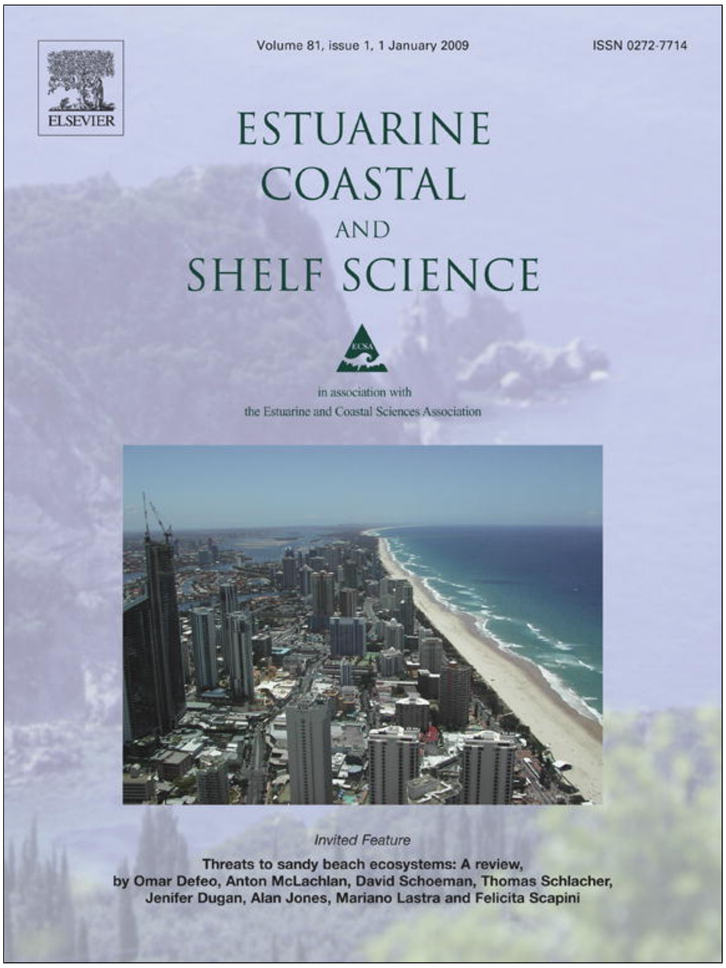

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Invited Feature

Threats to sandy beach ecosystems: A review,
by Omar Defeo, Anton McLachlan, David Schoeman, Thomas Schlacher,
Jenifer Dugan, Alan Jones, Mariano Lastra and Felicita Scapini

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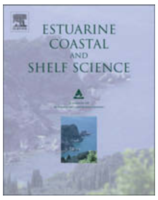

Ecophysiological characteristics of invasive *Spartina alterniflora* and native species in salt marshes of Yangtze River estuary, China

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ABSTRACT

Biological invasions represent one of the significant components of global change. A comparative study of invaders and co-occurring natives is a useful approach to gaining insights into the invasiveness of exotic plants. *Spartina alterniflora*, a C_4 grass, is a widespread invader in the coastal wetlands in China and other regions of the world. We conducted a comparative study of *S. alterniflora* and native C_3 species, *Phragmites australis* and *Scirpus mariqueter*, in terms of their gas exchange and efficiencies in resource utilization. We tested the hypothesis that *S. alterniflora* has growth-related ecophysiological advantages over the natives in its non-native range, which result in its rapid growth and enhance its invasiveness. Photosynthesis, leaf area index (LAI), specific leaf area (SLA), and the efficiency of resource use (light, water, and nitrogen) were examined monthly for eight months in 2004. Overall, *S. alterniflora* had greater LAI, higher maximal net photosynthetic rate (A_{max}), and longer growing season than those of the native species. On average, the efficiencies of *S. alterniflora* in light, water, and nitrogen utilization were respectively 10.1%, 26.1%, and 33.1% higher than those of *P. australis*, and respectively 70.3%, 53.5%, 28.3% higher than those of *S. mariqueter*. However, SLA of *S. alterniflora* was significantly lower than those of *P. australis* and *S. mariqueter*. Although there was no general pattern in the relationship between invasiveness and plant photosynthetic types, in this study, most of the ecophysiological characteristics that gave *S. alterniflora* a competitive advantage in the Yangtze River estuary were associated with photosynthetic pathways. Our results offer a greater understanding of the relationship between invasiveness and plant photosynthetic type. Our results also indicate that LAI and the length of the photosynthetic season, which vary with habitats, are also important in invasion success.

1. Introduction

Biological invasions are among the most serious environmental problems (Sala et al., 2000) and are considered to be one of the significant components of human-induced global change (Vitousek et al., 1997; Mack et al., 2000). The invasion of exotic species has various profound effects on native ecosystems, from the genetic to the ecosystem levels (Grosholz, 2002). For example, invasive species reduce biodiversity (McKinney and Lockwood, 1999; Rodríguez et al., 2005), alter nutrient cycling processes (Ehrenfeld, 2003; Windham and Ehrenfeld, 2003), affect ecosystem functioning (D'Antonio and Vitousek, 1992; Walker and Smith, 1997; Christian and Wilson, 1999), and even have evolutionary consequences (Mooney and Cleland, 2001).

Invasive plants are often characterized by rapid growth, so they can crowd out native species (Cronk and Fuller, 1995). Apart from their growth rates, other growth-related features that are probably associated with the competitive success of invasive species usually include high photosynthetic rates, low tissue construction costs (CC), and high total leaf area (McDowell, 2002). Specific leaf area (SLA) is an indirect indicator of leaf CC (Durand and Goldstein, 2001; McDowell, 2002). A lower CC (i.e. higher SLA) suggests a more efficient use of carbon resources because less energy is invested per unit leaf mass produced, which can potentially contribute to a higher growth rate (Lambers and Poorter, 1992; Durand and Goldstein, 2001). Invaders tend to have a higher SLA or a lower CC, giving them a growth advantage (Baruch and Goldstein, 1999; Nagel and Griffin, 2001; Smith and Knapp, 2001; Daehler, 2003).

