

Short-term C₄ plant *Spartina alterniflora* invasions change the soil carbon in C₃ plant-dominated tidal wetlands on a growing estuarine Island

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Abstract

Spartina alterniflora is an invasive C₄ perennial grass, native to North America, and has spread rapidly along the east coast of China since its introduction in 1979. Since its intentional introduction to the Jiuduansha Island in the Yangtze River estuary, *Spartina alterniflora* community has become one of the dominant vegetation types. We investigated the soil carbon in the *Spartina alterniflora* community and compared it with that of the native C₃ *Scirpus mariqueter* community by measuring total soil carbon (TC), soil organic carbon (SOC), total soil nitrogen (TN), and the stable carbon isotope composition ($\delta^{13}\text{C}$) of various fractions. TC and SOC were significantly higher in *Spartina alterniflora* in the top 60 cm of soil. However, there was no significant difference in soil inorganic carbon (IC) between the two communities. Stable carbon isotopic analysis suggests that the fraction of SOC pool contributed by *Spartina alterniflora* varied from 0.90% to 10.64% at a soil depth of 0–100 cm with a greater percentage between 20 and 40 cm deep soils. The $\delta^{13}\text{C}$ decreased with increasing soil depth in both communities, but the difference in $\delta^{13}\text{C}$ among layers of the top 60 cm soil was significant ($p < 0.05$), while that for the deeper soil layers (>60 cm) was not detected statistically. The changes in $\delta^{13}\text{C}$ with depth appeared to be associated with the small contribution of residues from *Spartina alterniflora* at greater soil depth that was directly related to the vertical root distribution of the species.

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1. Introduction

Soil is a major reservoir for carbon in terrestrial ecosystems. This carbon is derived almost exclusively from the residue of plants growing on the site. The differences in soil carbon after a shift in the dominance of plant community are therefore expected (Bernoux et al., 1998; Chiang et al., 2004). The changes in species composition may alter ecosystem structure (e.g., vertical root profile) and processes (e.g., nutrient cycling, carbon allocation)

(Ehrenfeld, 2001; Windham and Ehrenfeld, 2003), suggesting that soil carbon pools may consequently be changed. In many parts of the world, invasions of exotic species are recognized as a serious threat to native ecosystems (e.g., their biodiversity and functioning) (Lövel, 1997; Lonsdale, 1999). In particular, ecosystem production and the inputs of organic matter into the soil may be dramatically affected by invasive exotic plants if the production processes of the exotic species are different from those of native ecosystems (Ehrenfeld, 2001; Windham and Ehrenfeld, 2003). Thus, relating the invasion processes to ecosystem functioning in time and space is of great importance to ecology (Kriwoken and Hedge, 2000; Windham and Ehrenfeld, 2003).

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In 1979, *Spartina alterniflora* was transplanted into tidal marshes of coastal China from its native range, the USA (Qin and Zhong, 1992). While its rapid growth has greatly helped stabilize the tidal flats, the negative impacts to native ecosystems have also been significant (Thompson, 1991; Qin and Zhong, 1992; Daehler and Strong, 1997; Peng and Xiang, 1999; Bruno, 2000). In the Yangtze River estuary, there are several estuarine islands that were formed from large quantities of suspended sediments from the Yangtze River. These alluvial islands (e.g., Changxing, Chongming, Hengsha, and Jiuduansha) grow rapidly and provide critical habitats for many plants and animals (Fig. 1). Of them, Jiuduansha Island is the youngest one which became visible in 1954, had an area of 425 km² in 2003 and still continues to grow at approximate 70 m per year in radius (Chen, 2003). Native *Scirpus mariqueter* (a C₃ plant) has been the dominant species for over 30 years, while invasive *Spartina alterniflora* (a C₄ plant) was transplanted to Jiuduansha Island in 1997 under the Green Recovery for Biological Conservation program project in China (Chen, 2003). Because of its great seed production and germination rate on, *Spartina alterniflora* has rapidly spread on the island, and is replacing native species (Callaway and Josselyn, 1992; Bagwell and Lovell, 2000; Silliman and Zieman, 2001). Scientific explorations of various bio- and physical-changes and characteristics with the invasions are clearly needed to control or manage the invasive species on these islands. In this study, we focus specifically and rapid vegetative propagation the impact of C₄ plant *Spartina alterniflora* invasions on the soil carbon in C₃ plant-dominated tidal wetlands.

