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Invasion of *Spartina alterniflora* Enhanced Ecosystem Carbon and Nitrogen Stocks in the Yangtze Estuary, China

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Abstract

Whether plant invasion increases ecosystem carbon (C) stocks is controversial largely due to the lack of knowledge about differences in ecophysiological properties between invasive and native species. We conducted a field experiment in which we measured ecophysiological properties to explore the response of the ecosystem C stocks to the invasion of *Spartina alterniflora* (*Spartina*) in wetlands dominated by native *Scirpus mariqueter* (*Scirpus*) and *Phragmites australis* (*Phragmites*) in the Yangtze Estuary, China. We measured growing season length, leaf area index (LAI), net photosynthetic rate (Pn), root biomass, net primary production (NPP), litter quality and litter decomposition, plant and soil C and nitrogen (N) stocks in ecosystems dominated by the three species. Our results showed that *Spartina* had a longer growing season, higher LAI, higher Pn, and greater root biomass than *Scirpus* and *Phragmites*. Net primary production (NPP) was 2.16 kg C m^{-2} y^{-1} in *Spartina* ecosystems, which was, on average, 1.44 and 0.47 kg C m^{-2} y^{-1} greater than that in *Scirpus* and *Phragmites* ecosystems, respectively. The litter decomposition rate, particularly the belowground decomposition rate, was lower for *Spartina* than *Scirpus* and *Phragmites* due to the lower litter quality of *Spartina*. The ecosystem C stock (20.94 kg m^{-2}) for *Spartina* was greater than that for *Scirpus* (17.07 kg m^{-2}), *Phragmites* (19.51 kg m^{-2}) and the mudflats (15.12 kg m^{-2}). Additionally, *Spartina* ecosystems had a significantly greater N stock (698.8 g m^{-2}) than *Scirpus* (597.1 g m^{-2}), *Phragmites* ecosystems (578.2 g m^{-2}) and the mudflats (375.1 g m^{-2}). Our results suggest that *Spartina* invasion altered ecophysiological processes, resulted in changes in NPP and litter decomposition, and ultimately led to enhanced ecosystem C and N stocks in the invaded ecosystems in comparison to the ecosystems with native species.

Key words: ecosystem C and N stocks; leaf area index; litter decomposition; net primary production; photosynthesis; plant invasion; *Spartina alterniflora*; the Yangtze Estuary.

Introduction

Biological invasion is a significant element of global change. It not only threatens biodiversity and stability of native ecosystems worldwide (Vitousek

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and others 1997; Wilcove and others 1998; Ravit and others 2003), but also potentially alters ecosystem functioning and processes (Gordon 1998; Ehrenfeld 2003; Seabloom and others 2006). The carbon (C) cycle is an important component of ecosystem functioning and processes (Chapin and others 2002; Berg and McClaugherty 2003; Luo and Zhou 2006). Numerous studies, over the last several years, have addressed the issue of whether plant invasion changes C cycling (Christian and Wilson 1999; Hibbard and others 2001; Jackson and others 2002), but the conclusions are controversial. Some have suggested that plant invasions can enhance ecosystem C stocks (Stock and others 1995; Hibbard and others 2001), whereas others have argued against it (Christian and Wilson 1999; Scott and others 2001; Jackson and others 2002). These differing results among studies impede our understanding of whether and how biological invasion influences ecosystem biogeochemical cycles.

The controversial results from previous studies are partly due to the lack of knowledge about differences in ecophysiological properties between invasive and native plant species. For example, Hibbard and others (2001) showed that the ecosystem C stock increases as woody species expand into grasslands in the subtropical savannas. However, Jackson and others (2002) suggested that the woody plant invasion into grasslands along a precipitation gradient causes ecosystem C loss. The two studies did not provide much information on ecophysiological mechanisms underlying their results. Plant and soil processes such as net primary production (NPP), and litter decomposition, are crucial for understanding the changes in the ecosystem C stock caused by shifts in plant species composition (Chapin and others 2002). Plant ecophysiological properties, such as leaf area index (LAI), net photosynthetic rate (Pn), length of growing season, root biomass, and litter quality, determine NPP and litter decomposition. Higher LAI and Pn, longer growing season, and larger root biomass will all lead to larger NPP and greater plant biomass, resulting in more organic matter input into the soil via litterfall, roots, and their exudates (Chapin and others 2002). Lower litter quality leads to a lower rate of litter decomposition, which can reduce C release from litter, and hence more litter will be incorporated into the formation of soil organic matter (Berg and McClaugherty 2003). Previous studies have shown that invasive plant species differ in ecophysiological properties (for example, Baruch and Goldstein 1999; Nieva and others 2003), NPP (for example, Windham 2001) and decomposition rate (for example, Allison and Vitousek 2004) from native species. Thus, it is necessary to explore how ecophysiological properties of invasive species affect C stocks in the invaded ecosystems.

Spartina alterniflora Loisel. (*Spartina*) is a C_4 grass, native to the Atlantic and Gulf Coasts of North America. It was intentionally introduced to China in 1979 to accelerate sedimentation and land formation via so-called ''ecological engineering'', and to the Yangtze Estuary in 1990's (Tang and Zhang 2003). Since then, *Spartina* has rapidly invaded Yangtze estuarine marshlands (Chung and others 2004; Wang and others 2006), which used to be dominated by two native species *Scirpus mariqueter* Tang et Wang (*Scirpus*) and *Phragmites australis* (Cav.) Trin. Ex Steud (*Phragmites*). Both *Scirpus* and *Phragmites* are C_3 grasses (Chen 2003). *Spartina* has different ecophysiological properties, such as growth rate, duration of growth over seasons, stem density within canopy, and LAI, from *Scirpus* and *Phragmites* (Chen 2003).