The photosynthesis or growth rates of plants are usually limited by the available resources. Therefore, the efficient use of available resources is very important for competitive success among plants. For example, invasive species may more efficiently utilize light (Kloeppel and Abrams, 1995; Pattison et al., 1998; Durand and Goldstein, 2001), water (Kloeppel and Abrams, 1995; McDowell, 2002), and nitrogen than native plants (Kloeppel and Abrams, 1995; Baruch and Goldstein, 1999; McDowell, 2002), which facilitates

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their invasion. Photosynthetic rates and resource use efficiency are associated with the plant photosynthetic types. To the best of our knowledge, there is however no general pattern in the relationship between invasiveness and plant photosynthetic types (e.g., Symstad, 2000), although some researchers have reported that fast-growing C_4 annuals are more likely to invade C_3 grasslands (White et al., 2001).

Estuaries, which offer the greatest ecosystem services per unit area (Costanza et al., 1997), are among the most heavily invaded ecosystems in the world (Cohen and Carlton, 1998; Grosholz, 2002). Wetlands, including estuarine salt marshes, seem to be highly vulnerable to invasions (Zedler and Kercher, 2004). Wetlands in the Yangtze River estuary in China are under threat of an invasive perennial C_4 grass, *Spartina alterniflora*, which is native to the east and Gulf coasts of North America and has become a worldwide invasive species (Callaway and Josselyn, 1992; Daehler and Strong, 1996; CSCC, 2004; Zedler and Kercher, 2004; Li et al., 2008). In 1979, *S. alterniflora* was deliberately introduced into China from North America to check erosion and promote sediment accretion (Chung, 1993), but it has become highly invasive in many coastal wetlands in China. Although *S. alterniflora* still provides the anticipated ecological benefits in the Yangtze River estuary (e.g., Wang et al., 2008), its negative effects on the native ecosystems have become more and more obvious (Li et al., 2008). It has locally displaced the native dominant species *Phragmites australis* and *Scirpus mariqueter* (Chen et al., 2004; Wang et al., 2006a), altered the structure of the trophic functional groups of benthic nematode communities (Chen et al., 2007) and macroinvertebrates (Chen et al., 2005), and reduced the species richness and density of shorebirds by reducing habitat quality (Chen et al., 2004; Li et al., 2008).

It is well accepted that C_4 plants have ecophysiological advantages (e.g., Sage, 2004), which seems true in our case, judging from the observed growth advantages of *S. alterniflora*. Therefore, we conducted a comparative study of gas exchange characteristics and resource use efficiency throughout a growing season. Our purpose was to test the hypothesis that *S. alterniflora* has growth-related ecophysiological advantages over the native C_3 species, which result in its rapid growth and thus enhance its invasiveness in the Yangtze River estuary, China.

2. Materials and methods

2.1. Study site

The field study was conducted on the Jiuduansha Islands in the Yangtze River estuary (31°13′N, 121°58′E) for eight months in 2004. The Jiuduansha Islands are young alluvial islands which are about 50-years-old. The species composition of the vegetation on the islands is relatively simple (Chen et al., 2003). There are only three dominant species, *Scirpus mariqueter*, *Phragmites australis*, and *Spartina alterniflora*, each forming extensive monocultures. Since its first introduction to the islands in 1997, the invasive species *S. alterniflora* has been rapidly replacing the native species.

The Jiuduansha Islands have a subtropical monsoonal climate, featuring abundant precipitation and four distinct seasons. The mean annual precipitation is 1145 mm and the mean annual air temperature is 15.7 °C. Rainfall usually comes with high temperatures. Seasonal variations are characterized by cold winters and hot summers, and the length of the growing season is about 254 days. Monthly rainfall and air temperature of the Yangtze River estuary during the measuring period in 2004 are shown in Fig. 1.

2.2. Species

Spartina alterniflora Loisel. (Poaceae), an invasive perennial, grows much taller and stronger in non-native range than in its native habitats. The height of the erect stems can be taller than 2.5 m and the basal diameter of the stems can be more than 1 cm in our site. *S. alterniflora* is distributed in intertidal zone and has high tolerance to salinity and water logging. Leaves of *S. alterniflora* are with glands that can secrete salt absorbed by roots. *S. alterniflora* spreads asexually by a subterranean rhizome system or by seeds.

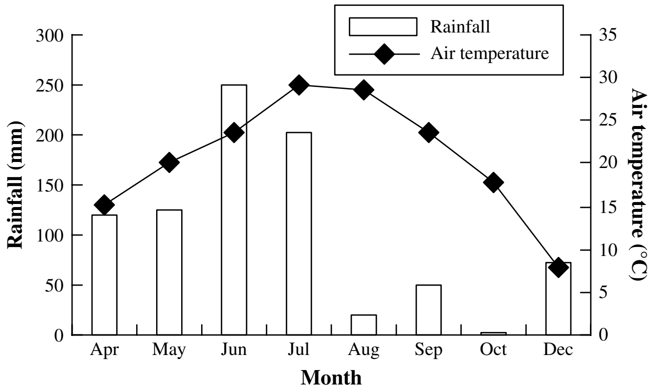

Fig. 1. Monthly rainfall and air temperature of the Yangtze River estuary during the measuring period in 2004 (data were provided by "The Island Investigation Project of Shanghai" processed by Shanghai Marine Environmental Forecasting Centre).

Phragmites australis (Cav.) Trin. ex Steud (Poaceae) is perennial grass and is distributed at higher elevation in coastal wetlands than *Spartina alterniflora* and *Scirpus mariqueter* because its adaptability to salinity is not as good as *S. alterniflora* and *S. mariqueter*. The erect stems of *P. australis* can grow up to 3 m tall. *P. australis* has long and dense rhizomes that can extend several meters away and is the main means by which *P. australis* spreads.

Scirpus mariqueter Tang et Zhang (Cyperaceae), a perennial, is endemic to China. This species can only grow in costal wetlands and is pioneer species on the mudflats playing an important role in the early stage of the salt marshes. It is distributed at the lowest elevation among the three dominant species on Jiuduansha Islands. The stems and leaves (0.5–0.8 m in height) of *S. mariqueter* are triangular prismatic. *S. mariqueter* produces rhizomes and corms mainly by which it forms new shoots at the beginning of the next growing season.

