Geoderma 145 (2008) 177–184

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Assessing the effects of short-term *Spartina alterniflora* invasion on labile and recalcitrant C and N pools by means of soil fractionation and stable C and N isotopes

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ARTICLE INFO

Article history:
Received 27 August 2007
Received in revised form 20 February 2008
Accepted 26 February 2008

Keywords:
C_3 and C_4 plant
Invasion
Soil fractionation
Soil organic matter
Stable C and N isotopes
Yangtze River estuary

ABSTRACT

An exotic grass *Spartina alterniflora* was intentionally introduced to Jiuduansha wetlands in Yangtze River estuary in 1997, and since then it had rapidly replaced native plant *Scirpus mariqueter* that used to dominate the estuarine salt marshes. We investigated consequences of *S. alterniflora* invasion to soil labile and recalcitrant C and N compared to the native *S. mariqueter* using soil fractionation and stable C and N isotopes. Results showed that *S. alterniflora* increased soil labile carbon (LC), recalcitrant carbon (RC), and soil recalcitrant nitrogen (RN) contents significantly ($P<0.05$) in the upper soil layers (0–60 cm) compared to the *S. mariqueter* soil. Soil labile nitrogen (LN) in the *S. alterniflora* soil, however, remained lower than that in the *S. mariqueter* soil ($P<0.01$), except for the surface soil layer (0–20 cm). The LC accounted for, on average, 36–38% of soil organic matter (SOM) in both communities, while labile N accounted for 32% of SOM in *S. alterniflora* soil and 48% in *S. mariqueter* soil. The $\delta^{13}C$ values in *S. alterniflora* soil showed that *S. alterniflora* contributed on average 8.6% and 3.3% to the LC and RC pools, respectively, within the 0–100-cm soil layer. The greatest labile C contribution derived from *S. alterniflora* was found at the 40-cm soil whereas the proportion of recalcitrant C originating from *S. alterniflora* showed a decreasing trend with soil depth. These changes appeared to be associated with vertical distributions of roots and rhizodeposition. We also found that the $\delta^{15}N$ values of SOM were more enriched in *S. alterniflora* soil compared to *S. mariqueter* soil, suggesting that greater SOM input by *S. alterniflora* residues would stimulate microbial activity rates that could lead to increased N turnover rates in *S. alterniflora* soil.

1. Introduction

Soil organic matter (SOM), a significant component of the global terrestrial carbon (C) and nitrogen (N) pools, is critically important in global C and N cycles (e.g., Jobbágy and Jackson, 2000; Del Galdo et al., 2003). SOM has a complex composition that generally consists of labile and recalcitrant pools (Rovira and Vallejo, 2002). The labile pool, small but highly bio-reactive, determines the instantaneous C and N fluxes, while the recalcitrant pool, large and long-lived, dominates long-term C and N storage (Trumbore et al., 1990). Labile pools of SOM are a direct reservoir of readily available nutrients, which are especially important because they control ecosystem productivity in the short term, and could be the most affected by altered environmental factors such as vegetation type and land cover change (Zak et al., 1993; Hu et al., 1997; Jobbagy and Jackson, 2000). Changes in the portions of inputs to labile and recalcitrant pools of SOM may not only lead to a new equilibrium of labile SOM condition in the short term but also influence the long-term terrestrial C and N pools (Zak et al., 1993). Previous studies have indicated that the soil fractionations vary significantly with an array of soil parent materials, vegetation characteristics, and disturbances and management practices (e.g. Harris et al., 1996). Understanding how the above factors influence the redistribution of labile and recalcitrant C and N pools is particularly important in predicting changes in ecosystem functioning.

The effects of plant invasions on soil processes and ecosystem functioning have been increasingly recognized in recent years in many parts of the world (Ehrenfeld et al., 2001; Ehrenfeld, 2003; Allison and Vitousek, 2004; Liao et al., 2008). Numerous authors (Hooper and Vitousek, 1998; Ehrenfeld, 2003; Liao et al., 2008) have reported that invasive species have direct effects on C and N cycles through altering pools of above-ground and below-ground C, N, and other elements, net primary productivity, plant growth rates, litter quality and quantity, and nutrient and C mineralization rates. Often, these changes in vegetation

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doi:10.1016/j.geoderma.2008.02.013

structure and composition are accompanied by altering SOM input and quality, which potentially change the distribution of inputs to labile and recalcitrant soil nutrient pools. The changes, however, in SOM, even when significant, are small when compared to the magnitude of the soil C and N reservoirs. For this reason, conventional methodologies usually cannot be used to examine the soil labile and recalcitrant pool within the short time frame of most experiments.

Numerous studies (Bernoux et al., 1998; Ehleringer et al., 2000; Accoe et al., 2002; Swap et al., 2004) have been successful in applying $\delta^{13}C$ in elucidating plant-soil SOM dynamics, making the stable isotopic analysis an appropriate approach. Theoretically, when one type of vegetation is replaced with another, $\delta^{13}C$ values could be used to identify SOM derived from residues in the native vegetation and the new vegetation, for example, where C_4 plant (with $\delta^{13}C$ values be reported as −19 to −9‰) grows on soil derived from a C_3 plant ($\delta^{13}C$ of −35 to −20‰) (Nyberg et al., 2000; Biedenbender et al., 2004; Staddon, 2004). Based on the change in ^{13}C signature of SOM, the relative contribution of new vs. old soil organic C can be quantified using the mass balance of stable isotope contents (e.g., Dawson et al., 2002; Del Galdo et al., 2003). As for N, several studies have reported strong correlations between enriched levels of leaf $\delta^{15}N$ and increased soil N (Högberg, 1990; Emmett et al., 1998), increased rates of N-cycling (Garten,1993), and increased loss of N (Högberg and Johannisson, 1993). Convincingly, analyzing the $\delta^{13}C$ and $\delta^{15}N$ of ecosystem components (leaves, litter and soils) could be used to assess the interplay of SOM related to plant growth (Lynch et al., 2006). Very few attempts, however, have been made to quantitatively evaluate the effect of invasive plants on SOM fractionations in wetland ecosystems. Here, we reported a case study of examining such effects of *Spartina alterniflora* invasions in the Yangtze River estuary.