Partitioning carbon contributions from different species to the soil carbon is challenging. Among the numerous methods, the carbon isotopic technique based on the difference in stable carbon isotope composition ($\delta^{13}\text{C}$) ratios between older soil carbon and inputs of new carbon appears promising. This technique studies soil carbon dynamics over a few years or several 100 years, and the results can help to understand the consequences of human-

induced land-use change (Bernoux et al., 1998; Hobbie et al., 2004). When species composition of vegetation changes from plants with a C₃ photosynthetic pathway to those with a C₄ pathway, or vice versa, changes in $\delta^{13}\text{C}$ in soil organic matter (SOM) over time can be used to identify sources of organic carbon in soil. Plants with a C₃ pathway have $\delta^{13}\text{C}$ values in the range of -35‰ to -20‰ ; those with a C₄ pathway have higher $\delta^{13}\text{C}$ values, ranging from -19‰ to -9‰ (O'Leary, 1988; Bernoux et al., 1998; Nyberg et al., 2000; Staddon, 2004). When one type of vegetation is replaced with another, $\delta^{13}\text{C}$ values can be used to identify SOM derived from residues in the native vegetation and the new vegetation. Several studies have shown the value of using stable isotopes to monitor the influence of vegetation changes on soil C dynamics (e.g., Boutton, 1996; Staddon, 2004). The isotopic signature of soil C reflects the relative contribution of C₃ and C₄ production to soil C accumulation, and integrates the species' contributions over long time periods (Boutton, 1996; Diels et al., 2001; Biedenbender et al., 2004). A natural abundance of $\delta^{13}\text{C}$ has been used to describe the dynamics of shifting forest-savanna boundaries (Mariotti and Peterschmitt, 1994; Nyberg et al., 2000), and to analyze the effects of young C₃ trees planted on C₄-dominated grasslands on SOM (Nyberg and Högberg, 1995; Nyberg et al., 2000). Therefore, the characteristics of the $\delta^{13}\text{C}$ of the vegetation serve as a marker to indicate the origin of SOM (Chiang et al., 2004). However, few attempts have been made to assess the effects of invasive plants on SOC in tidal salt marshes.

Here, we hypothesized that the invasive C₄ *Spartina alterniflora* in the Jiuduansha tidal wetlands would significantly change soil organic C distribution because it is different from native C₃ plant in several aspects (e.g., productivity, tissue chemistry, and plant morphology). Salt marshes on Jiuduansha provided an ideal model system where plant communities are experiencing a rapid succession, and where native C₃ plants are replaced by invasive C₄ plants. The major purpose of this study was to quantify

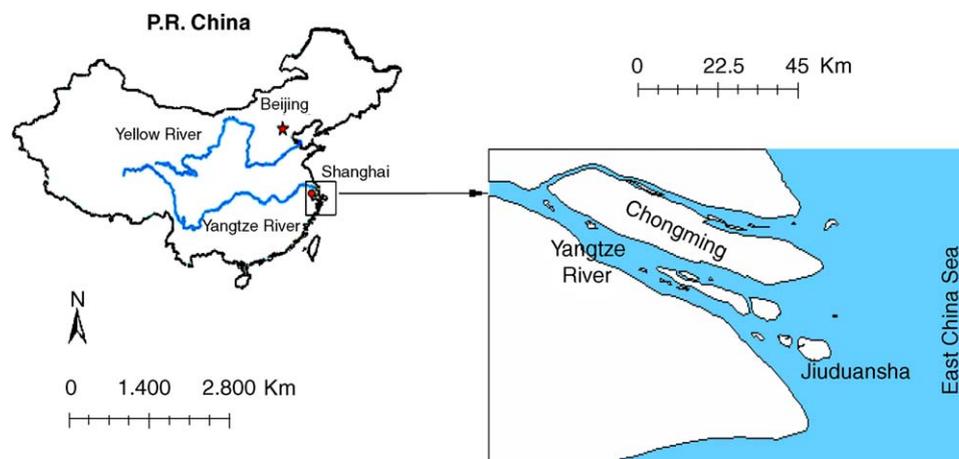


Fig. 1. Location of Jiuduansha Island, an estuarine island formed from deposits of suspended sediments from the Yangtze River in coastal Shanghai, PR China.

the soil C of a 7-year C_4 plant community (*Spartina alterniflora*) and a 30-year C_3 plant community (*Scirpus mariqueter*). Measurements of stable carbon isotopic composition, carbon concentration and nitrogen concentration in the soil down to a depth of 100 cm in the two communities allowed us to estimate the proportion of soil organic carbon (SOC) derived from *Spartina alterniflora*. We collected litter, root, and plant samples, and analyzed them for carbon concentration, nitrogen concentration, and isotopic composition with the goal to better understand the influence of invasive species C_4 plants on soil C.

2. Materials and methods

2.1. Study area

This study was conducted at Shanghai Jiuduansha Wetland Nature Reserve in the Yangtze River estuary (31°03′–31°17′N, and 121°46′–122°15′E) (Fig. 1). The climate is characterized by an annual precipitation of 1145 mm and a mean temperature of 15.7 °C, with monthly means of 36.6 °C for July and –7.7 °C for January. Jiuduansha has been developed as a stable island over a half century. The vegetation on the island consists of few species, and the structure of the plant community is relatively simple. The native species, *Scirpus mariqueter*, dominates the salt marshes on this island, in which *Spartina alterniflora* was introduced in 1997 (Chen, 2003).

