lathrop, 1999). The dramatic invasions of both *Spartina* and *Phragmites* have caused many ecological and economic problems in China and North America. However, it is interesting that in North America *Phragmites* is moving from high to low marshes to invade *Spartia*-dominated ecosystems, while in China *Spartina* is threatening high *Phragmites* salt marshes. 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 (Wang et al., 2006). Recently, it has been reported that increasing nutrient supply in coastal zones has positively promoted the invasion of both exotic species (Tyler et al., 2007), and analyzing the phenotypic plasticity of the two species in response to the increased nitrogen supply and culm density will enable us to examine the validity of this explanation for the range expansions of both species.

Here, the alien *Spartina* and native *Phramites* were studied by adjusting nitrogen level and culm density under greenhouse condition, while maintaining monocultures of the two species. The primary purpose was to evaluate statistically the impact of nitrogen level and culm density on the morphological characteristics, growth performances, and biomass allocation traits of two species and thus to identify optimal environmental conditions for plant growth. In particular, we wished to determine how phenotypic plasticity of the two species responded to different nitrogen level and culm density, and thus to explain and predict their invasive abilities in different coastal ecosystems.

Materials and methods

Plant and substrate materials

The individuals of two species and saline soil were collected at the end of March 2006 from the same area of Yancheng Natural Reserve (32°34′–34°28′N, 119°48′–121°150′E), Jiangsu Province, China. Table 1 shows the environmental background values of the two species on the coast of Jiangsu. For each species, individuals consisting of a single tiller with attached root material were separated, moved to the greenhouse and planted into plastic tanks (75 cm × 50 cm × 40 cm, length × width × height), which were filled with saline soil up to a depth of 20 cm. The plants were grown in the greenhouse for 4 weeks and watered daily to provide a large pool of healthy individuals for use in the following experiments.

Experimental design

Experiments were set up in the greenhouse of Nanjing University, China (32°10′37″N, 118°41′57″E) on 24 April 2006. They aimed to test the effects of nitrogen level (low, medium or high) and intra-specific competition on the morphology, growth and biomass allocation of *Spartina* and *Phragmites* growing at different densities. Thirty-six units of *Spartina* (34.4 ± 1.1 cm tall) and 36 *Phragmites* (44.6 ± 2.3 cm tall) were planted into 10 l plastic pots (28 cm in diameter, 25 cm in height) with 20 cm deep saline sand (12.5 kg dry weight) using 1, 2, and 3 stems per pot. This represented 4 repetitions × 2 species × 3 nitrogen levels × 3 densities. After planting, carbamide solution (with 46% available nitrogen) was added once every 2 weeks to the tanks from the top of the saline soil to maintain the soil nitrogen contents close to 0 mg/kg (N0 treatment), 60 mg/kg (N1) and 120 mg/kg (N2), to represent low, medium and high nitrogen treatments, respectively. The N loading expressed as 60 and 120 mg/kg of soil dry weight and calculated as available nitrogen (nitrogen weight/saline sand dry weight per tank). Each treatment has four replicate in this study. During the experiment, the salinity of substrates was maintained at 8–10‰ (to match field conditions) and all tanks were immersed to a depth of 3–5 cm above the sand. Salinity and water levels were monitored weekly, and adjusted to initial conditions by adding freshwater and crude salt.

Parameters measured

After treated with nitrogen for 15 weeks, all the plants were harvested and morphological and biomass allocation parameters were measured.

Parameters measured to reflect morphological characteristics were max-height of culm (MHC), stem diameter (SD), mean height of total culms (MHTC), total leaf areas (TLA), and specific leaf area (SLA, total leaf areas/total leaf weight). Those reflecting biomass allocation were above-biomass ratio (ABR, the above-ground biomass/the total biomass), below-biomass ratio (BBR, the belowground biomass/the total biomass), culm biomass ratio (CBR, culm biomass/the total biomass), leaf biomass ratio (LMR, leaf biomass/the total biomass), root biomass ratio

Table 1 The environment background values of *S.alterniflora* and *P. australis* on the coast of Jiangsu Province

Microhabitats	Elevation (m)	Soil available *N* concentration (mg/kg)	Soil organic carbon concentration (mg/g)	Salinity substrate (%)	Culm height (m)	Culm diameter (cm)
S. alterniflora	2.2–3.4	21–89	2.4–10	0.8–1.0	1.2–2.3	0.6–1.5
P. australis	3.1–4.2	32–78	3.8–12.7	0.8–1.0	1.5–2.5	0.7–1.1

(RMR, root biomass/the total biomass), rhizome biomass ratio (RhMR, rhizome biomass/the total biomass), root biomass/crown mass (R/C) and leaf area to root mass ratio (LARMR, total leaf areas/root biomass). Parameters measuring growth were RGR, NAR and LARm. For biomass allocation parameters, the plants from each replicate were divided into leaves and stems, and rhizomes and roots, which were, respectively, dried to constant weight at 80°C for 72 h and weighed (±0.1 mg). The weights of culm and leaves were combined to give the total aboveground biomass and those of roots and rhizomes to give the total belowground biomass of each plant.