To guide this study, we hypothesized that shifts in species composition caused by *Spartina* invasion alter ecophysiological processes and consequently result in changes in ecosystem C cycles and hence changes in C stocks in the invaded ecosystems. To test this hypothesis, we measured the length of growing seasons, LAI, leaf net photosynthesis, root biomass, NPP, litter quality and litter decomposition, C stocks in plants and soils in the ecosystems dominated, respectively, by *Spartina*, *Scirpus*, and *Phragmites*. Because C and nitrogen (N) cycles interact intimately in ecosystems, we also quantified ecosystem N stocks in the three ecosystems. In addition, *Spartina* rapidly spreads in the mudflats in many places (Tang and Zhang 2003; Chung and others 2004; Neira and others 2006), and thus, we also measured soil C and N stocks in the mudflats for comparison with those in the *Spartina* ecosystems.

Materials and Methods

Study Site and Materials

We conducted this study in Jiuduansha wetlands of the Yangtze Estuary. The Jiuduansha wetlands (30°10′N, 122°01′E) (Figure 1) occupy an area of 234 km^2 at an elevation of −2 m (2 m lower than sea level) (Chen 2003). Mean annual temperature is 15.7°C, with a mean temperature of the coldest and warmest months being 4.2°C in January and 27.3°C in July, respectively. Mean annual precipitation is 1,145 mm and concentrates in the

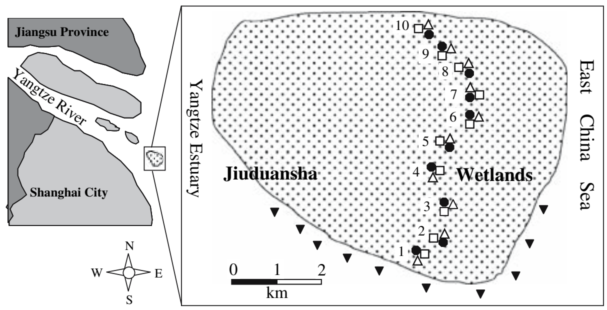

Figure 1. Locations of sampled ecosystems in Jiuduansha wetlands, the Yangtze Estuary, China. Note: *triangle*, *Spartina* (*Spartina alterniflora*) stands; *filled circle*, *Scirpus* (*Scirpus mariqueter*) stands; *square*, *Phragmites* (*Phragmites australis*) stands; *filled downward triangle*, Mudflats.

summer months. Mean annual salinity of seawater is about 11.7‰. The wetlands consist of vegetated marshlands and unvegetated mudflats. Two native plants, *Scirpus* and *Phragmites* dominated the marshlands before *Spartina* was introduced. In general, the natural community succession is rather rapid from mudflats to *Scirpus* to then *Phragmites* (Chen 2003).

Spartina was introduced into the Jiuduansha wetlands in 1997 with an initial planting area of 50 ha (Chen and others 2001). Since then, *Spartina* rapidly expanded in both *Scirpus* and *Phragmites* wetlands. By 2003, the *Spartina*-invaded marshlands covered an area of 1,080 ha (Wang and others 2006). All of the three species formed pure stands (monocultures) with clear boundaries among them. The three species are perennials with overwintering rhizomes for *Spartina* and *Phragmites*, and corm for *Scirpus*. Their ramets begin to emerge in spring, and turn senescent and die in autumn or winter.

Sampling Transects

Two transects, 3-km long, were established in the wetlands in November 2003 (Figure 1). One was in the marshlands along a transition zone from *Scirpus* to *Phragmites*, and the other in the mudflats. Ten sites were randomly selected on the marshland transect. At each site, we selected three stands, each dominated, respectively, by *Spartina*, *Scirpus* and *Phragmites* and all being close to each other and at the same elevation (Figure 1). The same elevation and the close proximity of the stands at each site were to minimize environmental heterogeneities (for example, salinity, redox potential, tidal inundation) for measurements in the estuarine wetlands (Delaune and others 1983). Most of the stands selected had an area of about 4 ha whereas a few stands had an area of less than 4 ha but larger than 1 ha. Sites 3–6 were positioned for measurements of both aboveground and belowground biomass. Sites 3–7 were also used for ecophysiological measurements such as area per leaf and the vertical pattern of root biomass. Sites 7–10 were selected for the litter decomposition experiment. Soil samples for measurements of C and N contents were taken at all ten sites. The mudflat transect was 100 m away from the edges of plant stands. Ten points were also positioned for soil sampling at 300-m intervals along the transect.

Ecophysiological Properties and Plant Biomass

Net photosynthetic rates (Pn) of newly fully expanded leaves (Baruch and Goldstein 1999) were measured monthly from April to November in 2004 with a LI-6400 and a standard Li-Cor chamber (6 cm^2) (Li-Cor Inc., Lincoln, NE, USA). Light response curves were obtained by measuring assimilation rates at different intensities of photosynthetically active radiation, from 2,500 to 0 $\mu mol\ m^{-2}\ s^{-1}$ following the operation instructions of LI-6400. We achieved the variation in light intensity by a red–blue light-emitting diode array. We made 3–5 light-response curves for each of the three stands at sampling sites 3–7. Leaf area index (LAI) was monitored monthly for each of the three types of stands at sampling sites 3–7, from April to December in 2004 by using a LI-3000A (Li-Cor Inc., Lincoln, NE, USA), and the measurements were made from 5 0.5×0.5 m quadrats for each stand at each site. Stem height, culm diameter, population density, and area per leaf were measured in 15 1×1 m quadrats in September 2004. In addition, the phenology of each species (that is, the dates to sprout, flower, seed, and senesce) was recorded.