2.2. Field sample collection

In October 2004, we collected samples of soils, leaves, litters, and roots from *Spartina alterniflora* and *Scirpus mariqueter* communities. Samples of soils were analyzed for total soil carbon (TC), total soil nitrogen (TN), SOC, and stable carbon isotopic composition ($\delta^{13}C$) of SOC, while samples of leaves, litters, and roots were analyzed for TC, TN and $\delta^{13}C$. Two transects were placed along a transitional zone from *Spartina alterniflora* to *Scirpus mariqueter*, each of which measured 50 m wide and 200 m long. Six 2 × 2 m² sampling plots were randomly positioned along each transect. Six replicates of plant leaves, roots, and litters were collected in each plot. We sampled newly produced leaves, litters, and roots in each plot (Lin et al., 1999). To minimize sampling error, each replicate was taken from several separate plants in each plot at each sampling time. Soil sampling was taken to a depth of 100 cm in the randomly assigned plots along each transect, using a 2.3-cm diameter stainless steel soil sampler. These soil samples were separated by depths at 0–5, 5–20, 20–40, 40–60, 60–80, and 80–100 cm for each plot. Several soil samples (up to 6) were taken in each plot, and soil from the same layer from the same plot was combined. All samples, including soil, leaves, roots, and litter, were immediately stored and sealed in glass vials and kept on ice in coolers, immediately transported to laboratory at Fudan University, and frozen at 5 °C before analysis.

2.3. Laboratory analyses

Soil samples were first physically cleaned of obvious plant materials with forceps, and then samples of leaves, roots, litter, and the soil were dried at 50 °C to constant weight and ground to pass through 20-mesh sieves (Lin et al., 1999; Chiang et al., 2004). An aliquot (about 10 g) of dried soil was treated with 1 N HCL for 24 h at room temperature to remove any inorganic carbon (IC), and the unhydrolyzed residue was categorized as SOC (Lin et al., 1999). Approximately 20 mg of leaves, roots, and litter subsamples were weighed and analyzed for TN and TC of plant materials. Non-HCL-treated soil subsamples (about 50 mg) were weighed and analyzed for soil TN and TC, while HCL-treated soil (about 50 mg) was weighed and analyzed for SOC. All these measurements were analyzed on a NC Soil Analyzer (Flash, EA, 1112 Series, Italy) based on the protocol developed in the lab (Fudan University, Shanghai, China). Precision for C and N measurements were ±5.4% and ±0.5%, respectively. The carbon isotope ratio of organic materials (leaves, roots, litter and HCL-treated soil) was measured on an isotope ratio mass spectrometer (Thermo Finnigan, Delta-Plus, Flash, EA, 1112 Series, USA). Urea and glycine were analyzed as accuracy and precision standards for isotopic ratios. Precision for $\delta^{13}C$ were ±0.15‰ based on repeated measurements of a lab working standard (Institute of Botany, Chinese Academy of Sciences, Beijing, China). The $\delta^{13}C$ of the organic matter was calculated from:

$$\delta^{13}C = [R_{\text{sample}}/R_{\text{PDB}} - 1] \times 1000, \quad (1)$$

where $R = {}^{13}C/{}^{12}C$. Pee Dee Belemnite (PDB) is the belemnite carbonate standard of the Peedee Formation in South Carolina, USA (Desjardins et al., 1996; Wooller et al., 2003; Chiang et al., 2004).

2.4. Calculation of carbon inputs

The proportion (f) of *Spartina alterniflora*-derived C in the soil requires knowledge of (1) the $\delta^{13}C$ of the soil after transplantation of *Spartina alterniflora* ($\delta^{13}C_{\text{new}}$), (2) the $\delta^{13}C$ of the soil before transplantation of *Spartina alterniflora* ($\delta^{13}C_{\text{old}}$), and (3) the $\delta^{13}C$ of *Spartina alterniflora* plant material entering the soil ($\delta^{13}C_{\text{mix}}$) (Chiang et al., 2004; Hansen et al., 2004):

$$\delta^{13}C_{\text{new}} = \delta^{13}C_{\text{mix}} \times f + \delta^{13}C_{\text{old}} \times (1 - f), \quad (2)$$

where $\delta^{13}C_{\text{mix}}$ is the mean $\delta^{13}C$ of *Spartina alterniflora* plant materials entering the soil, which is the mean value of litters, rhizomes, and roots from *Spartina alterniflora*; $\delta^{13}C_{\text{new}}$ is the mean $\delta^{13}C$ of the SOC in *Spartina alterniflora* community; $\delta^{13}C_{\text{old}}$ is the mean $\delta^{13}C$ of the SOC in *Scirpus mariqueter* community; f is the proportion of carbon from C_4 *Spartina alterniflora*, (1– f) is the proportion of carbon from *Scirpus mariqueter*. Eq. (2)

can be solved for f , yielding:

$$f = \frac{\delta^{13}C_{\text{new}} - \delta^{13}C_{\text{old}}}{\delta^{13}C_{\text{mix}} - \delta^{13}C_{\text{old}}} \times 100\%. \quad (3)$$