The relative growth rate (RGR), net assimilation rate (NAR) and mean leaf area ratio (LARm) were quantified using the methods of Poorter (1999):

$$\mathrm{RGR} = \frac{\ln W_2 - \ln \overline{W_1}}{\Delta t}$$

$$\mathrm{NAR} = \frac{W_2 - \overline{W_1}}{L_2 - \overline{L_1}} \times \frac{\ln L_2 - \ln \overline{L_1}}{\Delta t}$$

$$\mathrm{LARm} = \frac{\ln W_2 - \ln \overline{W_1}}{W_2 - W_1} \times \frac{L_2 - \overline{L_1}}{\ln L_2 - \ln \overline{L_1}}$$

where $\overline{W_1}$, $\overline{L_1}$ are measures of the dry weight of initial total biomass (g) and total leaf area (cm^2) ($n = 10$) of a plant, $\overline{W_2}$, $L_2$are measures of the dry weight of harvest total biomass (g) and total leaf area (cm^2), and Δt is the time with nitrogen treatment. Phenotypic plasticity index (PPI) was calculated according to the formulas given by Valladares et al. (2000). $\mathrm{PPI} = 1 - x/X$ where x and X are the minimum and the maximum mean values among the three density/N level treatments.

Data analysis

Two-way ANOVA was used to test the statistical difference of the effects on nitrogen treatments, culm density and their interactions on parameter variation. Tukey HSD test were conducted to examine the differences among the treatments. One-way ANOVA was used to test the statistical difference of the related parameters of the two species under the same nitrogen treatment/culm density. If necessary, biomass data were transformed (ln). Morphological data were transformed using either square root (max-height of culm, mean height of culms) or $\log_{10}$ (above-biomass ratio, below-biomass ratio and specific leaf area). All statistical analyses were conducted with SPSS 13.0 for Windows (SPSS Inc., USA). The figures are made with SigmaPlot 9.0.

Results

Effects of nitrogen levels and intraspecific competition on two species

Effects of nitrogen addition on two species

Nitrogen levels had a highly significant impact ($P < 0.0001$) on the morphological characteristic mean height of total culms of *Spartina*, with the individuals at medium nitrogen level producing the highest mean height of total culms (Table 2; Fig. 1a–d), while no significant effects of nitrogen on culm height were observed in *Phragmites* (Table 2; Fig. 2a–d). Nitrogen also showed highly significant effects ($P < 0.001$) on two growth parameters, relative growth rate and mean leaf area of *Spartina* but only on mean leaf area ratio of *Phragmites* (Table 2; Figs. 3a–c, 4a–c). In contrast, nitrogen had a similar, albeit slightly inconsistent, effects on biomass accumulation in both species with significant ($P < 0.05$) effects in one or both species for all parameters other than culm biomass ratio (Table 2; Figs. 5a–f, 6a–f). Under the same nitrogen level, *Spartina* generally had greater morphological parameter values and higher growth rate than *Phragmites* (Figs. 1, 2, 3, 4).

Effects of culm density on two species

High culm density had significant inhibitory effect on all morphological traits of *Spartina* (Table 2; Fig. 1e–h) but affected only specific leaf area ($P < 0.05$) of *Phragmites* (Table 2; Fig. 2e–h). Increased culm density significantly ($P < 0.001$) reduced the relative growth rate of *Spartina* (Table 2; Fig. 3d–f) but no significant effects of density on *Phragmites* growth were found (Table 2; Fig. 4d–f). Significant effects of density ($P > 0.05$) on biomass allocation were observed only in the rhizome biomass ratio of *Phragmites* despite six biomass accumulation parameters being measured for each species (Table 2; Figs. 5g–l, 6g–l). Under the same culm

Table 2 Results of Two-way ANOVA analysis of morphological, growth, and biomass allocation parameters for *S. alterniflora* and *P. australis*