Phragmites australis and *Scirpus mariqueter* form extensive and dense mono-specific stands on the Islands. Generally, the individuals of the invasive *Spartina alterniflora* arrive in the native stands of *P. australis* or *S. mariqueter* by seeds or subterranean rhizomes. Once starting its growth in the native stands, *S. alterniflora* can quickly spread by the subterranean rhizomes, crowd out the native species, and form dense mono-specific stands. Therefore, on the Jiuduansha Islands, extensive mono-specific stands of the above three dominant plant species are quite common while mixed stands of *S. alterniflora* and *P. australis* or *S. mariqueter* are very rare. To avoid possible confusion caused by environmental differences (e.g., elevation and salinity), we selected adjacent stands of each species to ensure that the differences measured were attributable to the plant species.

2.3. Measurements

Leaf area index (LAI) was measured monthly for consecutive eight months. For each species, five randomly selected $0.5 \times 0.5\ m^2$ plots were sampled in measuring the leaf area and leaf mass. Leaf area was measured using an area meter (model LI-3000A, LI-COR, Inc., Lincoln, NE, USA). Because the leaves of *Scirpus mariqueter* are triangular prismatic and the area of each plane is almost the same, the leaf area of this species was calculated by multiplying the projected area by 1.5. SLA was calculated by dividing the leaf area by the dried leaf mass.

Leaf gas exchange was also measured monthly. The plants used for the measurements of leaf gas exchange were randomly selected within each stand of a specific species. Leaf gas exchange was measured *in situ* using a portable photosynthesis system (model LI-6400, LI-COR, Inc., Lincoln, NE, USA) with the standard Li-Cor chamber (6 cm^2). Variations in light intensity were achieved with a red–blue light-emitting diode (LED) array. Light response curves were constructed by measuring the assimilation rates at different intensities of photosynthetically active radiation, from 2500 to 0 $\mu mol\ m^{-2}\ s^{-1}$. Other parameters inside the leaf chamber, such as temperature and relative humidity, varied with the ambient environments. For all of the light curves that we obtained, the variations of the temperature and relative humidity inside the chamber during the period that a curve was acquired were $2.5 \pm 0.9\ ^\circ C$ and $7.0 \pm 3.6\%$, respectively. In addition, the lasting time for constructing a light curve was 9.2 ± 2.5 min.

To make the results comparable and to avoid the possible effects of leaf age, when the seasonal changes were determined, all measurements of leaf gas exchange were made with relatively young leaves and from the same position in the canopy, i.e., the second fully expanded leaf from the top. Three to five individuals of *Spartina alterniflora* and *Phragmites australis* were sampled in total for each time.

Unlike the leaves of *Spartina alterniflora* and *Phragmites australis*, which are large enough to cover the standard 6 cm^2 chamber, the leaves of *Scirpus mariqueter* are too narrow to do so. To ensure that the CO_2 flux was high enough for infrared gas analyzer (IRGA) to be detected, 5 leaves from different *S. mariqueter* plants were lined up together inside the chamber for one measurement. Compared with the other two species, *S. mariqueter* had fewer leaves on each plant (usually 2–5 leaves). In fact, only one leaf was very vigorous on each plant. However, the CO_2 flux of the photosynthesis of only one leaf might be too small for the IRGA to be detected. Therefore, to make the data comparable among species, i.e., to measure the photosynthetic rates of vigorous leaves, we chose 5 vigorous leaves from different plants as replicates.

To understand the variation in photosynthesis with the canopies of *Spartina alterniflora* and *Phragmites australis*, light response curves for leaves from the different layers were measured in August. The canopy was partitioned into three layers for both species, the upper (Up), middle (Mid), and lower (Low) layers, by dividing the total leaves evenly into three parts according to their positions in the canopy of the plant. Three to four plants were sampled in total for each species. We did not measure the leaf gas exchange in different canopy layers for *Scirpus mariqueter*, because there were no obvious layers in this species.

All leaf gas exchange measurements were made in the morning on sunny days. The leaves were collected to determine the total nitrogen (TN) content immediately after the photosynthetic measurements were made. Leaf samples were dried at 50 °C to a constant mass and then ground, sieved, and analyzed for TN with an NC (nitrogen–carbon) Analyzer (model Flash EA1112 series, Thermo Electron Corporation, Waltham, MA, USA). Thirty leaves of *Spartina alterniflora* and *Phragmites australis* and 80 leaves of *Scirpus mariqueter* were used to establish the relationship between leaf area and dry mass, which was needed to transform the mass-based leaf TN into the area-based leaf TN. Pilot experiments indicated that the relationship between leaf area and dry mass in *S. mariqueter* was more variable than were those in the other two species. A larger sample size for *S. mariqueter* than for the other species was required to achieve similar precision in the measured data (r^2 of the regressions between leaf area and dry mass for *S. alterniflora*, *P. australis*, and *S. mariqueter* were 0.98, 0.87, and 0.65, respectively; and $P < 0.001$ for all three species).

The response of the leaf net photosynthetic rate (A) to light intensity was modelled with a non-rectangular hyperbolic equation proposed by Prioul and Chartier (1977):

$$A = \frac{\phi Q + A_{max} - \sqrt{(\phi Q + A_{max})^2 - 4 \phi Q k A_{max}}}{2k} - R_{day}$$

where A is the leaf net photosynthetic rate; Q is the light intensity; φ is the apparent quantum yield (QY); the maximal net photosynthetic rate (A_{max}) is the light-saturated A, i.e., the upper asymptote; R_{day} is day respiration, i.e., the release of CO_2 in the light by processes other than photorespiration; and k, denoting convexity, is required to describe the progressive rate of bending between the linear gradient and the maximal value. The light compensation point (LCP) and the apparent respiration were estimated from the intercepts. The light saturation point (LSP) was estimated by extrapolating the linear function described by φ and R_{day} to its intersection with A_{max} (Walker, 1989). The calculations for all these parameters were made using Photosynthesis Assistant (Dundee Scientific, Scotland, UK). Water use efficiency (WUE) was calculated as the ratio of instantaneous A to the transpiration rate at the saturated photosynthetic photon flux density (2000 $\mu mol\ m^{-2}\ s^{-1}$). Photosynthetic nitrogen use efficiency (PNUE) was calculated as the ratio of A_{max} to leaf TN expressed per unit leaf area.