S. alterniflora, a C_4 grass, was introduced to China from its native range, the United States in 1979 (Qin and Zhong, 1992). Since then, *S. alterniflora* has been widely planted in the tidal marshes on the eastern coast of China, and is now distributed from Tianjin to Guangxi, and covered an area of 112,000 ha by 2000 (An et al., 2007). *S. alterniflora* spread to most of the tidal lands in the Yangtze estuary through both intentional introductions and natural dispersal since it was first found in the estuary (Wang et al., 2006). Although many of its biological characters make *S. alterniflora* a good soil stabilizer, its effects on native ecosystems are multifold, including the displacement of native species, the changes of biodiversity, and ecosystem functioning (Daehler and Strong, 1997; Bruno, 2000; Chen et al., 2004; Chen et al., 2007a,b; He et al., 2007).

Jiuduansha is an estuarine island growing from constant deposition of sediments carried by the Yangtze River. *S. alterniflora* was transplanted to the island in 1997 under the Greening Engineering project, where native *Scirpus mariqueter* (a C3 plant), a pioneer species of mudflats, has dominated for over thirty years (Chen, 2003; Cheng et al., 2006b). *S. alterniflora* has rapidly spread on the island out-competing the habitats of native species because of its fast growth, and high seed production and germination rate (Qin and Zhong, 1992; Wang et al., 2006). Our previous study reported that short-term *S. alterniflora* invasion on Jiuduansha Island increased SOM significantly as a result of the greater above-ground and below-ground biomass of *S. alterniflora* compared to *S. mariqueter* (Cheng et al., 2006b; Liao et al., 2007). To guide this paper, we hypothesized that rapid invasion of *S. alterniflora* would significantly alter SOM fractionation due to its differences in ecophysiological processes from native *S. mariqueter*. Our capacity to predict the effect of *S. alterniflora* invasion on labile and recalcitrant SOM depends largely on a better understanding how vegetation changes affect SOM fractionation with soil depth. The specific objectives of this study were to: (1) compare the labile and recalcitrant pools of SOM to a depth of 100 cm between *S. alterniflora* and *S. mariqueter* soil; and (2) evaluate the influences of the *S. alterniflora* invasion on the labile and recalcitrant pools through stable C and N isotopic analyses of $\delta^{13}C$ and $\delta^{15}N$.

2. Materials and methods

2.1. Study area

This study was conducted at Shanghai Jiuduansha Wetland Nature Reserve (31°3′–31°17′N, and 121°46′–122°15′E) in the Yangtze River estuary (see Cheng et al., 2006b). Jiuduansha Island is an alluvial island in the Yangtze River, which had an area of 425 km^2 in 2003 and still continues to grow at 70 m per year in radius (Chen, 2003). The climate is characterized by an annual precipitation of 1145 mm and annual mean temperature of 15.7 °C, with monthly means of 36.6 °C in July and −7.7 °C in January. Currently, Jiuduansha has evolved into a stable island after a half-century of sediment deposition. The soil is silt and clay with pH 7.9–8.4 that is classified as coastal saline soil and damp soil (Chen, 2003; Zhou et al., 2006). The vegetation on the island consists of few species, so the plant community structure is relatively simple. The native plant *S. mariqueter* used to dominate the salt marshes on this island, to which *S. alterniflora* was introduced in 1997 (Chen, 2003; Cheng et al., 2006b).

2.2. Field sample collection

Two transects, 3 km long, along a transitional zone from *S. alterniflora* to *S. mariqueter* in the wetland were selected in April 2005 (details given in Liao et al., 2007). Because *S. alterniflora* and *S. mariqueter* could hardly co-exist, both of the two species form their respective monocultures. In Jiuduansha wetlands, *S. alterniflora* had replaced *S. mariqueter* for about eight years, while *S. mariqueter* had dominated the salt marshes for over 30 years (Chen, 2003). We randomly selected six sampling sites on each transect, each of which measured 50 m wide and 200 m long. At each site, several samples (up to 6) of leaf, litter, root, and soil samples were randomly collected. One replicate (leaves, litter, roots, and soil) was taken from several randomly-selected separate samples at each site. Newly produced leaves, litter, and roots were sampled at each site (Cheng et al., 2006b). Soil samples were taken to a depth of 100 cm with a 2.3-cm diameter stainless steel soil sampler in the randomly-selected locations. These soil samples were collected at 0–5-cm, 5–20-cm, 20–40-cm, 40–60-cm, 60–80-cm, and 80–100-cm soil depths for each plot. All samples were immediately sealed in glass vials, stored on ice in coolers, transported to the laboratory at Fudan University, and stored at 5 °C before analysis.