The aboveground and belowground biomass of the three species were sampled from November 2003 to December 2004, to characterize the peak biomass and mean annual plant C and N stocks. Due to the harsh working conditions in the estuary, we sampled the aboveground biomass nine times and belowground biomass only six times. In the sampling area, we collected the aboveground biomass within three quadrats of 1×1 m. The aboveground biomass was sorted into live parts (including senescent leaves attached to culms), and dead parts (aboveground litter standing in the air and fallen on the soil surface). We further separated standing and surface litter into that produced in the current and that produced in the previous years according to litter color. The belowground biomass was sampled to a depth of 100 cm below the ground using a large steel auger with an inner diameter of 14.2 cm in each quadrat after the aboveground biomass was taken. Twelve samples for both, the aboveground (4 sites × 3 quadrats) and belowground biomasses (4 sites × 3 soil cores) were obtained from the field for each species at each time. To characterize vertical patterns, root biomass was measured in six sections (0–5, 5–20, 20–40, 40–60, 60–80, and 80–100 cm) of the soil core using a small steel auger with an inner diameter of 2 cm, in September 2004. In total, 90 samples (5 sites × 3 soil cores × 6 sections) were taken for each of the three species.

All the samples were washed in clean water immediately by sieve with a mesh size of 0.45 mm. The belowground biomass from November 2003 to December 2004 was sorted in water, by color and texture (Valiela and others 1976; Ellison and others 1986), into three parts for *Spartina* and *Phragmites* (that is, live rhizome, live root, and litter) and two parts for *Scirpus* (that is, litter and live plants including corms and roots). All the samples were oven-dried at 50°C for 10 days to constant weight, and then weighed. To determine C and N concentrations, the aboveground and belowground plant samples were ground to powder in a Wiley mill. C and N analyses were performed on the *NC Analyzer* (*FlashEA* 1112 Series, Italy). The aboveground net primary production (ANPP) was estimated by harvesting peak standing live biomass (Roman and Daiber 1984), due to the low mortality of all three species during the growing season. The belowground net primary production (BNPP) was estimated using the method proposed by Lomnicki and others (1968).

Soil Properties

As described in the sampling of root biomass with the small auger, three soil cores were taken for each of the three species at each site along the vegetated transect, and at each sampling point along the mudflat transect in September 2004. Totally, 180 soil samples (10 sites × 3 soil cores × 6 sections) were obtained from each of the four ecosystem types, and air-dried. Subsamples of 250–300 mg untreated soil for each sample were used to determine soil C and N concentrations, and the residuals were oven-dried at 80°C to constant weight to determine soil bulk density. The air-dried soil for determining soil C and N concentrations was also used to calculate soil bulk density. The method of determining total C and N concentrations of soil samples was the same as that for plant materials. Soil C content was calculated by multiplying soil C concentration by its corresponding soil bulk density. The soil C stock was calculated by summing the soil C content of each soil layer multiplied by the thickness of the soil layers down to 100 cm depth. The calculation methods for soil N concentrations and stocks were similar to those for soil C.

Litter Decomposition Rate

We used the litterbag method to quantify litter decomposition rates although this method may not be very accurate (Wieder and Lang 1982). We measured the rates of aerial decomposition (AD) of standing litter in the air, surficial decomposition (SD) of the aboveground litter that fell on the soil surface, and belowground decomposition (BD) of rhizome and root litter in soils (Liao 2007). The litterbags (20 cm × 20 cm) were made of fiberglass net (1-mm-mesh). The litterbags were hung on plastic strings at a height of 1.3 m supported by PVC pipes for aerial decomposition, placed on the soil surface for surficial decomposition, and buried below the ground at a depth of 20 cm for belowground decomposition. The decomposition rate of litter was estimated from litter mass remaining by the log linear model, which has been suggested to be superior to other models (Wieder and Lang 1982). The amount of C released during litter decomposition was estimated through multiplying the decomposition rate by its corresponding litter mass (C) which was based on the assumption that litter C concentration varied little during decomposition in our study (Luo and Zhou 2006).

Statistical Analyses

To meet the assumptions for statistical analysis, most of the data sets were log or cube root transformed before ANOVA analysis was performed. Significance at the $P < 0.05$ level for differences of measured variables among four types of ecosystems was examined by a Duncan post hoc test. One-way ANOVA was used to test observed differences in ecophysiological properties, NPP, decomposition rates, and amounts of C released during litter decomposition among the three species. One-way ANOVA was also used to test differences in soil C and N stocks among the three species and mudflats. Repeated-measures ANOVA was used to test the differences in LAI, Pn, and plant C and N stocks among the three species. Data of root biomass, soil C and N concentrations and contents along the soil depth gradient among species were analyzed with a nested design ANOVA. All statistics were performed using STATISTICA 6.0 (StatSoft, Inc. (2001), http://www.statsoft.com).

Results

Ecophysiological Properties

The three species significantly differed in many of the ecophysiological properties examined (Table 1, and Figures 2, 3). Plant N concentrations of live and dead aboveground and belowground tissues of *Spartina* were all lower than those of *Scirpus* and *Phragmites* (Table 1). The rates of aerial, surficial and belowground decomposition of *Spartina* litter were lower than the respective rates of *Scirpus* litter. Decomposition rates were lower for belowground litter but higher for aerial and surficial litter of *Spartina* than the corresponding litter types of *Phragmites*. The length of the growing season was 270 days for *Spartina*, which was 80 and 50 days longer than that for *Scirpus* and *Phragmites*, respectively ($F_{2, 8} = 241$, $P < 0.001$; Figure 2A). The mean seasonal LAI of *Spartina* stands was 4.40 $m^2\ m^{-2}$, which was higher than that of *Scirpus* (2.95 $m^2\ m^{-2}$) and *Phragmites* stands (2.11 $m^2\ m^{-2}$) ($F_{2, 11} = 159$, $P < 0.001$; Figure 2B). Mean seasonal Pn of *Spartina* was 24.44 μmol $CO_2\ m^{-2}\ s^{-1}$, which was also higher than that of *Scirpus* (6.72 μmol $CO_2\ m^{-2}\ s^{-1}$) and *Phragmites* (15.85 μmol $CO_2\ m^{-2}\ s^{-1}$) ($F_{2, 11} = 126$, $P < 0.001$; Figure 2C). Root biomass under the *Spartina* stands was significantly higher than that under either *Scirpus* or *Phragmites* stands in September 2004 ($F_{2, 270} = 101$, $P < 0.001$; Figure 3).