2.4. Data analysis

For seasonal changes in LAI, A_{max}, LSP, LCP, R_{day}, QY, WUE, TN, PNUE, and SLA, repeated measures ANOVA was used to test the differences in the parameters among *Spartina alterniflora*, *Phragmites australis* and *Scirpus mariqueter*. For changes in A_{max}, LSP, LCP, R_{day}, QY, WUE, TN, and PNUE with canopy layers, nested design ANOVA was used to test the differences between *S. alterniflora* and *P. australis*. And post hoc tests were included in the above two kinds of statistics. All of the statistical analysis was performed with Statistic 6.0.

3. Results

3.1. Seasonal changes in LAI

LAI of the three species showed significant seasonal changes with higher values in summer (Fig. 2A; Table 1). There were significant differences among the three species, with which *Spartina alterniflora* exhibited greater mean LAI (1.74–6.86) than those of *Phragmites australis* (0.37–5.06) and *Scirpus mariqueter* (2.13–7.98), especially in the later half of the growing season. *S. alterniflora* had a longer photosynthetic season than the two native species. The time of shoot sprouting in spring was almost the same for *S. alterniflora* and *P. australis*, but was much later for *S. mariqueter*. At the end of the growing season, *S. alterniflora* senesced much later than the two native species. The two native species had only very low LAI in October, whereas *S. alterniflora* maintained a high LAI even in December.

3.2. Photosynthetic characteristics in relation to light

Most photosynthetic parameters for *Spartina alterniflora*, *Phragmites australis*, and *Scirpus mariqueter* were consistent with the general differences between C_4 and C_3 plants. Significant variations in A_{max} were detected in both species and seasons (Fig. 2B; Table 1). *S. alterniflora* showed higher A_{max}, of 11.7–40.6 $\mu mol\ m^{-2}\ s^{-1}$, than *P. australis* (17.0–28.0 $\mu mol\ m^{-2}\ s^{-1}$) in most months and *S. mariqueter* (6.7–17.0 $\mu mol\ m^{-2}\ s^{-1}$) in all of the measured months. *S. alterniflora* also had significantly higher R_{day}, of 0.18–4.90 $\mu mol\ m^{-2}\ s^{-1}$, than *P. australis* (0.78–2.64 $\mu mol\ m^{-2}\ s^{-1}$) and *S. mariqueter* (0.63–1.37 $\mu mol\ m^{-2}\ s^{-1}$,

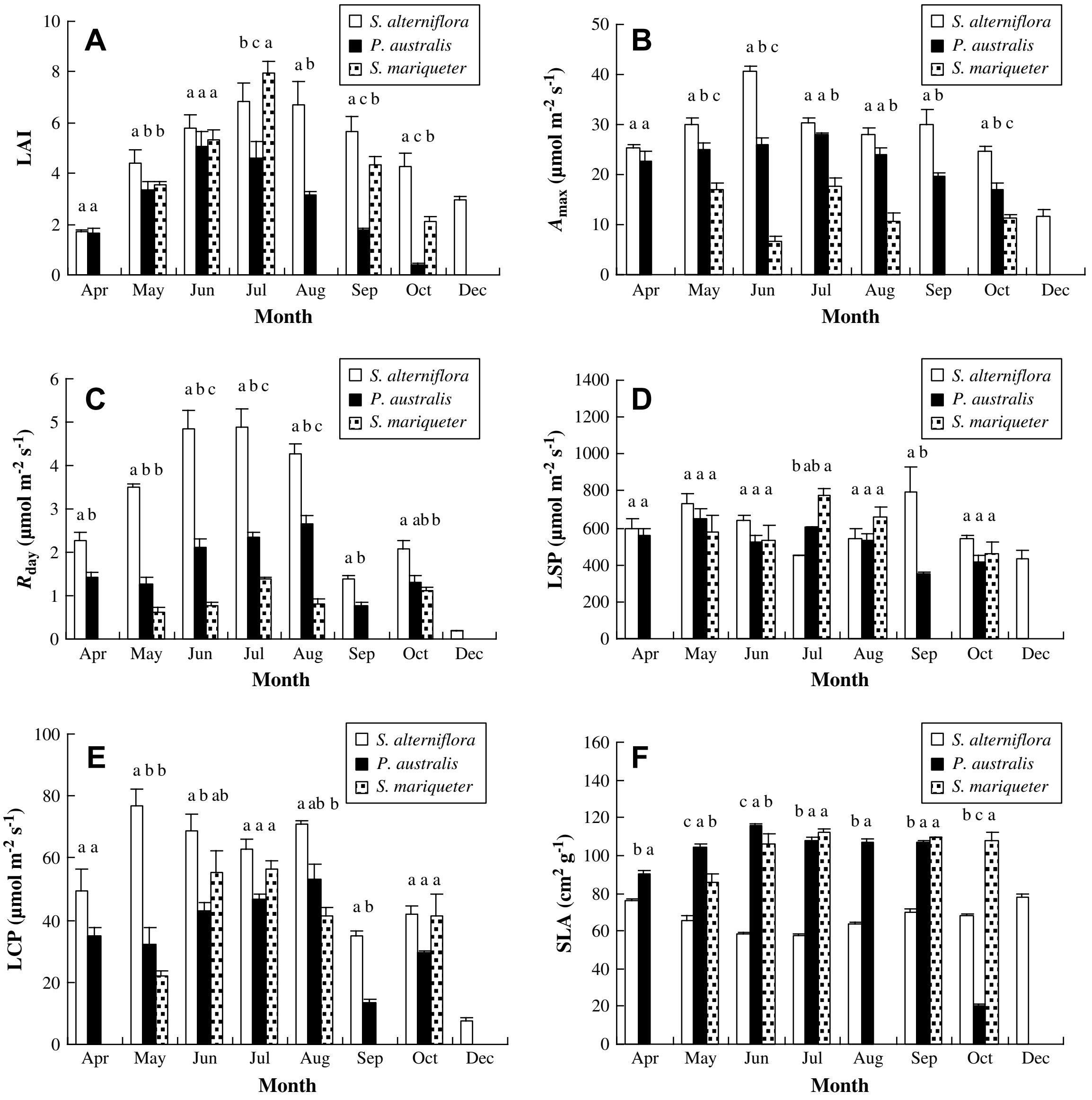

Fig. 2. Seasonal changes in the leaf area index (LAI, A), maximal net photosynthetic rate (A_{max}, B), day respiration (R_{day}, C), light saturation point (LSP, D), light compensation point (LCP, E), and specific leaf area (SLA, F) of *S. alterniflora*, *P. australis*, and *S. mariqueter* in the Yangtze River estuary. LAI and SLA were not measured in August and A_{max}, R_{day}, LSP, and LCP were not measured in September for *S. mariqueter*. In April, the leaves of *S. mariqueter* were too small to be measured. In December, *P. australis* and *S. mariqueter* were dead. The vertical bars represent the standard errors.