2.3. Laboratory analysis

Samples of leaf, root, litter, and soil were dried at 50 °C to constant weight and ground to pass through 20-mesh (0.84 mm) sieves (Cheng et al., 2006b). The soil samples were analyzed for soil labile C (LC), recalcitrant C (RC), soil labile N (LN), and recalcitrant N (RN) concentrations, $\delta^{13}C$ of LC and RC, and $\delta^{15}N$ of LN and RN. The leaf, litter, and root samples were analyzed for total carbon (TC), total nitrogen (TN), $\delta^{13}C$ and $\delta^{15}N$.

Soil labile and recalcitrant C and N were determined following the acid hydrolysis procedure described by Cheng et al. (2006b) and Rovira and Vallejo (2002). 1) Subsamples of soil were treated with 1 N HCL for 24 h at room temperature to remove any carbonate. This fraction was interpreted to be soil organic matter (SOM) pool. 2) Approximately 500 mg of the SOM sample was hydrolyzed with 20 ml of 5 N H_2SO_4 for 30 min at 105 °C in sealed Pyrex tubes. The hydrolysate was recovered by centrifugation and decantation. The residue was washed with 20 ml of water, and the washing was added to the hydrolysate. This hydrolysate was interpreted to be Labile Pool (I). The residue was dried at 60 °C. The remaining residue was hydrolyzed with 2 ml of 26 N H_2SO_4 overnight at room temperature while being continuously shaken. Then, water was added to dilute the acid to 2 N and the sample was hydrolyzed for 3 h at 105 °C with

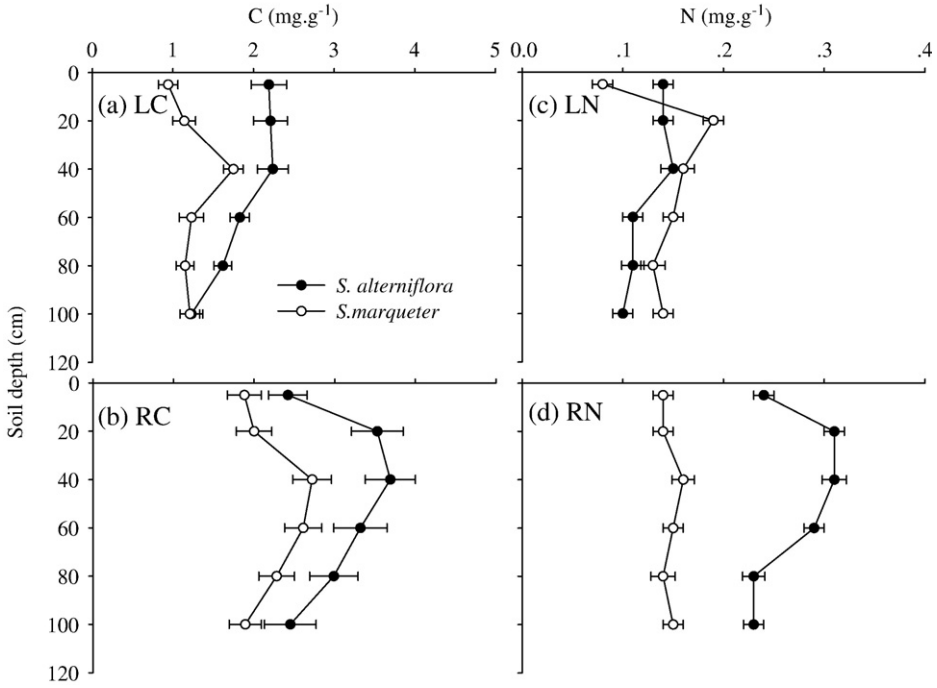

Fig. 1. Labile and recalcitrant C and N of *S. alterniflora* and *S. mariqueter* soil in Jiuduansha wetlands in coastal Shanghai, China. Error bars represent the ±1 standard error of the means (n=6).

occasional shaking. The hydrolysate was recovered by centrifugation and decantation. The residue was washed with 20 ml of water, and the washing was added to the hydrolysate. This hydrolysate was understood to be Labile Pool (II). Labile Pool (I) was added to Labile Pool (II) to obtain the total labile pool. 3) The remaining residue was rinsed twice with water, transferred to a pre-weighed crucible, and dried at 60 °C. This fraction was interpreted to be the Recalcitrant Pool.

Subsamples of leaf, root, litter, SOM, and recalcitrant pool were weighed, and analyzed for $\delta^{13}C$, $\delta^{15}N$, and C and N concentrations on an isotope ratio mass spectrometer (Thermo Finnigen, Delta-Plus, Flash, EA, 1112 Series, USA).

The carbon and nitrogen isotope ratio of the soil organic matter and plant materials was expressed as:

$$\delta^h X = \left[\left(\frac{X^h}{X^l}\right)_{\text{sample}} \Big/ \left(\frac{X^h}{X^l}\right)_{\text{standard}} - 1 \right] \times 1000 \quad (1)$$

where X is either carbon or nitrogen, h is the heavier isotope, l is the lighter isotope. Both CO_2 and N_2 samples were analyzed relative to internal, working gas standards. Carbon isotope ratios (^{13}C) are expressed relative to Pee Dee Belemnite ($\delta^{13}C$=0.0‰); nitrogen stable isotope ratios (^{15}N) are expressed relative to air ($\delta^{15}N$=0.0‰) (Wooller et al., 2003). Urea and glycine were analyzed as checks on the accuracy and precision of isotopic ratios and elemental compositions by the elemental analyzer. Precision for $\delta^{13}C$, C concentration, $\delta^{15}N$, and N concentration were ±0.15‰, ±5.4%, ±0.15‰, and ±0.5%, respectively.