Parameters	Variation	*S. alterniflora*		*P. australis*	
	Source	*F*	*P*	*F*	*P*
Morphological traits					
Max-height of culm, MHC	N	2.784	0.073	0.659	0.523
	D	3.989	0.026*	2.132	0.131
	N × D	0.563	0.691	0.335	0.853
Mean height of total culms, MHTC	N	14.006	<0.001**	2.219	0.138
	D	6.911	0.003**	2.765	0.090
	N × D	0.525	0.718	0.569	0.687
Stem diameter, SD	N	1.929	0.157	1.138	0.330
	D	9.835	0.001**	0.612	0.547
	N × D	0.721	0.582	0.144	0.965
Specific leaf area, SLA	N	0.095	0.910	0.101	0.904
	D	4.896	0.02*	3.406	0.043*
	N × D	2.201	0.110	1.595	0.194
Growth traits					
Relative growth rate, RGR	N	10.566	0.001**	1.627	0.209
	D	9.886	0.001**	2.415	0.118
	N × D	0.530	0.714	0.411	0.799
Net assimilation rate, NAR	N	2.269	0.132	0.913	0.409
	D	2.376	0.105	1.606	0.213
	N × D	0.189	0.943	0.189	0.943
Mean leaf area ratio, LARm	N	15.737	<0.001**	7.777	0.001**
	D	0.601	0.553	1.580	0.218
	N × D	0.188	0.944	0.069	0.991
Biomass allocation traits					
Culm biomass ratio, CBR	N	3.128	0.068	1.708	0.194
	D	1.748	0.187	0.498	0.611
	N × D	0.168	0.954	1.672	0.175
Leaf biomass ratio, LBR	N	23.708	<0.001**	6.342	0.004**
	D	0.519	0.599	0.909	0.411
	N × D	0.611	0.658	0.535	0.711
Root biomass ratio, RBR	N	2.867	0.083	5.257	0.009**
	D	2.768	0.075	0.032	0.969
	N × D	0.880	0.485	0.859	0.497
Rhizome biomass ratio, RhBR	N	5.328	0.009**	1.604	0.214
	D	1.142	0.329	4.988	0.019*
	N × D	1.710	0.167	0.445	0.775
Root mass/crown mass, R/C	N	2.918	0.066	4.229	0.022*
	D	2.614	0.086	0.015	0.985
	N × D	0.389	0.815	0.730	0.577

Table 2 continued

Parameters	Variation Source	*S. alterniflora* *F*	*S. alterniflora* *P*	*P. australis* *F*	*P. australis* *P*
Leaf area to root mass ratio, LARMR	N	12.212	<0.001**	8.139	0.001**
	D	1.039	0.363	0.394	0.677
	N × D	0.121	0.974	1.052	0.393

For each biomass variable, the *F* value (*F*) and probability (*P*) are shown with significant experimental effects indicated by *asterisks* (* $P < 0.05$; ** $P < 0.001$)

D Density, *N* Nitrogen, *D* × *N* Density × nitrogen

density conditions, *Spartina* generally had greater morphological parameter values and higher growth rate than *Phragmites* (Figs. 1, 2, 3, 4).

Effects of interactions of nitrogen addition and culm density on two species

Two-way ANOVA analysis showed that there were no significant interactions between nitrogen levels and culm density on the morphological parameters, growth performances parameters, and biomass allocation parameters of either species (Table 2).

Phenotypic plasticity of morphologic character, growth performance and biomass allocation traits in response to different nitrogen level and plant density

Phenotypic plasticity of two species in response to nitrogen levels under different culm density

Mean phenotypic plasticity indices (MPPI) of morphological and biomass allocation parameters of the two species in response to nitrogen level generally decreased gradually with the increase of the culm density except for the MPPI of biomass allocation

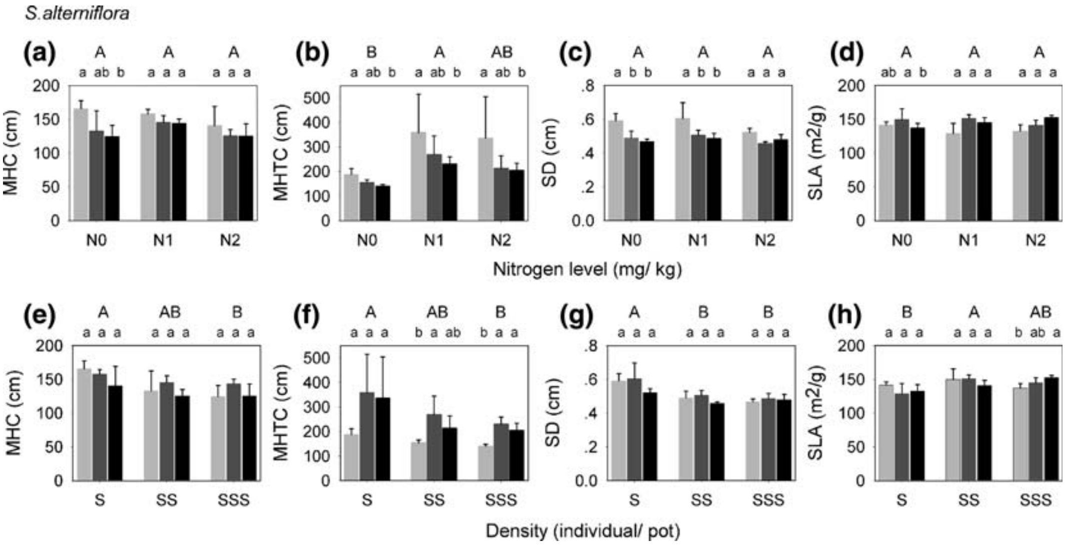


Fig. 1 Effects of nitrogen levels and culm density on morphological traits of individual *S. alterniflora*. **a–f** denotes, respectively: nitrogen levels (**a–d**) **a** MHC, **b** MHTC, **c** SD, **d** SLA; (□ S, ▨ SS, ■ SSS); culm density (**e–h**) **e** MHC, **f** MHTC, **g** SD, **h** SLA (□ N0, ▨ N1, ■ N2). N0, N1, N2: it means three nitrogen levels; N0 (0 mg kg^{-1}), N1 (60 mg kg^{-1}), N2 (120 mg kg^{-1}). S, SS, SSS: it represents different density series of *S. alterniflora*. Each letter corresponds to one individual plant of that species. Treatments with different code letters are significantly different at the significance level of 5% (Tukey HSD test): *uppercase letters* denote differences between nitrogen levels or culm density; *lowercase letters* denote differences between different culm density under the same nitrogen level or different nitrogen level under the same culm density