Fig. 2C; Table 1) throughout the growing season except in October for *P. australis*. C_4 plants are usually characterized by higher LSP and LCP than those by C_3 plants. However, in our case, we did not find any significant differences in LSP among the three species although the seasonal variations were significant (Fig. 2D, E; Table 1).

Consistent with the seasonal changes, analysis on the photosynthetic characteristics of different layers indicated that except for LSP, all the other parameters, including A_{max}, R_{day}, and LCP, showed significant differences between *Spartina alterniflora* and *Phragmites australis*, of which *S. alterniflora* had higher values of A_{max}, R_{day}, and LCP than *P. australis* (Fig. 3; Table 2). Overall, photosynthetic parameters of *S. alterniflora* and *P. australis* decreased significantly from the canopy top to the lower layers. A_{max} of both *S. alterniflora* and *P. australis* could be divided to three significantly different layers but R_{day}, LSP, and LCP of the middle layer of both *S. alterniflora* and *P. australis* did not significantly differ with either the upper layer or the lower layer.

3.3. Light, water, and nitrogen use efficiency

The measurements made across seasons showed that QY, WUE, TN, and PNUE had significant differences not only among species but also among different seasons (Fig. 4; Table 1). On average, QY of *Spartina alterniflora* was 10.1% and 70.3% higher than those of *Phragmites australis* and *Scirpus mariqueter*, respectively; and WUE of *S. alterniflora* was 26.1% and 53.5% higher than those of *P. australis* and *S. mariqueter*, respectively. The leaf TN values were significantly different among the three species. The leaf TN of *S. alterniflora* was significantly lower than that of *P. australis* except in April and October, but significantly higher than that of *S. mariqueter* throughout the growing season. With higher A_{max}, PNUE of *S. alterniflora* was 33.1% and 28.3% higher than those of *P. australis* and *S. mariqueter*, respectively.

Unlike the photosynthetic parameters, QY, WUE, and PNUE had no significant differences among canopy layers but significantly

Table 1
Summary of repeated measures ANOVA to test the differences of the parameters measured among species.

Parameters	Source of variation	df	*F*	*P*
Leaf area index (LAI)	Species	2, 12	149.6	< 0.0001
	Season	5, 60	63.4	< 0.0001
	Species × season	10, 60	5.1	<0.0001
Maximal net photosynthetic rates (A_{max})	Species	2, 6	340.2	<0.0001
	Season	5, 30	144.2	<0.0001
	Species × season	10, 30	18.4	<0.0001
Day respiration (R_{day})	Species	2, 6	158.8	<0.0001
	Season	4, 24	31.1	<0.0001
	Species × season	8, 24	12.7	<0.0001
Light saturation point (LSP)	Species	2, 6	1.3	0.34
	Season	4, 24	5.5	<0.01
	Species × season	8, 24	4.7	<0.01
Light compensation point (LCP)	Species	2, 6	18.7	<0.01
	Season	4, 24	20.1	<0.0001
	Species × season	8, 24	9.8	<0.0001
Quantum yield (QY)	Species	2, 6	175.7	<0.0001
	Season	5, 30	71.2	<0.0001
	Species × season	10, 30	8.8	<0.0001
Water use efficiency (WUE)	Species	2, 6	125.6	<0.0001
	Season	5, 30	16.4	<0.0001
	Species × season	10, 30	76.1	<0.0001
Total nitrogen (TN)	Species	2, 6	294.6	<0.0001
	Season	4, 24	22.7	<0.0001
	Species × season	8, 24	31.9	<0.0001
Photosynthetic nitrogen use efficiency (PNUE)	Species	2, 6	75.8	<0.0001
	Season	5, 30	147.2	<0.0001
	Species × season	10, 30	20.0	<0.0001
Specific leaf area (SLA)	Species	2, 12	358.5	<0.0001
	Season	4, 48	77.8	<0.0001
	Species × season	8, 48	106.6	<0.0001

differed between *Spartina alterniflora* and *Phragmites australis* (Fig. 5; Table 2). TN of both *S. alterniflora* and *P. australis* was not significantly different between the upper layer and the middle layer although the overall differences among canopy layers were significant.

3.4. Seasonal changes in SLA

SLA of the three species showed significant seasonal variations (Fig. 2F; Table 1). However, contrary to the general pattern of SLA between the invaders and natives, SLA of *Spartina alterniflora* (57.6–77.7 $cm^2 g^{-1}$) was significantly lower than that of *Scirpus mariqueter* (85.8–112.4 $cm^2 g^{-1}$) throughout the growing season, and significantly lower than that of *Phragmites australis* (20.7–115.8 $cm^2 g^{-1}$) except in October.

4. Discussion

Species invasiveness, habitat invasiveness, and the effects of invasion are three main topics in invasion biology (Alpert et al., 2000). Many studies have been conducted to compare the performances of invasive species and their co-occurring native species to explore whether invasive plants perform better than the natives. In the present study, because the spreading process of the invasive *Spartina alterniflora* is so quick that typical ongoing mixed stands of *S. alterniflora* and the native species *Phragmites australis* or *Scirpus mariqueter* were seldom found on the Islands, a comparative study between the invader and the natives was done in adjacent monospecific stands of the above three species.