Plant C and N Dynamics

Mean annual total plant C stock (aboveground plus belowground) in *Spartina* stands was 2.95 kg m^{-2}, 2.53 and 0.74 kg m^{-2} greater than that in *Scirpus* and *Phragmites* stands, respectively ($F_{2, 33} = 290$, $P < 0.001$; Figure 4A–C). Mean annual total plant N stock in *Spartina* stands (46.49 g m^{-2}) was significantly greater than that in *Scirpus* stands (14.15 g m^{-2}) ($F_{1, 22} = 399$, $P < 0.001$), but not different from that in *Phragmites* stands (49.91 g m^{-2}) ($F_{1, 22} = 1.5$, $P = 0.23$) (Figure 4D–F). The allocation of mean annual total plant C stock to the belowground was lower in *Spartina* stands (71.2%) than that in *Scirpus* (82.2%) and *Phragmites* stands (79.7%) ($F_{2, 33} = 31$, $P < 0.001$). Mean annual belowground plant C stock down to a depth of 100 cm was significantly greater under *Spartina* stands (2.11 kg m^{-2}) than that under *Scirpus* (0.33 kg m^{-2}) and *Phragmites* stands (1.77 kg m^{-2}) ($F_{2, 33} = 231$, $P < 0.001$).

In September of 2004, total plant C stock of *Spartina* stands was 3.83 kg m^{-2}, being 3.28 kg m^{-2} and 0.89 kg m^{-2} greater than that of *Scirpus* and *Phragmites* stands, respectively ($F_{2, 33} = 242$, $P < 0.001$) (Table 2 and Figure 4). Total plant N stock of *Spartina* stands was 57.21 g m^{-2}, being 37.40 g m^{-2} greater than that in *Scirpus* ($F_{1, 22} = 173$, $P < 0.001$) but 15.86 g m^{-2} lower than that of *Phragmites* stands ($F_{1, 22} = 5.6$, $P < 0.03$) (Table 2 and Figure 4).

Table 1. Comparison of Properties among *Spartina*, *Scirpus* and *Phragmites*

Properties	*Spartina*	*Scirpus*	*Phragmites*
Stem height (cm) ($n = 15$)	143.3 ± 5.1^{b}	40.4 ± 1.6^{c1}	212.9 ± 19.9^{a}
Population density (ramets m^{-2}) ($n = 15$)	86 ± 7^{b}	3735 ± 349^{a}	49 ± 2^{c}
Culm diameter (cm) ($n = 15$)	1.06 ± 0.01^{a}	0.19 ± 0.01^{c2}	0.65 ± 0.01^{b}
Area per leaf (cm^2) ($n = 15$)	76.5 ± 0.7^{a}	11.7 ± 0.3^{b3}	65.6 ± 0.7^{c}
Mean live aboveground plant N (%) ($n = 12$)	1.20 ± 0.02^{c}	1.49 ± 0.02^{b}	1.64 ± 0.04^{a}
Mean dead aboveground plant N (%) ($n = 12$)	0.60 ± 0.02^{c}	1.32 ± 0.02^{a}	0.70 ± 0.02^{b}
Mean belowground plant N (%) (n = 12)	0.61 ± 0.01^{c}	1.26 ± 0.01^{a}	0.85 ± 0.03^{b}
Aerial decomposition rate[4] (y^{-1}) ($n = 4$)	0.80 ± 0.04^{b}	1.77 ± 0.12^{a}	0.57 ± 0.03^{c}
Surficial decomposition rate[4] (y^{-1}) ($n = 4$)	1.69 ± 0.05^{b}	3.40 ± 0.23^{a}	1.20 ± 0.05^{b}
Belowground decomposition rate[4] (y^{-1}) ($n = 4$)	1.15 ± 0.05^{c}	1.89 ± 0.17^{a}	1.50 ± 0.13^{b}

Data are presented as means ± 1 SE. Different letters indicate significant differences among species within the row
[1]*Culm height*
[2]*One-third of culm perimeter based on the soil surface*
[3]*Surface area of culm*
[4]*Decomposition rates of litter from Liao (2007)*

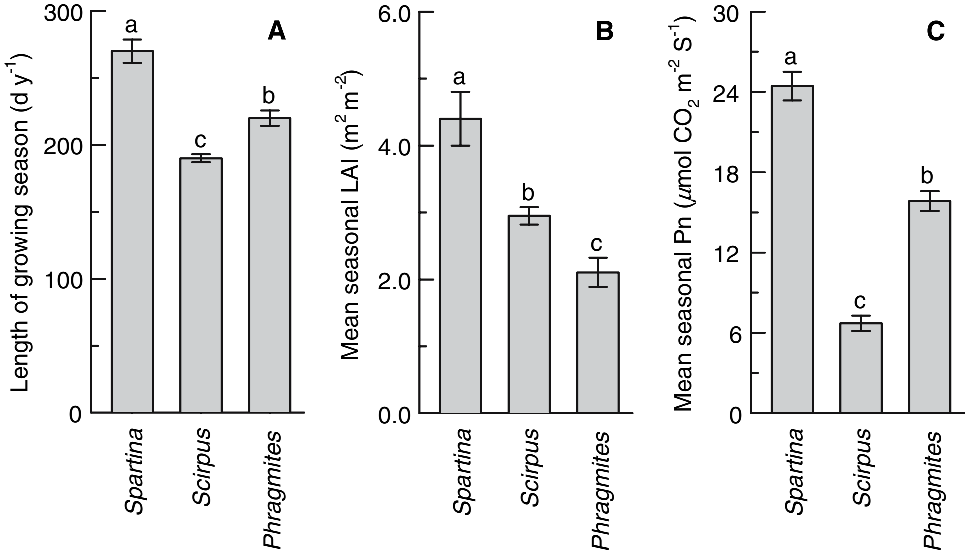

Figure 2. Comparison of growing season length (**A**), mean seasonal LAI (**B**), and mean seasonal Pn (**C**) among *Spartina*, *Scirpus* and *Phragmites* in 2004. *Bars* represent mean ± 1 Se (n = 3–5).