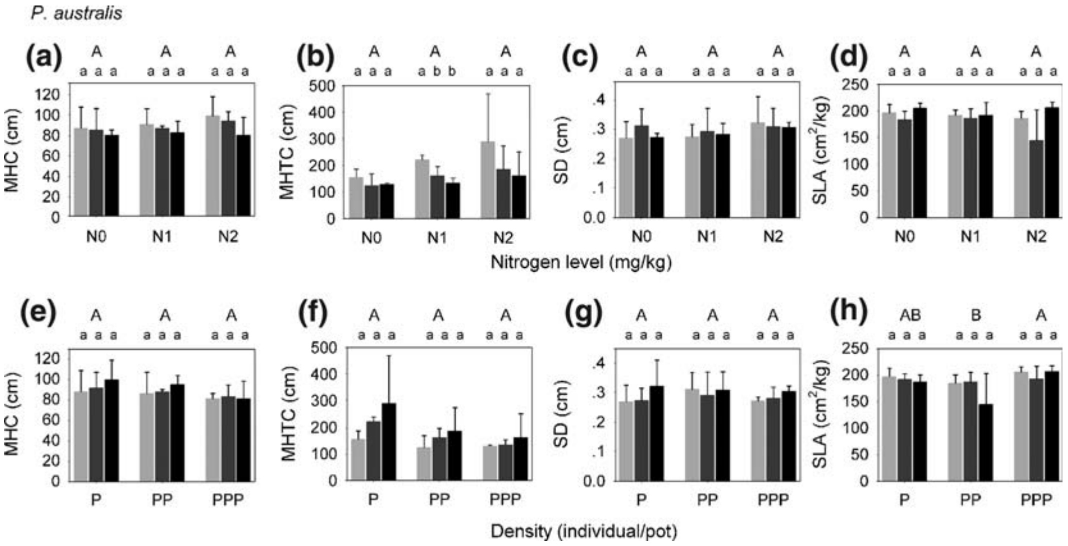
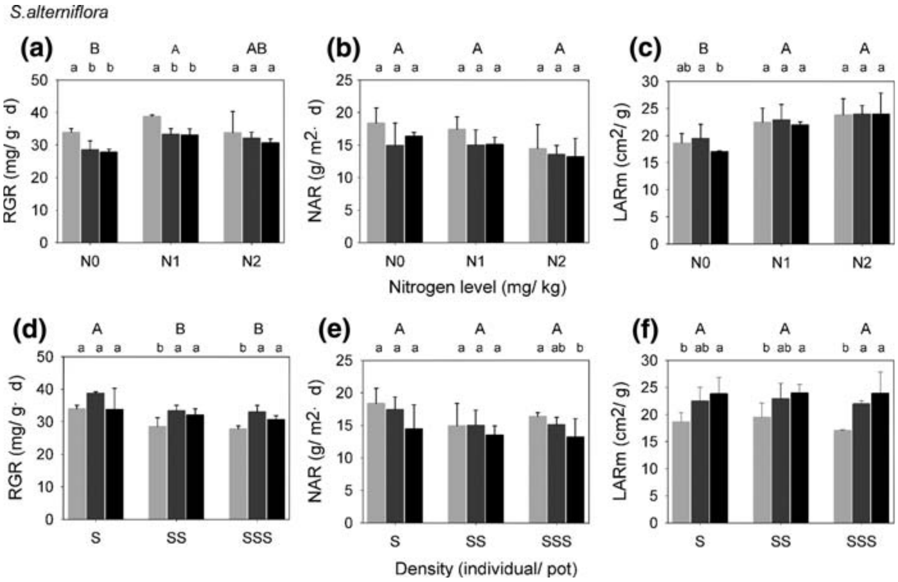


Fig. 2 Effects of nitrogen levels and culm density on morphological traits of individual *P. australis*. **a–f** denotes, respectively: nitrogen levels (**a–d**) **a** MHC, **b** MHTC, **c** SD, **d** SLA; (░ S, ▓ SS, ■ SSS); culm density (**e–h**) **e** MHC, **f** MHTC, **g** SD, **h** SLA(░ N0, ▓ N1, ■ N2). N0, N1, N2: it means three nitrogen levels; N0 (0 mg kg^{-1}), N1 (60 mg kg^{-1}), N2 (120 mg kg^{-1}). P, PP, PPP: it represents different density of *P. australis*. Each letter corresponds to one individual plant of that species. Letters denote see Fig. 1

Fig. 3 Growth traits changes of individual plant of *S. alterniflora*. Nitrogen levels (**a–c**) **a** RGR, **b** NAR, **c** LARm; culm density (**d–f**) **d** RGR, **e** NAR, **f** LARm. Notes see Fig. 1



parameters of *Phragmites*, which showed a trend of first decrease and then increase. For MPPI of growth parameters, *Spartina* had its lowest response to nitrogen at medium culm density and highest one at high culm density, whereas the response of *Phragmites* had a subdued response with a maximum under medium and high culm density (Table 3). Under the same culm density *Spartina* generally showed greater response to nitrogen than did *Phragmites*.