Most previous studies have found that the photosynthetic rates of invasive species are higher than those of natives (e.g., Pattison et al., 1998; Baruch and Goldstein, 1999; McDowell, 2002), whereas others have found no significant differences or even higher photosynthetic rates in the natives (e.g., Smith and Knapp, 2001; Bastlova and Kvet, 2002). Whether the photosynthetic rates of the invaders are higher than their native congeners seems to be related to the growing conditions (Daehler, 2003; Nagel and Griffin, 2004; Wang et al., 2006a). In our study, as expected from our general knowledge of the C_4 and C_3 photosynthetic pathways, we observed higher net photosynthetic rates and respiration rates in the invasive C_4 species *Spartina alterniflora* than in the native C_3 species

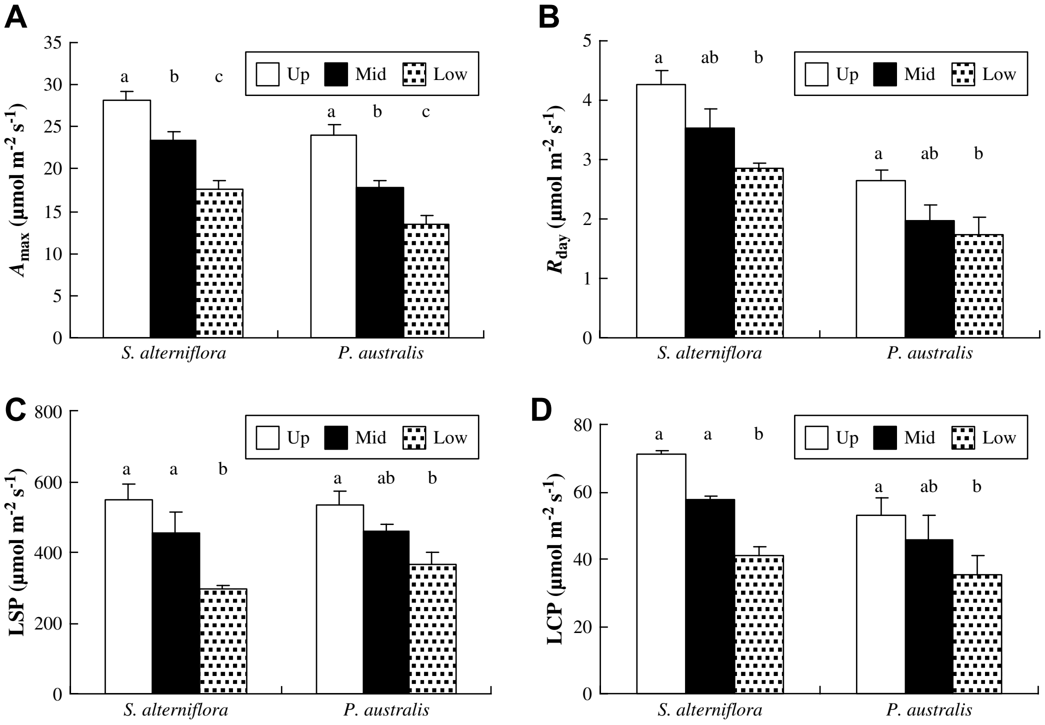

Fig. 3. Maximal net photosynthetic rate (A_{max}, A), day respiration (R_{day}, B), light saturation point (LSP, C), and light compensation point (LCP, D) of different layers of *S. alterniflora* and *P. australis* measured in August 2004, in the Yangtze River estuary. The vertical bars represent the standard errors.

Table 2
Summary of nested design ANOVA to test the differences of the parameters measured in different canopy layers between *Spartina alterniflora* and *Phragmites australis*.

Parameters	Source of variation	df	*F*	*P*
Maximal net photosynthetic rates (A_{max})	Species	1, 15	28.06	<0.0001
	Canopy layer	4, 15	23.72	<0.0001
Light saturation point (LSP)	Species	1, 15	0.46	0.51
	Canopy layer	4, 15	8.24	<0.01
Light compensation point (LCP)	Species	1, 15	8.56	<0.05
	Canopy layer	4, 15	5.74	<0.01
Day respiration (R_{day})	Species	1, 15	44.45	<0.0001
	Canopy layer	4, 15	5.12	<0.01
Quantum yield (QY)	Species	1, 15	34.31	<0.0001
	Canopy layer	4, 15	1.45	0.27
Water use efficiency (WUE)	Species	1, 15	89.60	<0.0001
	Canopy layer	4, 15	0.88	0.50
Total nitrogen (TN)	Species	1, 15	42.30	<0.0001
	Canopy layer	4, 15	10.21	<0.001
Photosynthetic nitrogen use efficiency (PNUE)	Species	1, 15	57.67	<0.0001
	Canopy layer	4, 15	2.79	0.06

Phragmites australis and *Scirpus mariqueter*. The higher net photosynthetic rates of *S. alterniflora* that might result in faster growth may help to explain why it has become so successful (Daehler, 2003) although the respiration rates of *S. alterniflora* were also higher than the native species. Furthermore, the photosynthetic rates of *S. alterniflora* as an invader at our site were much higher than those grown in their native habitats (e.g., Dai and Wiegert, 1996, 1997; Pennings et al., 2002; Farnsworth and Meyerson, 2003).

C_4 plants are characterized by higher LSP and LCP than C_3 plants. As for LCP, this was exactly the situation, but no significant difference in LSP was found between *Spartina alterniflora* and the other two species. These two C_3 species exhibited as high LSP as C_4 species probably because they always grow in high-light environments and may have been adapted to the high light.

Compared to photosynthesis, differences in the total leaf areas between invaders and natives are more consistent among studies, i.e., invaders usually have a significantly higher total leaf area than their co-existing native species (Daehler, 2003). In our study, as the general pattern, *Spartina alterniflora* had a higher LAI than *Phragmites australis* and *Scirpus mariqueter*. In addition, LAI of *S. alterniflora* at our site (4.80 on average) was much higher than that in their native habitats (Dai and Wiegert, 1996, 1997; Farnsworth and Meyerson, 2003).

Comparative studies on the length of the growing seasons of invaders and native species have not drawn a general conclusion (Daehler, 2003). As some studies showing that invaders tend to maintain net photosynthesis over a longer period of the year than non-invasive species (McDowell, 2002; Farnsworth and Meyerson, 2003), in our case, *Spartina alterniflora* maintained net photosynthesis at least one month longer than *Phragmites australis* and *Scirpus mariqueter*. The higher net photosynthetic rates, greater LAI, together with longer growing season might all have contributed to the higher net primary productivity of *S. alterniflora* (2.16 kg C m^{-2} yr^{-1}) than that of *P. australis* (1.69 kg C m^{-2} yr^{-1}) and *S. mariqueter* (0.72 kg C m^{-2} yr^{-1}) in the Yangtze River estuary (Liao et al., 2007).