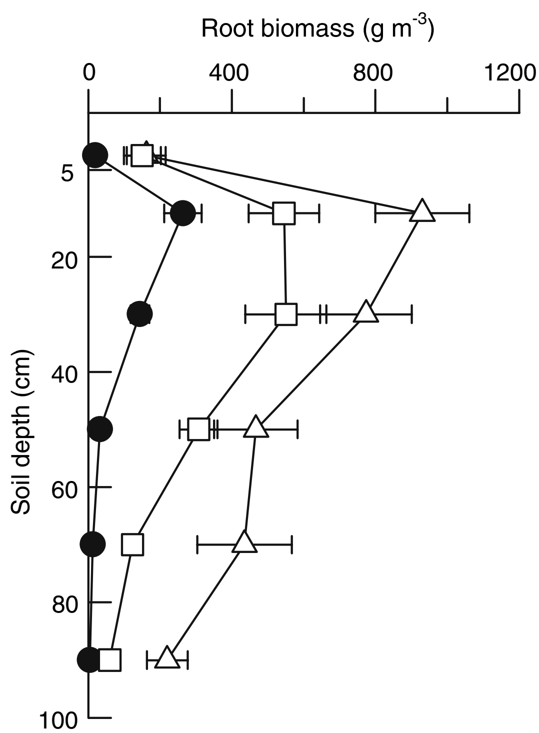

Figure 3. Distribution of root biomass in soil within a depth of 100 cm for three species in September of 2004. *Triangle, Spartina; filled circle, Scirpus; square, Phragmites. Bars* represents mean ± 1 Se (n = 15).

Ecosystem C Fluxes through NPP and Litter Decomposition

Net primary production (ANPP plus BNPP) was 2.16 kg C m^{-2} y^{-1} in *Spartina* ecosystems, which was, on average, 2 and 0.3-times higher than that in *Scirpus* and *Phragmites* ecosystems, respectively ($F_{2,\ 33}$ = 21, P < 0.001; Figure 5A). The total amount of C released during aerial (AD), surficial (SD), and belowground decomposition (BD) was 0.78 kg C m^{-2} y^{-1} from *Spartina* ecosystems, which did not differ from that of *Phragmites* ecosystems (0.76 kg C m^{-2} y^{-1}) ($F_{1,\ 22}$ = 0.3, P = 0.59) but was greater than that of *Scirpus* ecosystems (0.51 kg C m^{-2} y^{-1}) ($F_{1,\ 22}$ = 33, P < 0.001; (Figure 5B). As a result, the net carbon balance between NPP and decomposition (1.39 kg C m^{-2} y^{-1}) in *Spartina* ecosystems was greater than that in *Scirpus* (0.21 kg C m^{-2} y^{-1}) and *Phragmites* ecosystems (0.93 kg C m^{-2} y^{-1}), respectively ($F_{2,\ 33}$ = 16, P < 0.001).

C and N in the Soil

In September of 2004, soil total C concentration was, on average, 14.93 g C kg^{-1} dry soil down to a depth of 100 cm under *Spartina* stands being 0.85, 0.94, and 3.30 g C kg^{-1} higher than that under *Scirpus* and *Phragmites* stands ($F_{2,\ 495}$ = 76, P < 0.001), and in mudflats ($F_{1,\ 348}$ = 406, P < 0.001), respectively (Figure 6A). As a result, the soil total C stock was 17.11 kg m^{-2} within a depth of 100 cm under *Spartina* stands, which was 0.59, 0.54, and 1.99 kg m^{-2} greater than that under *Scirpus* and *Phragmites* stands ($F_{2,\ 60}$ = 6.2, P < 0.01) and in mudflats ($F_{1,\ 58}$ = 66, P < 0.001), respectively (Table 2). Similarly, soil total N concentrations, and N contents and N stocks were statistically greater under *Spartina* stands than those under *Scirpus* and *Phragmites* stands and in