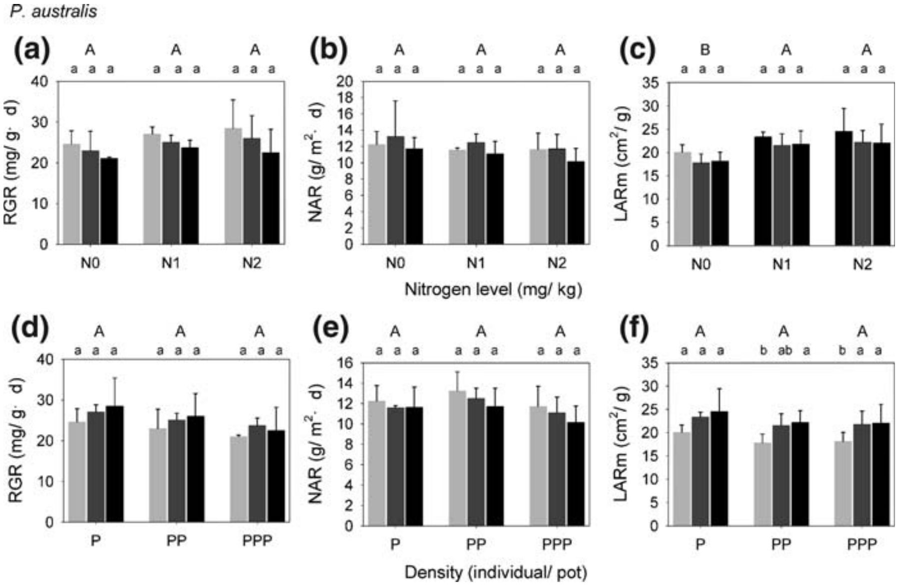


Fig. 4 Growth traits changes of individual plant of *P. australis*. Nitrogen levels (**a–c**) **a** RGR, **b** NAR, **c** LARm; culm density (**d–f**) **d** RGR, **e** NAR, **f** LARm. Notes see Fig. 1

Phenotypic plasticity of two species in response to intraspecific competition under different nitrogen levels

With increasing of nitrogen level, mean phenotypic plasticity indices (MPPI) of morphological traits of *Spartina* and *Phragmites* had a completely contrary trend in response to culm density, decreasing gradually for *Spartina* while increasing for *Phragmites*. For MPPI of growth parameters, *Spartina* had lowest response to culm density at medium nitrogen level and highest one at high nitrogen level, whereas the response of *Phragmites* was maximal under low nitrogen level. In addition, for the MPPI of the biomass allocation parameters, there was a decreased response for *Spartina* at the high nitrogen level, whereas for *Phragmites* the lowest response was at the intermediate nitrogen level. Under the same nitrogen level *Spartina* generally showed greater response to culm density than did *Phragmites* (Table 4).

Discussion

In the present study, *Spartina* responded more favorably to nitrogen availability and was less affected by culm density, which suggests that *Spartina* may acclimate better to high nitrogen environments and intraspecific competition than *Phragmites*. Nitrogen level had significant effects on several morphological (mean height of total culms), growth (the relative growth rate and mean leaf area ratio) and biomass allocation traits (leaf biomass ratio, rhizome biomass ratio, and leaf area to root mass ratio) of *Spartina*, while culm density only affected its morphological traits and the relative growth rate. Growth rate is thought to be an important trait associated with the invasiveness of plants. Grotkopp et al. (2002) found that invasive plants had higher relative growth rate than their noninvasive congeners and the relative growth rate was positively associated with invasiveness of invasive species. The higher relative growth rate of *Spartina* compared with *Phragmites* found in our study may contribute to its invasiveness. Net assimilation rate and mean leaf area ratio are regarded as two determinants of relative growth rate (Zheng et al., 2009). The higher net assimilation rate and mean leaf ratio of invaders may increase their relative growth rate, facilitating invasions of alien plants (Daehler, 2003; Zheng et al., 2009). Our results were consistent with these studies, with *Spartina* having higher net assimilation rate and mean leaf ratio of than *Phragmites* under the same nitrogen and culm density conditions, which may help the invader to form dense monoculture and outgrow native plant species, In addition, biomass allocation may also affect the success of invasive plants (Williams & Black, 1994; Wilsey & Polley, 2006). Our study provided support for this observation with the more