In contrast, in Farnsworth and Meyerson's study (2003), *Phragmites australis* was the invasive species while *Spartina alterniflora* was the native species. *P. australis* had a greater LAI and a longer growing season than *S. alterniflora*. In our case, all relationships were reversed. However, photosynthetic rates kept consistent between the two studies, i.e., *S. alterniflora* had higher

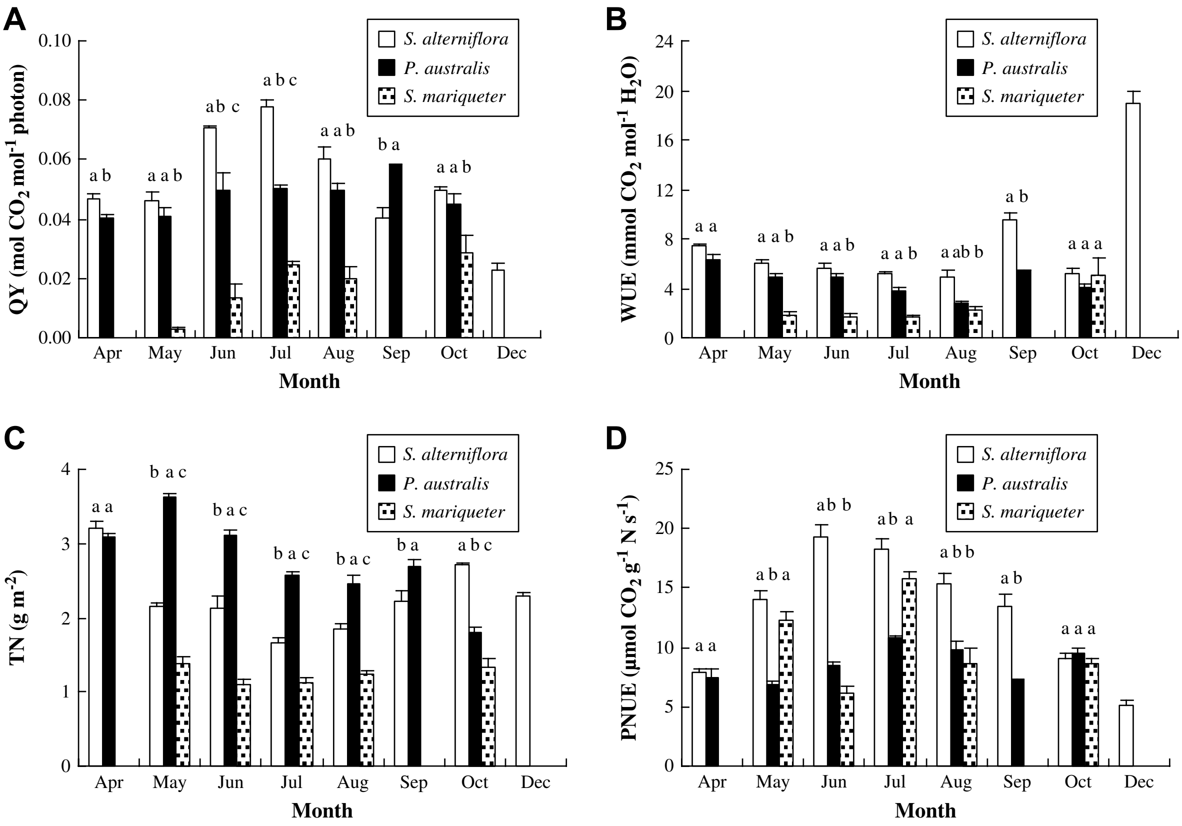

Fig. 4. Seasonal changes in quantum yield (QY, A), water use efficiency (WUE, B), leaf total nitrogen (TN, C), and photosynthetic nitrogen use efficiency (PNUE, D) of *S. alterniflora*, *P. australis*, and *S. mariqueter* in the Yangtze River estuary. QY, WUE, TN, and PNUE for *S. mariqueter* were not measured in September. In April, the leaves of *S. mariqueter* were too small to be measured. In December, *P. australis* and *S. mariqueter* were dead. The vertical bars represent the standard errors.