2.4. Calculation

Because the hydrolysate of the labile pool cannot be directly measured on isotope ratio mass spectrometer, the $\delta^{13}C$ and $\delta^{15}N$ of the soil labile pool were not available. However, a linear mixing model (Eq. (2)) can be used to estimate the $\delta^{13}C$ and $\delta^{15}N$ of soil labile pool based on the $\delta^{13}C$ and $\delta^{15}N$ values of SOM and recalcitrant pool and the concentration of SOM and recalcitrant pool (Cheng et al., 2006a).

$$\delta X_{\text{LP}} = \delta X_{\text{RP}} + (\delta X_{\text{SOM}} - \delta X_{\text{RP}}) \times \frac{\theta_{\text{SOM}}}{\theta_{\text{LP}}} \quad (2)$$

where δX_{LP} represents the δX value of labile pool; δX_{RP} symbolizes the δX value of recalcitrant pool, δX_{SOM} is the δX value of SOM, θ_{SOM} represents the concentration of SOM, θ_{LP} is the concentration of labile pool.

The calculation of the proportion (f) of *S. alterniflora*-derived LC and RC was determined by the following linear mixing model (Del Galdo et al., 2003; Hansen et al., 2004):

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

where f is the proportion of C from C_4 *S. alterniflora* plant, $\delta^{13}C_{\text{new}}$ is the $\delta^{13}C$ of the LC and RC in *S. alterniflora* soil; $\delta^{13}C_{\text{mix}}$ is the $\delta^{13}C$ of *S. alterniflora* plant material entering the soil which is an average value of litter, rhizomes, and roots from *S. alterniflora*; $\delta^{13}C_{\text{old}}$ is the $\delta^{13}C$ of the LC and RC in *S. mariqueter* soil, assuming no shift in the C_3/C_4 ratio in the *S. mariqueter* plant soil in the past 30 years (Del Galdo et al., 2003; Cheng et al., 2006b).

2.5. Data analyses

Before ANOVA analysis, the data sets were checked for normality, and log or cube root transformed to meet the assumptions for statistical analysis. The data analyses were performed using Stat Soft's Statistica, statistical software for Windows (Version 6.0, StatSoft, Inc., 2001).

Subtracting the recalcitrant pool from SOM on each sample allowed us to obtain the labile pool. The labile and recalcitrant pools and SOM on statistically paired samples were used to obtain the proportion of SOM. The C:N ratios of soil components were obtained by dividing LC, RC, LN, and RN on each sample. Within each depth, community (*S. alterniflora* vs. *S. mariqueter*) was the main factor in the model, with SOM fraction and replicate as secondary factors (see Del Galdo et al., 2003). Two-way ANOVAs were performed to examine the differences in the LC, RC, LN, RN, the values of $\delta^{13}C$ of LC and RC, the values $\delta^{15}N$ of LN and RN, the proportion of SOM and the C:N ratios of soil components between two communities in relation to soil depth (Cheng et al., 2006b). t-tests (t-test for independent samples by

Table 1
Statistically significant differences of soil C and N contents, $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) in SOM fractionations between *S. alterniflora* and *S. mariqueter* communities based on a two-way ANOVA and *t*-test

Source of variation	LC		RC		LN		RN	
	(kg m^{-2})	$\delta^{13}C$	(kg m^{-2})	$\delta^{13}C$	(kg m^{-2})	$\delta^{15}N$	(kg m^{-2})	$\delta^{15}N$
Community	*	**	**	n.s.	*	***	***	**
Depth	n.s.	**	n.s.	n.s.	n.s.	**	n.s.	n.s.
0–5	*	n.s.	*	*	*	*	*	*
5–20	*	*	*	*	*	*	*	*
20–40	*	*	*	*	*	*	*	n.s.
40–60	*	*	*	*	*	*	*	n.s.
60–80	*	*	*	n.s.	*	*	*	*
80–100	n.s.	*	*	n.s.	*	*	*	n.s.
Community*depth	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Note: n.s. = not significant; *P<0.05; **P<0.01; ***P<0.001.
LC: labile carbon; RC: soil recalcitrant carbon; LN: labile nitrogen, RN: soil recalcitrant nitrogen.

Table 2
The C:N ratios in labile and recalcitrant pools of *S. alterniflora* and *S. mariqueter* soils in Jiuduansha wetlands in coastal Shanghai, China

Community	Depth (cm)	Labile pool	Recalcitrant pool
S. alterniflora	0–5	15.64±1.02	10.08±1.72
	5–20	15.79±0.88	11.38±0.27
	20–40	14.93±1.63	10.71±1.15
	40–60	16.63±0.74	12.72±1.59
	60–80	10.45±0.86	13.00±1.20
	80–100	16.20±0.90	10.65±2.43
S. mariqueter	0–5	11.75±1.34	13.42±2.09
	5–20	6.00±1.91	14.29±2.52
	20–40	13.94±0.79	16.31±3.21
	40–60	8.07±2.63	18.13±4.87
	60–80	9.46±1.77	16.29±1.04
	80–100	12.50±1.70	12.60±2.28
Source of variation			
Community		***	***
Depth		n.s.	n.s.
Community×depth		n.s.	n.s.