Because $\delta^{13}C_{\text{mix}}$, $\delta^{13}C_{\text{new}}$, and $\delta^{13}C_{\text{old}}$ are independently measured, the standard errors (SE) of f associated with the use of the mass-balance approach can be calculated using partial derivatives (Taylor, 1982; Phillips and Gregg, 2001) as

$$\sigma_f^2 = \left(\frac{\partial f}{\partial \delta_{\text{mix}}}\right)^2 \sigma_{\delta_{\text{mix}}}^2 + \left(\frac{\partial f}{\partial \delta_{\text{new}}}\right)^2 \sigma_{\delta_{\text{new}}}^2 + \left(\frac{\partial f}{\partial \delta_{\text{old}}}\right)^2 \sigma_{\delta_{\text{old}}}^2. \quad (4)$$

This can be reduced to:

$$\sigma_f^2 = \frac{1}{(\delta_{\text{new}} - \delta_{\text{old}})^2} [\sigma_{\delta_{\text{mix}}}^2 + f^2 \sigma_{\delta_{\text{new}}}^2 + (1-f)^2 \sigma_{\delta_{\text{old}}}^2], \quad (5)$$

where $\sigma_{\delta_{\text{mix}}}^2$, $\sigma_{\delta_{\text{new}}}^2$ and $\sigma_{\delta_{\text{old}}}^2$ represent variances of the mean $\delta^{13}C_{\text{mix}}$, $\delta^{13}C_{\text{new}}$, and $\delta^{13}C_{\text{old}}$, respectively. The σ_f is the SE of the proportion (f) estimate (Phillips and Gregg, 2001).

2.5. Statistical analyses

Subtracting SOC from TC on statistically paired samples allows us to obtain an estimate of soil IC. TC, SOC, IC, and TN concentrations and $\delta^{13}C$ in SOC of each soil layer were averaged over six soil samples. Two-way ANOVA was performed to examine the differences in TC, IC, SOC, TN, and $\delta^{13}C$ in SOC between the two communities in relation to soil depth. The t -tests were further employed to compare the difference in TC, IC, SOC, TN, and $\delta^{13}C$ in SOC at the same soil layer between the two communities. One-way ANOVA was used to examine the variation in TC, IC, SOC, TN and $\delta^{13}C$ in SOC with soil depth within

each community. TN and TC values of plant materials (leaf, litter and root) on statistically paired samples were used to obtain C:N ratios. $\delta^{13}C$ and C:N ratio of plant materials were averaged over six replicates. t -test was used to examine the difference in $\delta^{13}C$ and C:N ratio of plant materials between two species.

3. Results

TC and SOC of *Spartina alterniflora* community were generally higher than those of *Scirpus mariqueter* community (Table 1), except at deeper layers (>60 cm, $P>0.05$) (Table 1), and TN of *Spartina alterniflora* community was also relatively higher than that of *Scirpus mariqueter* community at all soil layers (Table 1). TC and SOC concentrations of surface soil (0–5 cm) in both communities were, respectively, relatively low and high at the soil depth of 20–60 cm, and then decreased with soil depth from 60 to 100 cm (Table 1). TN did not change with depth in either of soil profiles (Table 1). IC of *Spartina alterniflora*

Table 2

Stable carbon isotopic composition ($\delta^{13}C$) and C:N ratio of C_3 and C_4 plants in Jiuduansha wetlands in the Yangtze River estuary, China

Species		$\delta^{13}C$ (‰)	C:N ratio
<i>Spartina alterniflora</i> (C_4)	Leave	-12.8 ± 0.3^a	32.7 ± 1.8^a
	Litter	-13.4 ± 0.3^a	34.9 ± 2.5^a
	Root	-13.1 ± 0.3^a	32.1 ± 0.8^a
<i>Scirpus mariqueter</i> (C_3)	Leave	-26.7 ± 0.3^b	26.3 ± 2.7^b
	Litter	-27.9 ± 0.3^b	31.7 ± 1.6^b
	Root	-26.6 ± 0.2^b	27.2 ± 1.1^b

Values are mean ($n=6$) with standard error. The superscript letters indicate significant differences between two species (t -test, $P<0.05$).

Table 1

Soil carbon and nitrogen of *Spartina alterniflora* and *Scirpus mariqueter* communities in Jiuduansha wetlands in the Yangtze River estuary, China

Community	Depth (cm)	TC % (g 100 g ⁻¹)	IC % (g 100 g ⁻¹)	SOC % (g 100 g ⁻¹)	TN % (g 100 g ⁻¹)
<i>Spartina alterniflora</i>	0–5	1.33 ^a	0.87 ^a	0.46 ^a	0.040 ^a
	5–20	1.39 ^a	0.82 ^a	0.57 ^a	0.047 ^a
	20–40	1.47 ^a	0.91 ^a	0.56 ^a	0.048 ^a
	40–60	1.33 ^a	0.81 ^a	0.52 ^a	0.039 ^a
	60–80	1.30 ^a	0.89 ^a	0.41 ^a	0.034 ^a
	80–100	1.28 ^a	0.88 ^a	0.40 ^a	0.034 ^a
<i>Scirpus mariqueter</i>	0–5	1.14 ^b	0.86 ^a	0.28 ^b	0.023 ^b
	5–20	1.24 ^b	0.93 ^a	0.31 ^b	0.026 ^b
	20–40	1.29 ^b	0.81 ^a	0.48 ^b	0.034 ^b
	40–60	1.27 ^b	0.88 ^a	0.39 ^b	0.028 ^b
	60–80	1.25 ^a	0.90 ^a	0.35 ^b	0.026 ^b
	80–100	1.29 ^a	0.92 ^a	0.36 ^a	0.027 ^b
Source of variation					
Community		***	n.s.	***	***
Depth		*	n.s.	*	*
Community × Depth		n.s.	n.s.	n.s.	**

Values are means ($n=6$). Statistically significant differences are given after two-way ANOVA (n.s. = not significant; * $P<0.05$; ** $P<0.01$; *** $P<0.001$). The superscript letters indicate significant differences at the same soil layer between two species after t -test ($P<0.05$). TC: total soil carbon; IC: soil inorganic carbon; SOC: soil organic carbon; TN: total soil nitrogen.