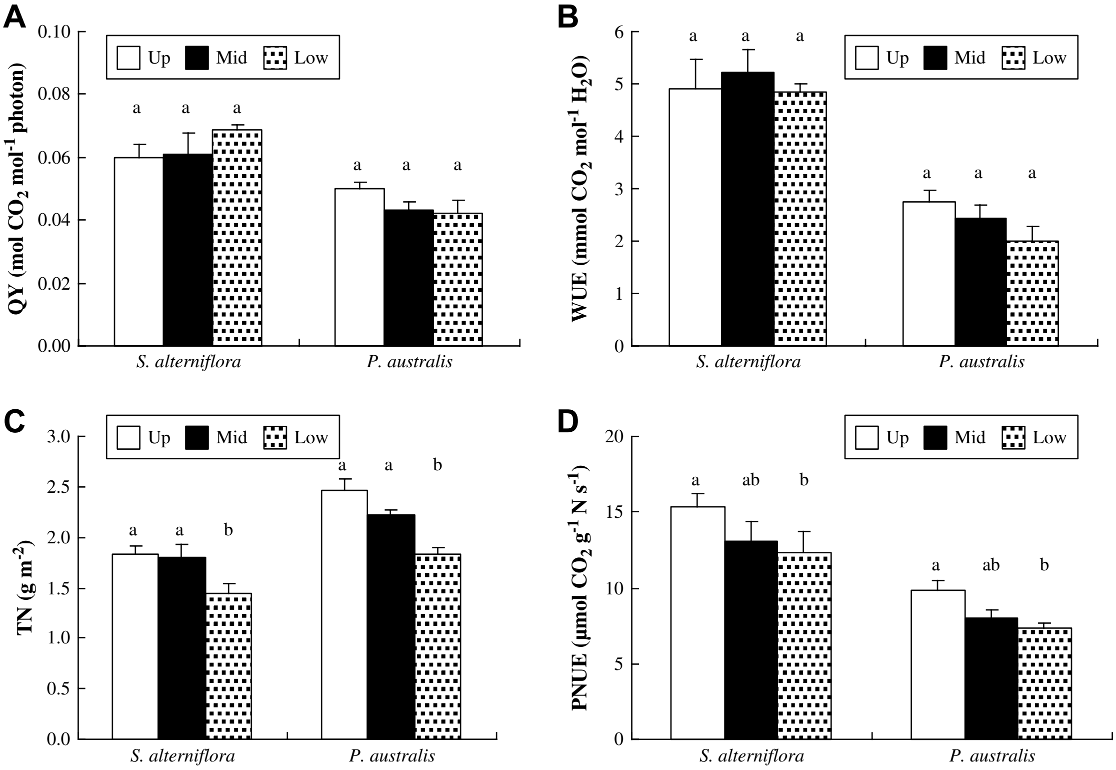

Fig. 5. Quantum yield (QY, A), water use efficiency (WUE, B), leaf total nitrogen (TN, C), and photosynthetic nitrogen use efficiency (PNUE, D) of different layers of *S. alterniflora* and *P. australis* measured in August 2004, in the Yangtze River estuary. The vertical bars represent the standard errors.

photosynthetic rates. These results suggested that LAI and growing season length, which depend on the habitats, play very important roles in invasion success. If a species with a great invading capacity encounters a habitat in which the species experiences a longer photosynthetic season and can express an increased LAI, it tends to become invasive. Ecophysiological differences, like LAI and growing season length, between invasive *P. australis* and native *S. alterniflora* in the USA were considered to result from variations in the soil salinity of the salt marshes (Burdick et al., 2001; Gratton and Denno, 2005; Vasquez et al., 2006). In the Yangtze River estuary, the greater LAI and longer growing season of *S. alterniflora* compared with those of *P. australis* may also be associated with the soil salinity of the habitat and climatic conditions (Wang et al., 2006b).

Invasion by plants may also be achieved by the more efficient use of available resources relative to native species. Pattison et al. (1998) point out that invasive species appear to be better suited than native species to capturing and utilizing light resources. The efficient use of light is important for *Spartina alterniflora* because its stands were usually very dense and canopy shading was quite common at our site. QY, an indicator of light use efficiency, was higher in *S. alterniflora* than in *Phragmites australis* or *Scirpus mariqueter*, which was favourable for *S. alterniflora* to sequester carbon. WUE of *S. alterniflora* was also higher than were those of the other two native species. A higher WUE is essential for plants growing in salt marshes because the major effect of salt stress is water deficit (Hester et al., 2001). PNUE of *S. alterniflora* was not only higher than were those of *P. australis* and *S. mariqueter* at our site but also higher than that in its native habitats (Dai and Wiegert, 1997). The capacity of *S. alterniflora* to use light, water, and nitrogen more efficiently may help it outperform its co-occurring native species. These results also followed the theoretical patterns of plant photosynthetic types that C_4 species display higher “efficiencies” in radiation, nutrient, and water utilization than C_3 species, and hence achieve higher productivity (Sage, 2004).

TN of *Spartina alterniflora* was lower than that of *Phragmites australis* but was higher than that of *Scirpus mariqueter*, which is inconsistent with our understanding of the differences between C_4 and C_3 plants. This might correlate with leaf morphology of triangular prismatic of *S. mariqueter*. Wetland plants grown under saline conditions often develop smaller leaves (Shea et al., 1975; Hester et al., 1998). *S. mariqueter* should have high salt tolerance because it is distributed only at very low elevations near mudflats (Sun et al., 2001), which might partially benefit from its leaf shape in terms of water conservation (Van den Boogaard and Villar, 1998; Hester et al., 2001; McDowell, 2002). This kind of leaf shape results in smaller photosynthetic area and therefore less photosynthetic enzymes, which are the major existing form of leaf nitrogen.

Whereas most of the indices examined here conferred a growth advantage on *Spartina alterniflora*, SLA (other than LCP and R_{day}) seems to be disadvantageous for *S. alterniflora* in the accumulation of carbon. SLA is important in regulating plant performance, including carbon assimilation and allocation (Lambers and Poorter, 1992; Reich et al., 1997). A larger SLA can usually bring about rapid growth (Lambers and Poorter, 1992; Reich et al., 1997). However, contrary to the general relationship between invaders and native species, in this study, *S. alterniflora* had a lower SLA (or higher CC) than *Phragmites australis* and *Scirpus mariqueter*. SLA is one of the morphometric variables that influence transpiration water loss. A lower SLA (i.e., thicker leaves) increases the distance through which water must diffuse out of the leaf, and thus leads to water conservation (Van den Boogaard and Villar, 1998; McDowell, 2002). Therefore, the lower SLA of *S. alterniflora* might have contributed to its increased WUE and resulted in higher salt tolerance of *S. alterniflora* at our site (Wang et al., 2006b).

No general pattern of the relationship between invasiveness and plant photosynthetic type has been drawn until now. However, in this study, most growth-related ecophysiological advantages of the invasive *Spartina alterniflora* over the native species might be attributed to their different photosynthetic pathways. These advantages enhanced the invasion capacity of *S. alterniflora* in the Yangtze River estuary, China. Our results further our understanding of the relationship between invasiveness and plant photosynthetic type, i.e., some ecophysiological advantages resulting from different photosynthetic pathways may help to explain the success of invasion when a C_4 species invades the ecosystem dominated by C_3 species.

5. Conclusions

In the Yangtze River estuary, the invasion of *Spartina alterniflora* has changed the vegetation composition by replacing the native species. Invasive *S. alterniflora* exhibited growth-related ecophysiological advantages, including a higher A_{max}, greater LAI, longer growing season, and higher efficiency of resource utilization, which might all have contributed to its successful invasion of this region. Most of the results support the general pattern that invaders usually tend to express a high growth rate. Furthermore, most of these differences can be attributable to different photosynthetic pathways. As well as these ecophysiological characteristics associated with photosynthetic pathways, LAI and photosynthetic season length are also important in determining invasion success.

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