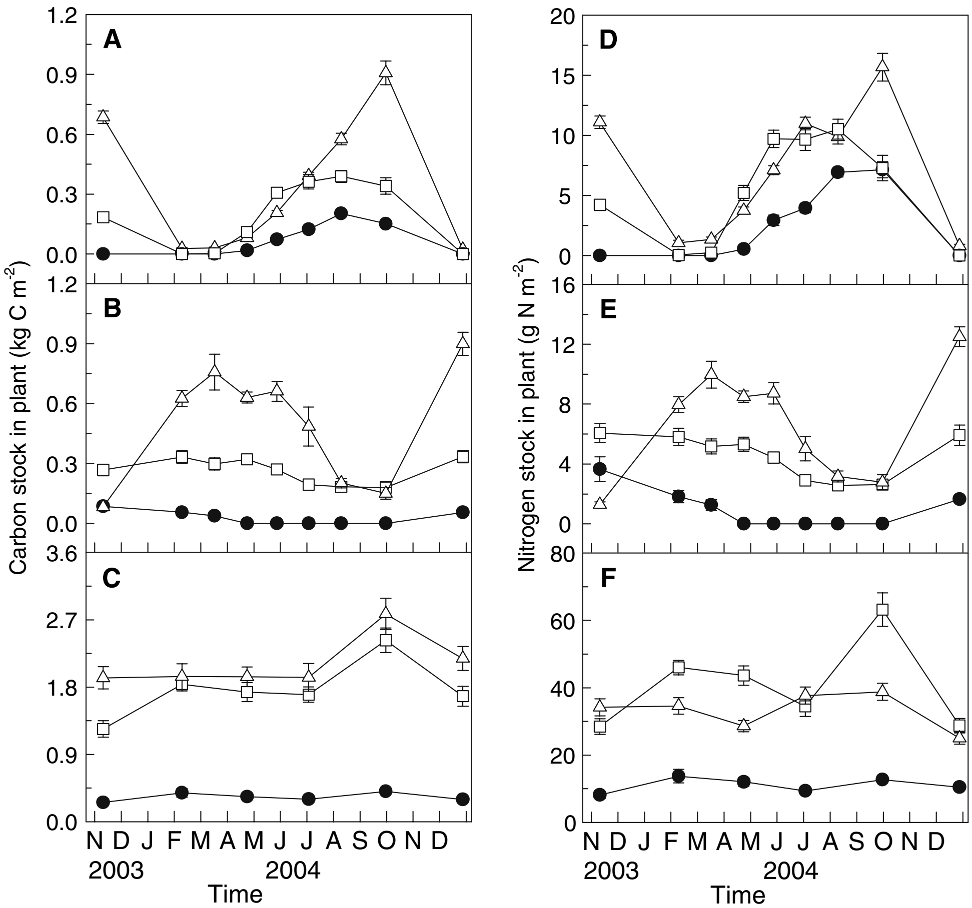

Figure 4. Seasonal variation of C and N stocks in live aboveground plant (**A**, **D**), dead aboveground plant (**B**, **E**), and total belowground plant biomass (**C**, **F**) for *Spartina*, *Scirpus* and *Phragmites* from November 2003 to December 2004, respectively. *Triangle*, *Spartina*; *filled circle*, *Scirpus*; *square*, *Phragmites*. *Bars* represent mean ± 1 Se (n = 12).

Table 2. Carbon and Nitrogen Stocks and Total Net Changes of C and N Stocks after *Spartina* Invasion, Calculated Using Data Collected in September 2004

Type	Mudflats C stock (kg m^{-2})	*Scirpus*	*Phragmites*	*Spartina*	Mudflats → *Spartina* Net C change (kg m^{-2})	*Scirpus* → *Spartina*	*Phragmites* → *Spartina*
Plant[1]	0	0.56	2.94	3.83	3.83	3.28	0.89
Soil[2]	15.12	16.51	16.57	17.11	1.99	0.59	0.54
Total	15.12	17.07	19.51	20.94	5.82	3.87	1.43
Type	**Mudflats N stock (g m^{-2})**	*Scirpus*	*Phragmites*	*Spartina*	**Mudflats → *Spartina* Net N change (g m^{-2})**	*Scirpus* → *Spartina*	*Phragmites* → *Spartina*
Plant[1]	0	19.8	73.1	57.2	57.2	37.4	−15.9
Soil[2]	375.1	577.3	505.1	641.6	266.5	64.4	136.6
Total	375.1	597.1	578.2	698.8	323.7	101.8	120.7

[1]*Belowground plant C and N stocks were up to a depth of 100 cm*
[2]*Soil C and N stocks were up to a depth of 100 cm*

mudflats (for all $P < 0.001$; Figure 6B, D). Total soil N stock was 641.62 g m^{-2} in *Spartina* ecosystems, which was 64.37, 136.55 and 266.46 g m^{-2} greater than that in *Scirpus*, *Phragmites* ecosystems, and mudflats, respectively (for all $P < 0.001$; Table 2).

Consequently, total ecosystem C stock, which is a sum of plant and soil C stocks, in September of 2004 was 20.94 kg m^{-2} in *Spartina* stands, 3.87, being 1.43, and 5.82 kg m^{-2} greater than that in *Scirpus* and *Phragmites* stands and mudflats,

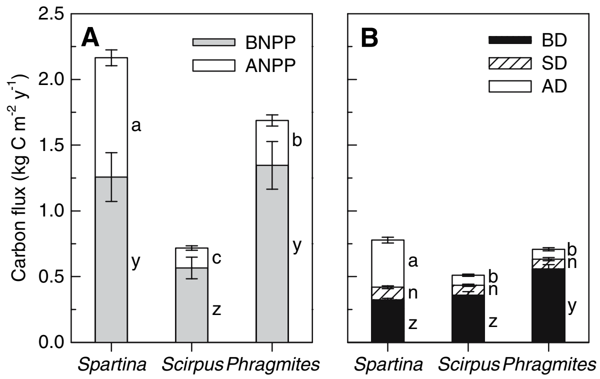

Figure 5. Carbon input by NPP (**A**) and release through litter decomposition (**B**) for *Spartina*, *Scirpus* and *Phragmites* ecosystems. Different letters of *a*, *b* and *c* indicate significant differences in aboveground *ANPP* and aerial decomposition (*AD*) among the three species; *y* and *z* indicate significant differences in *BNPP* and belowground decomposition (*BD*); and the letter *n* indicates no significant difference in surficial decomposition (*SD*). *Bars* represent mean ± 1 Se (*n* = 12).