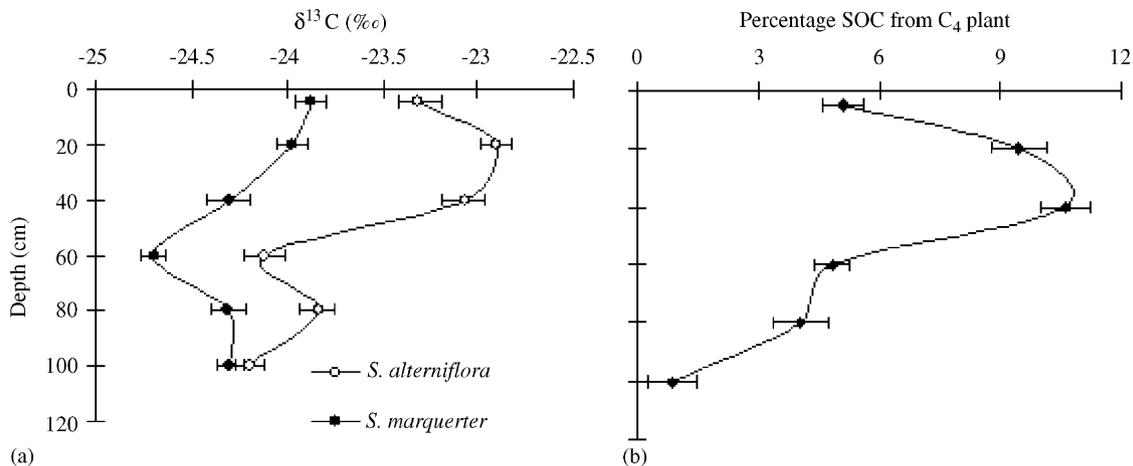


Fig. 2. (a) Vertical changes in $\delta^{13}\text{C}$ (‰) of soil organic carbon (SOC) at two communities and, (b) contribution (%) of invasive *Spartina alterniflora* (C_4 plant) to the SOM in Jiuduansha wetlands. Error bars represent the ± 1 standard deviation of the means ($n = 6$).

community was not significantly different from that of *Scirpus mariqueter* community ($P > 0.05$) (Table 1).

The $\delta^{13}\text{C}$ values of *Spartina alterniflora* leaves, litters, and roots varied from -12.8% to -13.4% , which is typical of C_4 plants; *Scirpus mariqueter* leaves and litters had a mean value of -26.7% , which is typical of C_3 plants (Table 2). C:N ratios of *Spartina alterniflora* were higher than those of *Scirpus mariqueter* (Table 2, $P < 0.05$).

There were significant differences in $\delta^{13}\text{C}$ between the two communities in the surface layers (0–60 cm) (Fig. 2a; $P < 0.05$). The values of $\delta^{13}\text{C}$ at deeper layers between 80 and 100 cm in *Spartina alterniflora* community were similar to those in *Scirpus mariqueter* community (Fig. 2a). The proportion of SOC from *Spartina alterniflora* appeared to be greater in the upper soil layers (0–60 cm), but the greater proportion of soil carbon (9.48–10.64%) from C_4 sources was found between 20 and 40 cm in depth (Fig. 2b). The SE for the proportion estimate calculated from Eq. (5) ranged from 0.31% to 0.59% (Fig. 2b). The proportion of SOC of *Spartina alterniflora* decreased with increasing depth, and the contribution of *Spartina alterniflora* to SOC at a depth of 100 cm decreased (Fig. 2b).

4. Discussion

Plant invasions have been previously found to alter various components of the nutrient cycle (e.g., Ehrenfeld, 2001; Windham and Ehrenfeld, 2003). Our results showed that a seven-year invasion of *Spartina alterniflora* in the Yangtze River estuary increased the carbon and nitrogen concentrations at most soil depths examined (Table 1). TC, SOC, and TN were higher in the soil dominated by *Spartina alterniflora* than those in that dominated by native *Scirpus mariqueter*, except at deeper soil layers (> 80 cm, Table 1). More importantly, we found that there was no significant difference in IC between *Spartina alterniflora* and *Scirpus mariqueter* communities. This result is critical because IC is substantial in the Jiuduansha wetland

ecosystem, which is carried down from the Yangtze River (Fig. 1 and Table 1). Therefore, we could conclude that the short-term invasion by *Spartina alterniflora* increased soil carbon concentration through increasing SOC concentrations (Table 1).