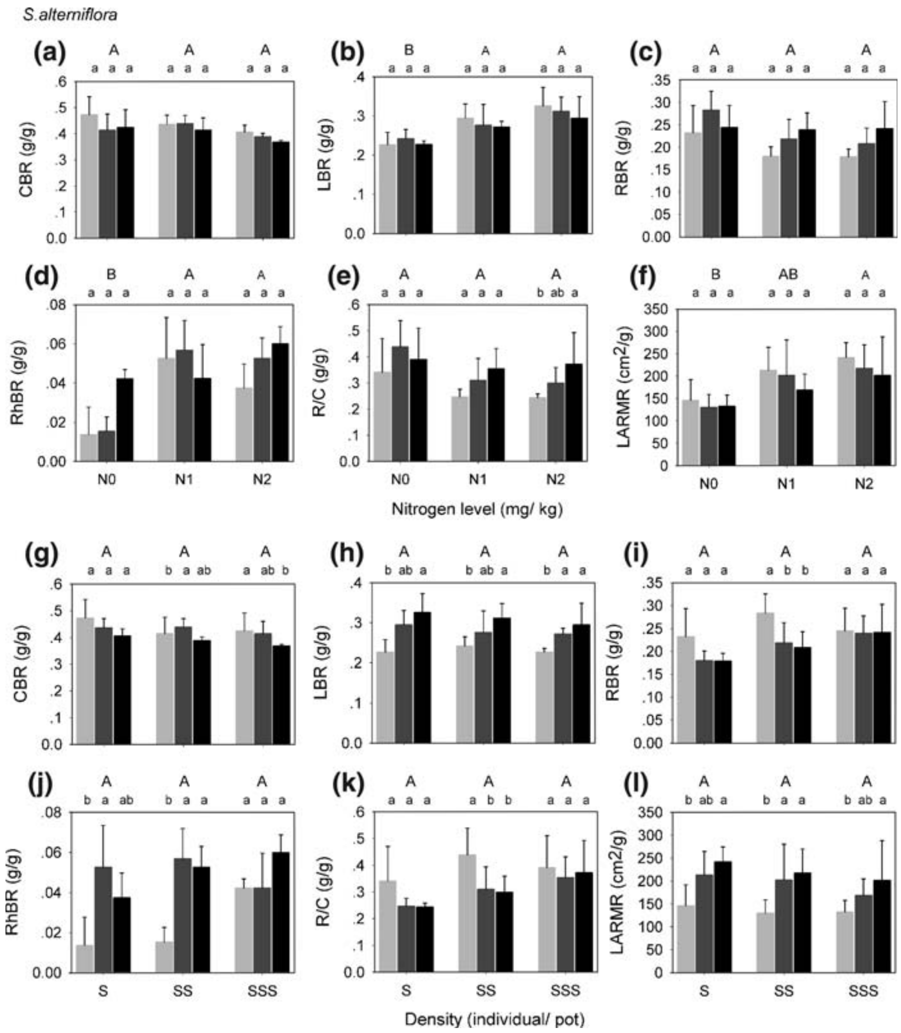


Fig. 5 Biomass allocation traits changes of individual plant of *S. alterniflora*. Nitrogen levels (**a**–**f**) **a** CBR, **b** LBR, **c** RBR, **d** RhBR, **e** R/C, **f** LARMR; culm density (**g**–**l**) **g** CBR, **h** LBR, **i** RBR, **j** RhBR, **k** R/C, **l** LARMR. Notes see Fig. 1

invasive *Spartina* allocating more biomass to leaves and less to roots than *Phragmites* did (see also Williams & Black, 1994; Wilsey & Polley, 2006). Meanwhile, we also found that the nitrogen promoted an increase in the leaf biomass ratio and the leaf area to root mass ratio of *Spartina*, which suggests that more biomass was invested into the assimilative organ as nitrogen increased. This is likely to lead to greater carbon accumulation in *Sparina* and thus increase its relative growth rate and improve the competitive ability of this species.

It has been long suggested that high phenotypic plasticity is a characteristic of invasive species (Callaway et al., 2003; Funk, 2008). We found that *Spartina* exhibited higher plasticity for more morphological, growth, and biomass allocation traits than *Phragmites* in response to nitrogen and culm density. Difference in phenotypic plasticity between native and invasive species will influence how these species will respond to changing environmental conditions (Funk, 2008). Superior ability to capitalize on abundant resources is likely to enable a species to invade habitats with high resource availability (Vitousek, 1986; Jean & Alice, 2006). In our study, the high plasticity that we observed in *Spartina*, in terms of positive responses to nitrogen availability, may override the negative effects of plant density that most plants experience, and thus, in situations of high nitrogen availability *Spartina* may experience little intraspecific competition.