Note: Values are mean (n=6) with standard error. Statistically significant differences are given after two-way ANOVA (n.s. = not significant; *P<0.05; **P<0.01; ***P<0.001).

variables) were further employed to compare the difference in LC, RC, LN, RN, the values of $\delta^{13}C$ of LC and RC, the values $\delta^{15}N$ of LN and RN, and the C:N ratios of soil components at the same soil layer between the two communities. The C and N values of plant components on each sample were used to obtain C:N ratios. A *t*-test was used to examine the difference in $\delta^{13}C$ and C:N ratio of plant materials between the two communities.

3. Results

3.1. Labile and recalcitrant C and N

Labile and recalcitrant C and N of the *S. alterniflora* soil were significantly different (P<0.05) from those of the *S. mariqueter* soil (Fig. 1, Table 1). Within each community, higher labile and recalcitrant C and N were found between 20- and 60-cm soil layers compared to other soil layers (Fig. 1). On average, LC of the *S. alterniflora* soil was significantly higher (P<0.05) in the upper soil layers (0–60 cm) than that of the *S. mariqueter* soil (Fig. 1a, Table 1). RC and RN of the *S. alterniflora* soil were significantly higher ($F_{1,\ 34}$=10.5, P=0.008; and $F_{1,\ 34}$=105, P=0.0003, respectively) than those of the *S. mariqueter* soil in all soil layers (Fig. 1b, d). However, LN of the *S. alterniflora* soil was lower than that of the *S. mariqueter* soil, except for the surface soil (0–5 cm) (Fig. 1c). Generally, LC accounted for a smaller proportion (averaged 36% to 38%) of SOM compared to RC in both two communities (Fig. 2a). But, LN proportions of SOM *S. alterniflora* soil (on average, 32%) were obviously lower than those in *S. mariqueter* soil (averaged 48%) except for the surface soil layer (0–5 cm) (Fig. 2c).

Significant differences (P<0.001) in the C:N ratio in labile and recalcitrant pools were found between the *S. alterniflora* and the *S. mariqueter* communities (Table 2). The C:N ratio in the labile pool

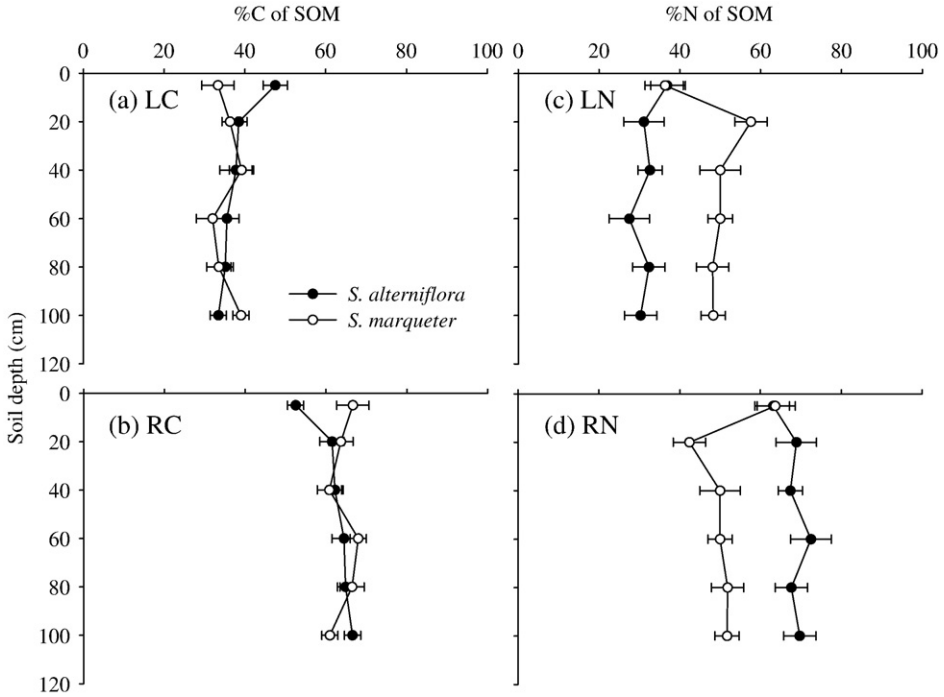

Fig. 2. The labile and recalcitrant C and N proportions of SOM of *S. alterniflora* and *S. mariqueter* soil in Jiuduansha wetlands in coastal Shanghai, China. Error bars represent the ±1 standard error of the means (n=6).

Table 3
The values of $\delta^{13}C$, $\delta^{15}N$, and C:N ratio of *S. alterniflora* and *S. mariqueter* plants in Jiuduansha wetlands in coastal Shanghai, China

Species		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N ratio
S. alterniflora (C_4)	Leaf	−12.8±0.3[a]	5.9±0.3[a]	32.7±1.8[a]
	Litter	−13.4±0.3[a]	3.3±0.4[a]	34.9±2.5[a]
	Root	−13.1±0.3[a]	4.6±0.3[a]	32.1±0.8[a]
S. mariqueter (C_3)	Leaf	−26.7±0.3[b]	6.6±0.3[b]	26.3±2.7[b]
	Litter	−27.9±0.3[b]	5.3±0.4[b]	31.7±1.6[b]
	Root	−26.6±0.2[b]	5.1±0.4[b]	27.2±1.1[b]

Note: Values are mean (n=6) with standard error. Different suffixes indicate significant differences between two species (t-test, P<0.05).

under *S. alterniflora* soil was higher than that in the *S. mariqueter* soil, while the C:N ratio in the recalcitrant pool of the *S. alterniflora* soil was lower than that of the *S. mariqueter* soil (Table 2). A two-way ANOVA showed no significant interactive effects (P>0.05) of community and depth on the C:N ratio of LC and RN (Table 2).