Although it is unclear as to how much of this change is attributable to plant community structure or post-invasion to the organic matter pool, the high SOC concentrations in *Spartina alterniflora* soils are the result of significantly greater rhizome and root biomass, and decomposition rates in *Spartina alterniflora* plant residuals. Previous studies have indicated that *Spartina alterniflora* has considerably higher production potential on the east coast of China (Qin and Zhong, 1992; Chen, 2003). Our results showed that C:N ratio of *Spartina alterniflora* was higher than that of *Scirpus mariqueter* (Table 2). This finding was consistent with the generalization that C_4 plants have higher C:N ratios than C_3 plants because the latter have more Rubisco proteins (Long, 1999; Still et al., 2003), indicating *Spartina alterniflora* has a higher photosynthetic efficiency than that of *Scirpus mariqueter*. The higher photosynthesis efficiency and production further suggests that *Spartina alterniflora* could fix more carbon and potentially provide great residual inputs to soil. Related field investigations conducted in the same system have found that *Spartina alterniflora*'s root biomass is significantly higher than *Scirpus mariqueter*, although the distribution of root biomass with soil depth followed a similar pattern for both species (i.e., root biomass concentrated on the upper 60 cm soil) (Liao et al., 2006, unpublished data). Interestingly, we found that the vertical patterns of the SOC and TN concentrations varied from low to high to medium in the upper 60 cm soil, and then decreased with depth in deeper soils in both two communities (Table 1), which might be related to C movement through the profile associated with the distribution of belowground roots, root exudate input, and residue decomposition (Henderson et al., 2004; Hobbie et al., 2004).

Another interesting observation is that the vertical distributions of $\delta^{13}\text{C}$ in the two communities differed relative to soil depth (Fig. 2a). There is evidence that the $\delta^{13}\text{C}$ values in C_3 SOM discriminate differently along the soil profile from C_4 SOM (e.g., Nyberg et al., 2000; Hobbie et al., 2004). Previous studies have shown that several factors influence ^{13}C values in SOC, including relative amount of C_3 and C_4 plant residual composition in SOM, genesis of soils and plants, and decomposition rate of plant litter (Nyberg et al., 2000; Osher et al., 2003; Hobbie et al., 2004; Chiang et al., 2004). Our stable isotopic analysis suggests that the $\delta^{13}\text{C}$ abundance in SOC was different between *Spartina alterniflora* and *Scirpus mariqueter* soils (Fig. 2a). The $\delta^{13}\text{C}$ in SOC of *Spartina alterniflora* seemed to be more enriched than that in SOC of *Scirpus mariqueter* (Fig. 2a), which might be a result of contribution from C_4 *Spartina alterniflora* residuals (Nyberg et al., 2000; Hobbie et al., 2004). Furthermore, we found that the $\delta^{13}\text{C}$ decreased with depth in the two communities, but the difference in $\delta^{13}\text{C}$ was significant only in the top layers (0–60 cm). This finding was not consistent with the pattern of previously reported $\delta^{13}\text{C}$ distributions in soil, in which the $\delta^{13}\text{C}$ value increased with increasing depth related to the contribution from enriched- ^{13}C carbon resources (Follet et al., 1997; Ehleringer et al., 2000). This depletion in $\delta^{13}\text{C}$ with increasing depth, however, has been observed (Kindscher and Tieszen, 1998; Collins et al., 1999; Henderson et al., 2004; Hansen et al., 2004), and was explained by the presence of SOC derived from ^{13}C -depleted C_3 vegetation (Hansen et al., 2004). One explanation for $\delta^{13}\text{C}$ depletion with soil depth in this study is that the residues from ^{13}C -enriched C_4 *Spartina alterniflora* contributed less to SOC than those from ^{13}C -depleted C_3 *Scirpus mariqueter* because of its short-term invasion on the island (i.e., <7 years), in which the *Scirpus mariqueter* monoculture has been the dominant community on the island over 30 years (Chen, 2003).

The trend in ^{13}C values versus depth might not only be related to the plant residue input combined with vertical transport of C within the soil profile, but also to the multiple pools of SOM with different C turnover rates (Kindscher and Tieszen, 1998; Henderson et al., 2004). The proportion of SOC originating from *Spartina alterniflora*, calculated by the mixing model, was 5.11% in the top 5 cm, and 9.48%–10.64% in the 20–40 cm soil layer. *Spartina alterniflora* carbon accounted for a relatively larger proportion of SOC (Fig. 2b), suggesting that some *Spartina alterniflora*-derived carbon might have been deposited at those depths (Fig. 2b; Hansen et al., 2004). The $\delta^{13}\text{C}$ and smaller proportion of SOC below 60 cm (Fig. 2b), however, suggests that little carbon derived from *Spartina alterniflora* was deposited even after 7-year invasion. Small contributions from *Spartina alterniflora* to SOC at the top layer (0–5 cm) suggested that the new carbon at the top was rapidly lost, possibly through soil respiration and incomplete decomposition of organic matter in residuals (Chiang et al., 2004). Further, differential rooting patterns