In the USA, nitrogen loading has promoted the invasion of *Spartina* in Willapa Bay and the invasion

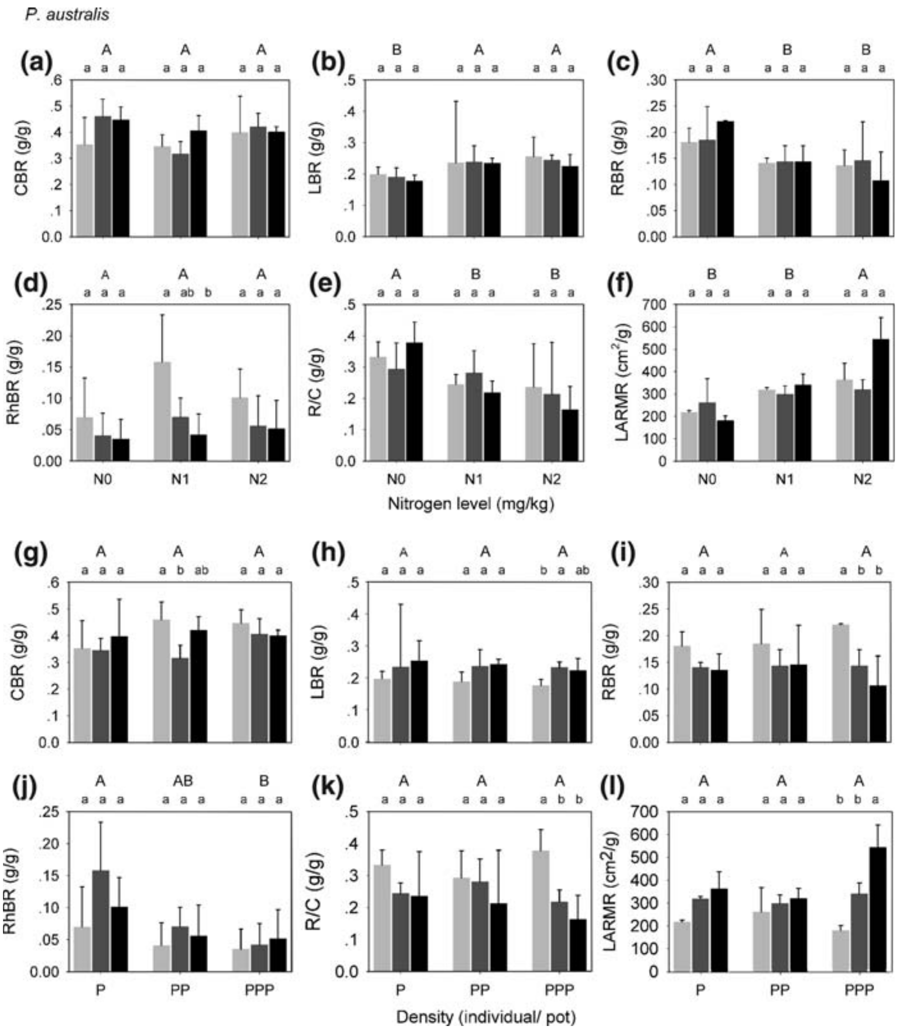


Fig. 6 Biomass allocation traits changes of individual plant of *P. australis*. Nitrogen levels (**a**–**f**) **a** CBR, **b** LBR, **c** RBR, **d** RhBR, **e** R/C, **f** LARMR; culm density (**g**–**l**) **g** CBR, **h** LBR, **i** RBR, **j** RhBR, **k** R/C, **l** LARMR. Notes see Fig. 1

of its hybrid (*S. alterniflora* × *S. foliosa*) in San Francisco Bay, and the high response of *Spartina* to nitrogen has greatly contributed to its invasiveness, especially for the trait of aboveground to belowground biomass ratio in response to different nitrogen levels, which could strengthen not only aboveground but also belowground competition dominance relative to native species (Tyler et al., 2007). In our study no significant effect of nitrogen on biomass allocation below and aboveground was observed but the strong growth response, in terms of mean height of total culms and leaf biomass ratio, to nitrogen in *Spartina* compared with *Phragmites* will certainly enhance its aboveground competition dominance and thus its successful invasion, which is consistent with previous studies (Zhao et al., 2008). In China, eutrophication of coastal zones has been one of the most pressing environmental problems accompanying rapid economic growth and human development. The level of dissolved inorganic nitrogen in both seawater and sediments has significantly increased in the past two decades along the Chinese coast (Shen et al., 2001; Wang, 2006; Li et al., 2007). This recent increase in nitrogen availability may further facilitate invasions by *Spartina* and endanger the remaining *Phragmites* stands.