3.2. The $\delta^{13}C$ and $\delta^{15}N$ values of plant, soil labile and recalcitrant pools

The $\delta^{13}C$ values of *S. alterniflora* leaf and litter varied from −12.8‰ to −13.4‰, while *S. mariqueter* leaf and litter had a mean value of −26.8‰ (Table 3). The $\delta^{15}N$ values for leaf and litter varied from 5.9‰ to 3.3‰, and 6.6‰ to 5.3‰ for *S. alterniflora* and *S. mariqueter* communities, respectively (Table 3). The C:N ratios of *S. alterniflora* were significantly higher (P=0.038, $F_{1,\ 24}$=4.8) than those of *S. mariqueter* (Table 3).

The $\delta^{13}C$ values of LC and RC and the $\delta^{15}N$ values of LN and RN were generally more enriched in *S. alterniflora* soil than those in *S. mariqueter* soil (Fig. 3). For both communities, the $\delta^{13}C$ value of LC was higher than that of RN except for the 40-cm soil layer in *S. mariqueter* soil (Fig. 3a vs. b). Similarly, $\delta^{15}N$ of LN was higher than that of RN (Fig. 3c vs. d). The $\delta^{13}C$ values of LC tended to decrease within the top 40-cm soil (Fig. 3a), but not for the $\delta^{13}C$ values of RC in either of the communities (Fig. 3b). In contrast, $\delta^{15}N$ values of LN were the highest in the deepest soil layer (80–100 cm) for *S. alterniflora* and in the surface sediments (0–20 cm) for *S. mariqueter* (Fig. 3c). There appeared no discernible $\delta^{15}N$ of RN trend with depth in both two communities (Fig. 3b).

A two-end member linear model Eq. (5) was used to calculate the percent of SOM derived from C_4 residues in *S. alterniflora* soil. The proportion of LC that came from *S. alterniflora* (C_4 plant) varied from 0.55% to 12.2% (Fig. 4). The lowest proportion of LC (0.55%) from C_4 sources was found in the surface soil (0–20 cm), while the greatest proportion of LC (8%–12%) from C_4 sources was observed in the top 40-cm soil, and then decreased from 60-cm to 100-cm soil (Fig. 4). However, the greatest proportion of RC (4.8%–5.8%) from C_4 sources was found in the surface soil (0–20 cm), and decreased with increasing depth (Fig. 4).

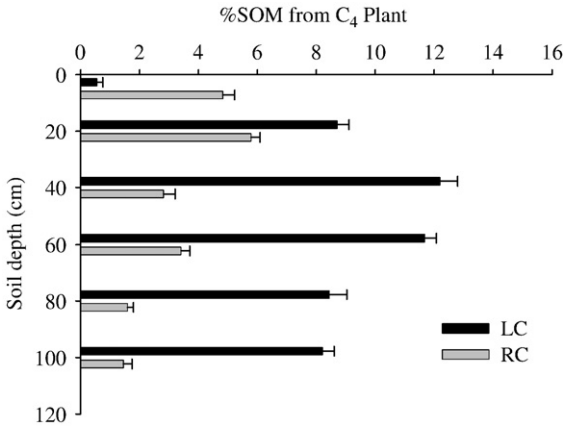

Fig. 4. Percentage contribution of *S. alterniflora* to labile and recalcitrant C in Jiuduansha wetlands in coastal Shanghai, China. Error bars represent the ±1 standard error of the means (n=6).

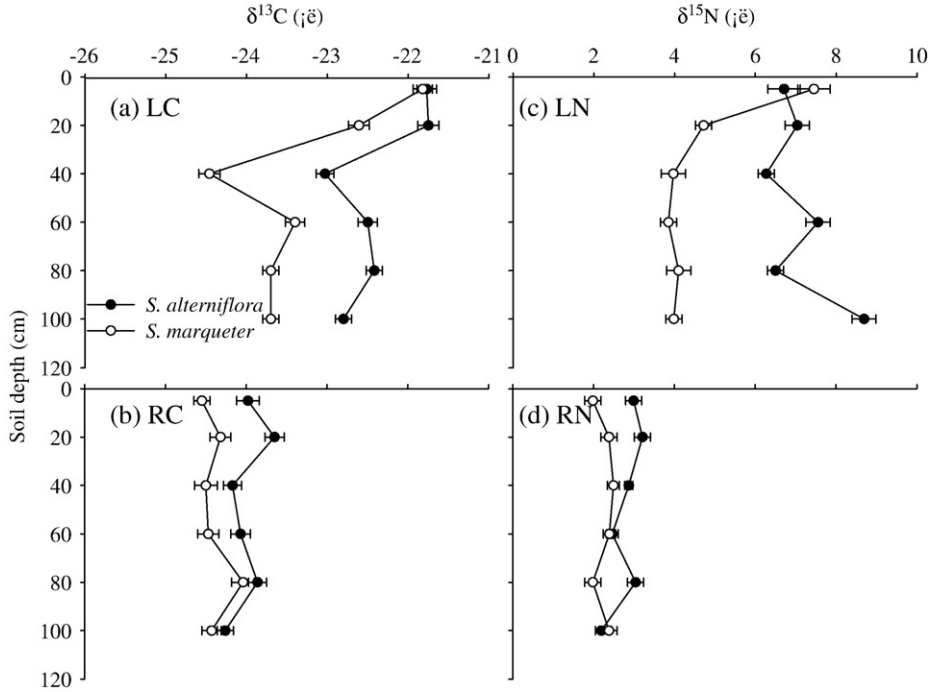

Fig. 3. The values of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) in labile and recalcitrant C and N of *S. alterniflora* and *S. mariqueter* soils in Jiuduansha wetlands in coastal Shanghai, China. Error bars represent the ±1 standard error of the means (n=6).