might have also resulted in variation in ^{13}C with depth when little or no redistribution from leaching is assumed (Henderson et al., 2004). Because roots dominate inputs of SOC, root exudates might also be important, although we lacked means by which to estimate their contribution (Rogers et al., 1994; Hobbie et al., 2004). As mentioned above, a larger proportion of *Spartina alterniflora* and *Scirpus mariqueter* roots are distributed in the upper soil layers (0–60 cm). It can be concluded that the greater contribution to SOC derived from C_4 plants between the soil layers of 20–40 cm is caused by larger root biomass, while contributions to SOC below 60 cm decline as root biomass decreases. This conclusion is based on a general decrease in biological activity with increasing soil depth and agrees with decreased root biomass with greater depth in other studies (Jackson et al., 1996; Hobbie et al., 2004).

It is important to note that prediction of how plant invasions alter soil C and N within a wetland ecosystem is complicated, depending on sediment redox potential, microbial processes, and organic matter deposition (e.g., Treseder and Allen, 2000; Windham and Ehrenfeld, 2003), all of which illustrate that long-term monitoring of the changes of SOC and controlled experiments are needed in future studies. Furthermore, we lacked the data on residue distribution in relation to soil depth and root decomposition rates, thus, we are not in a position to relate *Spartina alterniflora* invasion to C translocation. Nevertheless, the significance of our results tentatively demonstrates the short-term C_4 plant *Spartina alterniflora* invasions enhance soil carbon storage by increasing production and residue input in soil. On the contrary, the changes in soil nutrient components may reflect the shift in community composition and biodiversity (Wilcove et al., 1998; Cox, 1999; Ehrenfeld, 2001).

To conclude, we found that *Spartina alterniflora* invasion on Jiuduansha Island over the past 7 years was associated with increased SOC and TN concentration, but was not associated with a change in IC concentration. TC, SOC, and TN were higher in *Spartina alterniflora* soils than those in *Scirpus mariqueter* soils, except in deeper soil layers (>60 cm). The change in $\delta^{13}\text{C}$ ratio revealed that a fraction of the SOC pool was accounted for 0.9–10.6% of the SOC present at 0–100 cm soil layers by *Spartina alterniflora*-derived carbon, and a greater contribution derived from *Spartina alterniflora* was found between 20 and 40 cm deep soils.