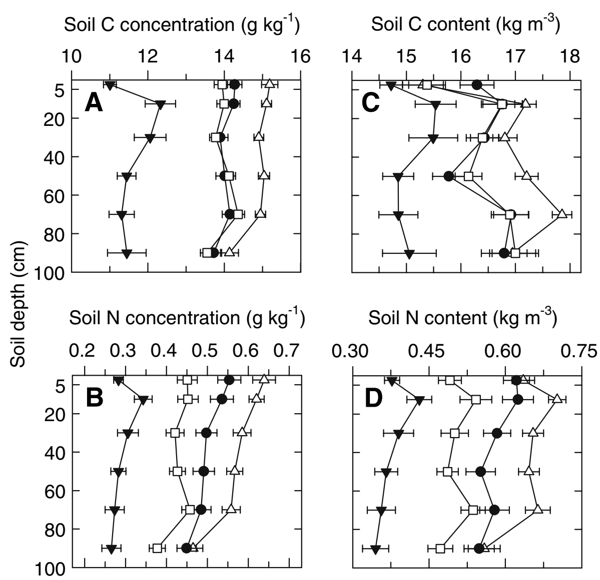

Figure 6. Performances of soil total C and N concentrations (**A**, **B**), and soil total C and N contents (**C**, **D**) within a depth of 100 cm under *Spartina*, *Scirpus* and *Phragmites* stands, and in mudflats in September of 2004. *Triangle*, *Spartina*; *filled circle*, *Scirpus*; *square*, *Phragmites*; *filled downward triangle*, Mudflats. *Bars* represent mean ± 1 Se (*n* = 30).

respectively (Table 2). Similarly, total ecosystem N stock in *Spartina* stands was 698.83 g m^{-2}, being 101.70, 120.60, and 323.70 g m^{-2} greater than that in *Scirpus* and *Phragmites* stands, and mudflats, respectively.

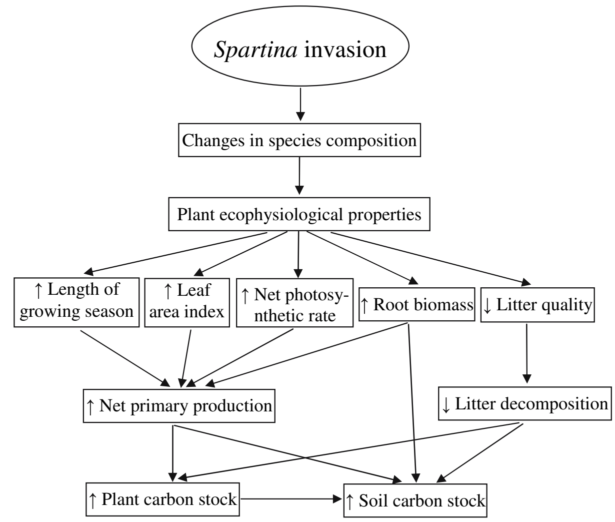

Figure 7. The pattern of the effects of *Spartina* invasion on ecosystem C stocks. Note: *up-arrow*, increase in response to *Spartina* invasion; *down-arrow*, decrease in response to *Spartina* invasion.

Discussion

Our study demonstrated that through the shift in plant species composition in invaded ecosystems, *Spartina* invasion instigated a suite of changes in ecophysiological properties, stimulated NPP, and decreased litter decomposition, and ultimately resulted in net accumulation in ecosystem C and N stocks (Figure 7). Ecophysiological properties are determinant drivers in regulating carbon input into plant and soil pools (Chapin and others 2002). For example, *Spartina* ramets began to grow earlier, and senesced later than *Scirpus* and *Phragmites*. All else being equal, species with longer growing seasons can synthesize more atmospheric CO_2 into carbohydrate by leaves through photosynthesis, and thus increase plant production.

Leaf area index (LAI) and Pn are important ecophysiological parameters that determine plant growth and NPP. To be successful competitors, plant species often have the potential to produce high LAI for harvesting light (Ehrenfeld 2003; Allison and Vitousek 2004; Reinhart and others 2006), and therefore, enhancing CO_2 assimilation per unit time and per unit area. Our results indicate that *Spartina* stands had higher mean seasonal LAI than both *Scirpus* and *Phragmites* stands (Figure 2B). In addition, *Spartina* is a C_4 grass whereas *Scirpus* and *Phragmites* are C_3 plants. C_4 grasses generally have higher Pn than C_3 grasses (Zhou and others 2007), which is consistent with our result that *Spartina* had higher mean seasonal Pn than *Scirpus* and *Phragmites* (Figure 2C). Our result is also supported by the study of Baruch and Goldstein (1999), in which the average P_n of 30 invasive species was found to be higher than that of 34 native species in Hawaii, independent of photosynthetic pathways. Consequently, the combination of a longer growing season, greater mean seasonal LAI, and higher mean seasonal Pn resulted in greater NPP for *Spartina* ecosystems than *Scirpus*, and *Phragmites* ecosystems in Jiuduansha wetlands.

In comparison with *Scirpus* and *Phragmites* ecosystems, increased production and decreased decomposition (Table 1) resulted in much higher soil C and N stocks under *Spartina* stands than those in the mudflats (Table 2 and Figure 6). The lower plant N concentration belowground (Table 1) could result in more soil humus accumulation due to the lower decomposition rate of belowground litter. Other studies have also shown that increases in NPP and decreases in litter decomposition rate can stimulate ecosystem C accumulation (Knops and Tilman 2000; Schuur and others 2001; O'Connell and others 2003; Silver and others 2004). Our observed enhancement in ecosystem C stock in *Spartina* ecosystems relative to *Scirpus* and *Phragmites* ecosystems was also supported by a study from Cheng and others (2006) in the same wetlands. In their study, the δ^{13}C analysis suggests that the C fraction contributed by *Spartina* to the soil organic C pool varies from 0.90 to 10.64% in the top 100-cm layer, with a greater contribution from the layer between 20 and 40 cm, when *Spartina* is compared to *Scirpus* in Jiuduansha wetlands. In our study, the percentage of net C change in soils from *Scirpus* (16.51 kg C m^{-2}) to *Spartina* (17.11 kg C m^{-2}) was on average 3.6% (Table 2), which falls within the range given by Cheng and others (2006).