4. Discussion

Invasion of *S. alterniflora* on Jiuduansha Islands exerted a profound influence on soil C and N pools. Our previous study has reported that the observed increases in soil organic C and N pools under the *S. alterniflora* soil are primarily attributable to high substrate organic inputs from *S. alterniflora* plant residuals (Cheng et al., 2006b). In the present study, an 8-year invasion of *S. alterniflora* in Jiuduansha wetlands caused a significant increase in labile C, recalcitrant C, and recalcitrant N, but a decrease in labile N in soil compared to *S. mariqueter* soil (Fig. 1). Meanwhile, we found that the greater labile and recalcitrant C and N were distributed between 20 and 40 cm in the soil, and then decreased with depth in deeper soils in both two communities (Fig. 1), which might be related to the spatial distribution of root residual input and decomposition (Jobbagy and Jackson, 2000; Cheng et al., 2006b; Liao et al., 2007).

Previous studies have demonstrated that the amount of labile C is proportional to the SOM input to the soil, and LC is more impacted than RC by land management practices (i.e., vegetation change) (e.g., Ruhlmann, 1999; Biasi et al., 2005). Our results indicated that the *S. alterniflora* invasion increased the labile C content in the upper soil layers (0–60 cm) (Fig. 1a) resulting from the high substrate organic inputs from *S. alterniflora* plant residuals (Cheng et al., 2006b; Ravit et al., 2006; Liao et al., 2007). Several studies have shown that a high supply of labile C could result in an increased recalcitrant pool (Berg and Matzner, 1997; Rovira and Vallejo, 2002). We found that the recalcitrant C and N pools in the *S. alterniflora* soil were higher than those in the *S. mariqueter* soil (Fig. 1b, d), possibly from the higher SOM input into *S. alterniflora* soil (Cheng et al., 2006b). Interestingly, we found labile N content in the *S. alterniflora* soil was lower than that in the *S. mariqueter* soil (Fig. 1c). Wetland vegetation may result in N loss both through uptake and incorporation in plant biomass directly, and through stimulation of microbial processes in the rhizosphere indirectly (Schade et al., 2001). Therefore, there are two possible explanations for the low labile N content in the *S. alterniflora* soil. First, because of a large amount of below-ground biomass of *S. alterniflora*, this input of SOM would stimulate microbes in the rhizosphere, which could lead to significant labile N loss by increased rates of N cycle (e.g. Pinay et al., 1993; Schade et al., 2001; Ravit et al., 2006). Second, a great demand for N by the *S. alterniflora* plants for growth may limit the availability of labile N in the *S. alterniflora* soil (Ehrenfeld et al., 2001; Hamersler and Howes, 2005). Generally, 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), suggesting *S. alterniflora* has a higher photosynthetic efficiency and production than *S. mariqueter* (Cheng et al., 2006b). The higher C:N ratio in the *S. alterniflora* soil was consistent with higher overall C:N ratio of *S. alterniflora* tissue compared to *S. mariqueter* (Tables 2 and 3), which may potentially control ecosystem productivity in the short term (Weintraub and Schimel, 2003).

We found that the labile C accounted for 36–38% of SOM and labile N 32–48% of SOM in the two communities (Fig. 2a), and the labile C and N were much higher than most of the other values reported for labile fractionations in terrestrial soils (e.g., Hu et al., 1997; Gu et al., 2004). Numerous studies indicated that wetland soil had significantly higher labile fraction organic matter content compared with other soils e.g., upland forest, abandoned cultivated, and cultivated soils (e.g., Ravit et al., 2006; Zhang et al., 2006). In wetland soils, low O_2 concentration limited cellulolytic enzymes activity (Freeman et al., 2001), which could lead to an increase in accumulation of labile C. Moreover, the Jiuduansha wetlands were flooded daily, suggesting potential input of dissolved organic C (DOC) and dissolved organic N (DON) from the floodwaters (Chen, 2003). This additional input of C and N may likely increase the total labile pool.