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References

- Bagwell, C.E., Lovell, C.R., 2000. Microdiversity of culturable diazotrophs from the rhizoplanes of the salt marsh grasses *Spartina alterniflora* and *Juncus roemerianus*. *Microbial Ecology* 39, 128–136.
- Bernoux, M., Cerri, C.C., Neill, C., De Moraes, J.F.L., 1998. The use of stable carbon isotopes for estimating soil organic matter turnover rates. *Geoderma* 82, 43–58.
- Boutton, T.W., 1996. Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change. In: Boutton, T.W., Yamasaki, S. (Eds.), *Mass Spectrometry of Soils*. Marcel Dekker, Inc., New York, pp. 47–82.
- Biedenbender, S.H., McClaran, M.P., Quade, J., Weltz, M.A., 2004. Landscape patterns of vegetation change indicated by soil carbon isotope composition. *Geoderma* 119, 69–83.
- Bruno, J.F., 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology* 81, 1179–1192.
- Callaway, J.C., Josselyn, M.N., 1992. The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. *Estuaries* 15, 218–226.
- Chen, J.K., 2003. A comprehensive Survey on Jiuduansha Island. Science Press, Beijing.
- Chiang, P.N., Wang, M.K., Chiu, C.Y., King, H.B., Hwang, J.L., 2004. Change in the grassland-forest boundary at Ta-Ta-Chia long term ecological research (LTER) site detected by stable isotope ratio of soil organic matter. *Chemosphere* 54, 217–224.
- Collins, H.P., Blevins, R.L., Bundy, L.G., Christenson, D.R., Dick, W.A., Huggins, D.R., Pau, A., 1999. Soil carbon dynamics in corn-based agroecosystems: results from carbon-13 natural abundance. *Soil Science Society of America Journal* 63, 584–591.
- Cox, G.W., 1999. *Alien Species in North American and Hawaii*. Island Press, Washington, DC.
- Daehler, C.C., Strong, D.R., 1997. Reduced herbivore resistance in introduced smooth cord grass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia* 110, 99–108.
- Desjardins, T., Carneirofilho, A., Mariotti, A., Chauvel, A., Girardin, C., 1996. Changes of the forest-savanna boundary in Brazilian Amazonia during the Holocene revealed by stable isotope ratio of soil organic carbon. *Oecologia* 108, 749–756.
- Diels, J., Vanlauwe, B., Sanging, N., Coolen, E., Merckx, R., 2001. Temporal variation in plant $\delta^{13}\text{C}$ values and implications for using the ^{13}C technique in long-term soil organic matter studies. *Soil Biology & Biochemistry* 33, 1245–1251.
- Ehleringer, J.R., Buchmann, N., Flanagan, L.B., 2000. Carbon isotope ratios in below ground carbon cycle processes. *Ecological Applications* 10, 412–422.
- Ehrenfeld, J.G., 2001. Plant–soil interactions. In: Levin, S. (Ed.), *Encyclopedia of Biodiversity*. Academic Press, San Diego, CA, USA, pp. 689–707.
- Follet, R.F., Paul, E.A., Leavitt, S.W., Halvorson, A.D., Lyon, D., Peterson, G.A., 1997. Carbon isotope ratios of Great Plains soils in wheat-fallow systems. *Soil Science Society of America Journal* 61, 1068–1077.
- Hansen, E.M., Christensen, B.T., Jensen, L.S., Kristensen, K., 2004. Carbon sequestration in soil beneath long-term *Miscanthus* plantations as determined by ^{13}C abundance. *Biomass & Bioenergy* 26, 97–105.
- Henderson, D.C., Ellert, B.H., Naeth, M.A., 2004. Utility of ^{13}C for ecosystem carbon turnover estimation in grazed mixed grass prairie. *Geoderma* 119, 219–231.
- Hobbie, E.A., Johnson, M.G., Rygielwicz, P.T., Tingey, D.T., Olszyk, D.M., 2004. Isotopic estimates of new carbon inputs into litter and soils in a four-year climate change experiment with Douglas-fir. *Plant and Soil* 259, 331–343.
- Jackson, R.B., Canadel, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108, 389–411.
- Kindscher, K., Tieszen, L.L., 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. *Restoration Ecology* 6, 181–196.
- Kriwoken, L.K., Hedge, P., 2000. Exotic species and estuaries: managing *Spartina anglica* in Tasmania, Australia. *Ocean & Coastal Management* 43, 573–584.
- Lin, G.H., Ehleringer, J.R., Rygielwicz, P.T., Johnson, M.G., Tingey, D.T., 1999. Elevated CO_2 and temperature impacts on different components of soil CO_2 efflux in Douglas-fir terracosms. *Global Change Biology* 5, 157–168.
- Lonsdale, W.M., 1999. Global patterns of plant invasions and concept of invisibility. *Ecology* 80, 1536–1552.
- Long, S.P., 1999. Environmental responses. In: Sage, R.F., Monson, R.K. (Eds.), *C₄ Plant Biology*. Academic Press, New York, pp. 215–249.
- Lövel, G., 1997. Global change through invasion. *Nature* 388, 627–628.
- Mariotti, A., Peterschmitt, E., 1994. Forest savanna ecotone dynamics in India as revealed by carbon isotope ratio of soil organic matter. *Oecologia* 97, 475–780.
- Nyberg, G., Högborg, P., 1995. Effects of young agroforestry trees on soils in on-farm situations in western Kenya. *Agroforestry System* 31, 45–52.
- Nyberg, G., Ekblad, A., Buresh, R.J., Högborg, P., 2000. Respiration from C₃ plant green manure to a C₄ plant carbon dominated soil. *Plant and Soil* 218, 83–89.
- O’Leary, M.H., 1988. Carbon isotopes in photosynthesis. Fractionation techniques may reveal new aspects of carbon dynamic in plants. *Bioscience* 38, 328–329.
- Osher, L.J., Matson, P.A., Amundson, R., 2003. Effect of land use change on soil carbon in Hawaii. *Biogeochemistry* 65, 213–232.
- Peng, S.L., Xiang, Y.C., 1999. The invasion of exotic plants and effects of ecosystems. *Acta Ecologica Sinica* 19, 560–569.
- Phillips, D.L., Gregg, J.W., 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia* 127, 171–179.
- Qin, P., Zhong, C.X., 1992. *Applied studies on Spartina*. Ocean Press.
- Rogers, H.H., Runion, G.B., Krupa, S.V., 1994. Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution* 83, 155–189.
- Silliman, B.R., Zieman, J.C., 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology* 82, 2830–2845.
- Staddon, P.L., 2004. Carbon isotopes in functional soil ecology. *Trends in Ecology and Evolution* 19, 148–153.
- Still, C.J., Berry, J.A., Ribas-Carbo, M., Helliker, B.R., 2003. The contribution of C₃ and C₄ plants to the carbon cycle of a tallgrass prairie: an isotopic approach. *Oecologia* 136, 347–359.
- Taylor, J.R., 1982. *An Introduction to Error Analysis*. Oxford University Press, Oxford.
- Thompson, J.D., 1991. The biology of an invasive plant: what makes *Spartina anglica* so successful? *Bioscience* 41, 393–400.
- Treseder, K.K., Allen, M.F., 2000. Mycorrhizal fungi have a potential role in soil carbon storage elevated CO_2 and nitrogen deposition. *New Phytologist* 147, 189–200.
- Wilcove, D., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48, 607–616.
- Windham, L., Ehrenfeld, J.G., 2003. Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. *Ecological Applications* 13, 883–897.
- Wooler, M., Smallwood, B., Jacobson, M., Fogel, M., 2003. Carbon and Nitrogen stable isotopic in *laguncularia racemosa* (L.) (white mangrove) from Florida and Belize: implications for trophic level studies. *Hydrobiologia* 499, 13–23.