When *Scirpus* and *Phragmites* ecosystems were invaded by *Spartina*, the soil total N stock increased (Figure 6), most likely due to epiphytic N fixation. Epiphytic N fixation occurs in *Spartina* stems and sheath litter (Currin and Paerl 1998). In our study, estimated exogenous N input via epiphytic N_2 fixation into standing stems and sheath litter reached at least 4.8 g N m^{-2} y^{-1} during aerial decomposition of *Spartina* in the field (Liao 2007). This amount was higher than that estimated (2.6 g N m^{-2} y^{-1}) in a previous study in *Spartina*'s native habitats in North Carolina, USA (Currin and Paerl 1998). This difference may be attributed partially to the higher aboveground biomass of *Spartina* in Jiuduansha wetlands than in its native habitats.

Table 3. Comparison of *Spartina* and *Phragmites* Performance Grown in China and the USA

	This study	Other studies	Locations	Cited
ANPP (kg m^{-2} y^{-1})				
Spartina	2.21	1.49	Delaware (N)	Roman and Daiber (1984)
Phragmites	0.95	2.94	Delaware (I)	
BNPP (kg m^{-2} y^{-1})				
Spartina	2.33	6.50	Delaware (N)	Roman and Daiber (1984) (soil depth of 35 cm)
Phragmites	2.66	5.80	Delaware (I)	
Peak total live biomass (kg m^{-2})				
Spartina	8.47	1.31	New Jersey (N)	Windham and others (2003) (soil depth of 30 cm)
Phragmites	5.79	2.34	New Jersey (I)	
Peak live aboveground biomass (kg m^{-2})				
Spartina	2.21	1.07	Delaware (N)	Gratton and Denno (2005)
Phragmites	0.95	2.27	Delaware (I)	
Leaf N concentration (% of mass)				
Spartina	1.40	1.47	Delaware (N)	Gratton and Denno (2005)
Phragmites	1.46	2.59	Delaware (I)	
Surficial litter decomposition rate (y^{-1})				
Phragmites	1.20	0.25	New Jersey (I)	Windham (2001)
Soil total C concentration (% of mass)				
Spartina	1.49	5.09	Delaware (N)	Gratton and Denno (2005) (soil depth of 5 cm)
Phragmites	1.39	3.86	Delaware (I)	
Soil total N concentration (% of mass)				
Spartina	0.06	0.46	Delaware (N)	Gratton and Denno (2005) (soil depth of 5 cm)
Phragmites	0.04	0.35	Delaware (I)	

N = native species; I = invasive species

Fixed N during litter decomposition can be incorporated into soil organic matter and then increase soil total N stocks (Knops and others 2002). The amount of additional N input into ecosystems by epiphytic N fixation is substantial in comparison with rhizospheric N_2-fixation and other N influxes for *Spartina* (Patriquin and Denike 1978; Currin and Paerl 1998). Conversely, N-content did not increase during decomposition of *Scirpus* and *Phragmites* litter, indicating minimal epiphytic N-fixation in the two ecosystems.

Compared to both *Scirpus* and *Phragmites* ecosystems, the relative increase in the total plant C stock was higher than that in the soil C stock for *Spartina* ecosystems in September of 2004, showing that *Spartina* invasion had a larger impact on plant than soil C stocks. Conversely, the relative increase in the total plant N stock was lower than that in the soil total N stock for *Spartina*, showing that *Spartina* invasion also had a greater impact on soil than plant N stock. The total plant N stock was higher for *Spartina* than for *Scirpus*, but it did not differ between *Spartina* and *Phragmites*. *Spartina* had the largest aboveground litter N stock among the three species (Figure 4E) due to epiphytic N fixation during aerial decomposition. *Spartina* stands covered an area of 4,553 ha (21.4% of total area) in the Yangtze estuarine wetlands (Huang and others 2005) by 2003, and 1.12×10^5 ha on the east coast of China by 2002 (Wang and others 2006). *Spartina* is still spreading rapidly on the east coast of China (Tang and Zhang 2003; Wang and others 2006).

Interestingly, *Phragmites* is an aggressive species that has rapidly invaded *Spartina* marshlands on the east coast of the USA (Windham and others 2003; Gratton and Denno 2005). By comparing the performances of *Spartina* and *Phragmites* grown in China and the USA (Table 3) (Liao 2007), we found that there were distinctive differences in many characteristics. For example, *Phragmites* ecosystems had higher NPP, higher leaf N concentrations, and lower surficial decomposition rates in the USA than those in China. At the same time, *Phragmites* ecosystems also had higher ANPP, peak live aboveground biomass, peak live total biomass, and higher leaf N concentration, but lower soil total C and N concentrations than the native *Spartina* ecosystems in the USA. However, the soil C and N levels were lower in China than in the USA for both *Spartina* and *Phragmites* stands. Those contrasting changes indicate that more information about ecophysiological properties is needed to draw a general conclusion on effects of plant invasion on ecosystem C and N cycles.

In conclusion, the invasive *Spartina* has a number of ecophysiological properties, for example, a longer growing season, higher LAI, higher Pn, greater root biomass, and lower plant N concentration, which enhance carbon assimilation into plants and soils relative to the two native species, *Scirpus* and *Phragmites*. Ecosystem C and N stocks are substantially greater in *Spartina*-invaded ecosystems than those in the native ecosystems. All of these changes in ecophysiological properties, NPP, litter decomposition, and plant and soil C and N stocks suggest that *Spartina* invasion alters ecosystem functioning and processes in the east coastal wetlands of China.

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