It is well known that the $\delta^{13}C$ values in C_3 SOM discriminate differently along the soil profile from C_4 SOM (e.g. Nyberg et al., 2000; Henderson et al., 2004; Hansen et al., 2004). Our data suggest that the $\delta^{13}C$ abundance in labile and recalcitrant C in the *S. alterniflora* soil was more enriched than in the *S. mariqueter* soil (Fig. 3), suggesting that the $\delta^{13}C$ values in the *S. alterniflora* soil were clearly shifted toward the typical C_4 signal likely due to *S. alterniflora* residual input. Our previous study showed that the C fraction contributed from *S. alterniflora* to the soil organic C ranged from 0.90–10.64% in the top 100-cm soil layer (Cheng et al., 2006b); while Liao et al. (2007) further indicated that the percentage of net C change in soils from *S. mariqueter* (16.51 kg C m^{-2}) to *S. alterniflora* (17.11) was averaged 3.6%. In this present study, we found that the proportion of labile and recalcitrant C from *S. alterniflora* in the 0–100-cm soil layers averaged 8.3% and 3.3%, respectively, which is consistent with the ranges given by Cheng et al. (2006b) and Liao et al. (2007). The greatest proportion of labile C originating from *S. alterniflora* was distributed in the 40-cm soil layer and the smallest proportion in the soil surface soil layer (0–20 cm). The vertical variation in *S. alterniflora*-derived contribution to labile C pattern seemed associated with the vertical distribution of roots and rhizodeposition (Wedin et al., 1995; Hansen et al., 2004) because a larger proportion of *S. alterniflora* roots were concentrated in the upper 40 cm of the profile (Liao et al., 2007). The smallest proportion of labile C derived from *S. alterniflora* was in the top soil layer (0–20 cm), presumably due to both the rapid physical turnover by moving water of tides and incomplete decomposition of residuals in the soil respiration process (Wedin et al., 1995; Gu et al., 2004). In contrast, the recalcitrant C was resistant to decomposition and had longer turnover time compared to labile C (e.g., Hu et al., 2004; Biasi et al., 2005). The proportion of recalcitrant C originating from *S. alterniflora* showed a decreasing trend with depth, which was contrary to the vertical changes in labile C with the depth (Fig. 2a vs. b). The explanation for this trend may be that the LC fractionation is controlled by root inputs from the vegetation, but RC reflects slower turnover rate with depth in the soil profile.

Interestingly, the $\delta^{15}N$ values of labile and recalcitrant N were more enriched in the *S. alterniflora* soil than those in the *S. mariqueter* soil (Fig. 4). Previous studies have suggested that nutrient-rich ecosystems tended to be isotopically enriched where the nitrogen cycle is more open to N loss through denitrification and leaching compared to nutrient-poor sites (Martinelli et al., 1999; Swap et al., 2004). It is worth noting that the total N (labile N plus recalcitrant N) was higher in the *S. alterniflora* soil than that in the *S. mariqueter* soil (Fig. 1), presumably due to more exogenous N input via epiphytic N fixation and more SOM inputs in *S. alterniflora* community compared to *S. mariqueter* (Cheng et al., 2006b; Liao et al., 2007). Additionally, high N levels have been found in *S. alterniflora* sediments in native habitats via N fixation associated with microbial community (Piehler et al., 1998; Windham and Ehrenfeld, 2003). More N fixation causes lower $\delta^{15}N$ in *S. alterniflora* plant than *S. mariqueter* plant because the $\delta^{15}N$ signature of the atmosphere is around 0‰ (Table 3). However, the $\delta^{15}N$ in *S. alterniflora* soil was higher than that in *S. mariqueter* (Fig. 4). The natural abundance of ^{15}N in soil became enriched in ^{15}N by the processes of losses of N from soil (Högberg and Johannisson, 1993; Eshetu, 2004). As stated earlier, labile N loss in *S. alterniflora* soil might be caused by increased N turnover rates resulting from a large amount of root biomass that would stimulate microbes in the rhizosphere of *S. alterniflora* (e.g. Pinay et al., 1993; Schade et al., 2001). The N-rich and labile N rapid loss in *S. alterniflora* soil would explain the enrichment of $\delta^{15}N$. Our results were consistent with the evidence that the natural abundance of $\delta^{15}N$ was higher in systems where nutrients were not limiting (Martinelli et al., 1999; Swap et al., 2004). It is also important to note that the variation in soil $\delta^{15}N$ patterns are complex process that is controlled by multiple factors like N transformation processes, microbial activities, substrates, and vegetation (e.g., Schade et al., 2001; Eshetu, 2004; Watzka et al., 2006). We should acknowledge the lack of seasonal soil labile and recalcitrant C and N pools fluctuation patterns and the predictions of modified microbial activity due to *S. alterniflora* below-ground root geometry and nutrient pumping

effects. Nevertheless, our results tentatively extrapolated the short-term impact of *S. alterniflora* invasion on soil labile and recalcitrant C and N pools at temporal scales.

In summary, an 8-year invasion of *S. alterniflora* in Jiuduansha wetlands caused a significant increase in labile C, recalcitrant C, and recalcitrant N but a decrease in labile N in soil compared to *S. mariqueter* soil. The labile C accounted for an average of 36–38% of SOM in both two communities, while labile N accounted for 32% of SOM in *S. alterniflora* and 48% in *S. mariqueter*. The $\delta^{13}C$ values in *S. alterniflora* soil showed that *S. alterniflora* contributed on average 8.6% and 3.3% to the LC and RC pools, respectively, within the 0–100-cm soil layer. The greatest labile C contribution derived from *S. alterniflora* was found in the top 40-cm soil whereas the proportion of recalcitrant C originating from *S. alterniflora* showed a decreasing trend with depth. These changes appeared to be associated with vertical distributions of roots and rhizodeposition. The higher $\delta^{15}N$ values of SOM in *S. alterniflora* soil compared to *S. mariqueter* soil suggested higher denitrification rates resulting from higher microbial activity rates stimulated by greater SOM input in *S. alterniflora* soil.

Acknowledgements

This work was supported by the National Basic Research Program of China (grant no. 2006CB403305), the Natural Science Foundation of China (grant no. 30670330), and the Ministry of Education of China (grant no. 105063). We thank Ronghao Peng, Yongjian Gu, Haiqiang Guo, Chenghuan Wang, Leyi Li, and Jared DeForest for their assistance in the field samplings, lab analyses, or constructive comments on early draft of the manuscript.

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