In our study, within the area where *Phragmites* occurs as a native species, *Phragmites* had lower morphological and growth trait values and lower phenotypic plasticity than invasive *Spartina*, whereas

Table 3 Phenotypic plasticity index (PPI) for traits related to the morphology, growth and biomass allocation in response to nitrogen in *S. alterniflora* and *P. australis* under different culm densities

Parameters	*S. alterniflora*			*P. australis*		
	S	SS	SSS	P	PP	PPP
Morphological traits						
Max-height of culm, MHC	0.151	0.138	0.133	0.117	0.094	0.026
Mean height of total culms, MHTC	0.479	0.424	0.393	0.463	0.329	0.202
Stem diameter, SD	0.136	0.097	0.039	0.163	0.064	0.108
Specific leaf area, SLA	0.089	0.066	0.102	0.054	0.226	0.068
Mean value	0.214	0.181	0.167	0.199	0.178	0.101
Growth traits						
Relative growth rate, RGR	0.127	0.144	0.159	0.137	0.117	0.113
Net assimilation rate, NAR	0.213	0.099	0.192	0.055	0.115	0.133
Mean leaf area ratio, LARm	0.217	0.186	0.288	0.182	0.199	0.180
Mean value	0.139	0.107	0.160	0.094	0.108	0.107
Biomass allocation traits						
Culm biomass ratio, CBR	0.141	0.115	0.132	0.131	0.313	0.104
Leaf biomass ratio, LBR	0.303	0.224	0.229	0.156	0.222	0.240
Root biomass ratio, RBR	0.231	0.265	0.021	0.246	0.223	0.515
Rhizome biomass ratio, RhBR	0.741	0.730	0.296	0.558	0.422	0.314
Root mass/crown mass, R/C	0.285	0.316	0.094	0.291	0.271	0.525
Leaf area to root mass ratio, LARMR	0.397	0.402	0.343	0.402	0.184	0.668
Mean value	0.350	0.342	0.186	0.297	0.273	0.394

S, SS, SSS and P, PP, PPP: see Figs. 1 and 2

in its invasive range, *Phragmites* has been reported to have higher biomass and relative growth rate than *Spartina* (Farnsworth & Meyerson, 2003). There are several hypothesis to explain the mechanism of successful invasion for invasive plants, such as the natural enemies, evolution of invasiveness, empty niche, disturbance, and novel weapons hypotheses (Hierro et al., 2005). Because no adequate studies on *Phragmites* have been undertaken within its invasive range, it is difficult to develop explanations of why it outperforms *Spartina* in such areas. Further studies of *Phragmites*, both in its native and introduced ranges, are be required to explore the mechanism of its successful invasion of North America while it is declining in China.

Conclusions

Spartina and *Phragmites* are extensively invasive species around the world. The two species have strong ability to adapt to various habitats and to tolerate harsh environmental conditions, such as high salinity, high sulfur, changing nitrogen levels, and intraspecific competition. Our case study supports the idea that invasive species display high trait plasticityNitrogen level had significant effects on many morphological (mean height of total culms), growth (the relative growth rate and mean leaf area ratio) and biomass allocation traits (leaf biomass ratio, rhizome biomass ratio, and leaf area to root mass ratio) of *Spartina*, while culm density only affected its morphological traits and the relative growth rate. On average *Spartina* displayed higher trait plasticity compared with *Phragmites* in response to altered nitrogen availability and culm density. Understanding how the growing conditions alter the trait plasticity of invasive species has important implications for the management of plant invasions. However, this study examined the effects of two environmental factors on trait plasticity of the two species in China, thus further study should focus on comparative studies of two species in their native and invasive range to explore the mechanism of their successful invasions.

Table 4 Phenotypic plasticity index (PPI) for traits related to the morphology, growth, and biomass allocation in response to culm density in *S. alterniflora* and *P. australis* under different nitrogen levels

Parameters	*S. alterniflora*			*P. australis*		
	N0	N1	N2	N0	N1	N2
Morphological traits						
Max-height of culm, MHC	0.151	0.138	0.133	0.078	0.089	0.187
Mean height of total culms, MHTC	0.479	0.424	0.393	0.199	0.392	0.439
Stem diameter, SD	0.209	0.195	0.125	0.136	0.063	0.051
Specific leaf area, SLA	0.089	0.066	0.102	0.105	0.037	0.301
Mean value	0.232	0.206	0.188	0.130	0.145	0.245
Growth traits						
Relative growth rate, RGR	0.127	0.144	0.159	0.144	0.124	0.208
Net assimilation rate, NAR	0.213	0.099	0.192	0.113	0.111	0.130
Mean leaf area ratio, LARm	0.217	0.186	0.288	0.115	0.077	0.102
Mean value	0.186	0.143	0.213	0.124	0.104	0.11
Biomass allocation traits						
Culm biomass ratio, CBR	0.141	0.115	0.132	0.234	0.221	0.054
Leaf biomass ratio, LBR	0.303	0.224	0.229	0.105	0.015	0.118
Root biomass ratio, RBR	0.231	0.265	0.021	0.182	0.020	0.267
Rhizome biomass ratio, RhBR	0.741	0.730	0.296	0.494	0.402	0.491
Root mass/crown mass, R/C	0.285	0.316	0.094	0.225	0.166	0.238
Leaf area to root mass ratio, LARMR	0.397	0.402	0.343	0.307	0.122	0.413
Mean value	0.350	0.343	0.186	0.309	0.158	0.264

PPI phenotypic plasticity index; N0, N1, N2: See Fig. 1

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