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Litter pool sizes, decomposition, and nitrogen dynamics in *Spartina alterniflora*-invaded and native coastal marshlands of the Yangtze Estuary

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Abstract Past studies have focused primarily on the effects of invasive plants on litter decomposition at soil surfaces. In natural ecosystems, however, considerable amounts of litter may be at aerial and belowground positions. This study was designed to examine the effects of *Spartina alterniflora* invasion on the pool sizes and decomposition of aerial, surficial, and belowground litter in coastal marshlands, the Yangtze Estuary, which were originally occupied by two native species, *Scirpus mariqueter* and *Phragmites australis*. We collected aerial and surficial litter of the three species once a month and belowground litter once every 2 months. We used the litterbag method to quantify litter decomposition at the aerial, surficial and belowground positions for the three species. Yearly averaged litter mass in the *Spartina* stands was 1.99 kg m^{-2}; this was 250 and 22.8% higher than that in the *Scirpus* (0.57 kg m^{-2}) and *Phragmites* (1.62 kg m^{-2}) stands, respectively. The litter in the *Spartina* stands was primarily distributed in the air (45%) and belowground (48%), while *Scirpus* and *Phragmites* litter was mainly allocated to belowground positions (85 and 59%, respectively). The averaged decomposition rates of aerial, surficial, and belowground litter were 0.82, 1.83, and 1.27 year^{-1} for *Spartina*, respectively; these were 52, 62 and 69% of those for *Scirpus* litter at corresponding positions and 158, 144 and 78% of those for *Phragmites* litter, respectively. The differences in decomposition rates between *Spartina* and the two native species were largely due to differences in litter quality among the three species, particularly for the belowground litter. The absolute amount of nitrogen increased during the decomposition of *Spartina* stem, sheath and root litter, while the amount of nitrogen in *Scirpus* and *Phragmites* litter declined during decomposition for all tissue types. Our results suggest that *Spartina* invasion altered the carbon and nitrogen cycling in the coastal marshlands of China.

Keywords Aerial decomposition of litter · Coastal marsh · Litter allocation · Litter nitrogen dynamics · Plant invasion · *Spartina alterniflora* · Yangtze Estuary

Introduction

Biological invasions not only threaten the integrity of native ecosystems worldwide but also potentially alter ecosystem biogeochemical cycles. Litter decomposition is a significant component of the carbon (C) and nitrogen (N) cycles. How plant invasions alter litter decomposition is a major issue in invasion ecology. A review by Ehrenfeld (2003) of 12 reported cases of invaded ecosystems found that—in comparison with the respective native ecosystems—litter mass increased in six of the cases, decreased in five, and remained unchanged only in one case. In general, invasive plants tend to have higher rates of litter

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decomposition than native species, resulting in accelerated N cycling in invaded ecosystems (Ehrenfeld 2003; Allison and Vitousek 2004; Liao et al. 2008). The increased rate of litter decomposition can be attributed primarily to a higher litter quality, such as a higher N concentration in the litter of the invasive plant species relative to that of the native plants (e.g., Allison and Vitousek 2004; Liao et al. 2008).

Past studies have mainly focused on the effects of invasive plants on litter C and N dynamics at soil surfaces. In natural ecosystems, however, aboveground litter does not necessarily fall onto the soil surface immediately after shoot death, resulting in a considerable amount of aboveground litter remaining in the air (the so-called 'aerial litter') for a substantial period (Kuehn et al. 2004). An abundance of fungal and bacterial taxa has been recorded in aerial litter (e.g., Poon and Hyde 1998; Denward et al. 1999). A large amount of CO_2 can be released from aerial litter by microbial decomposition (e.g., Kuehn et al. 2004) and by photodegradation (Denward and Tranvik 1998; Denward et al. 1999; Gessner 2001; Austin and Vivanco 2006). In addition, belowground litter production is substantial (e.g., Roman and Daiber 1984; Gross et al. 1991). To better understand the effects of plant invasion on C and N cycles, it is necessary to quantify the pool sizes, decomposition rates, and N dynamics of both aerial and belowground litter, especially when these two components account for large fractions of the total litter mass.

Spartina alterniflora Loisel, a C_4 grass native to the east coast of North America, was intentionally introduced to China in 1979 and has rapidly invaded marshlands on the east coast of China since then. The Yangtze Estuary is one of the regions heavily invaded by *Spartina* (Wang et al. 2006; Li et al. 2008). *Spartina* has rapidly spread throughout marshlands, which were previously dominated by the native species *Scirpus mariqueter* Tang et Wang and *Phragmites australis* (Cav.) Trin. Ex Steud, forming dense pure stands. Both *Scirpus* and *Phragmites* are C_3 grasses. *Spartina* has a larger biomass than *Scirpus* and *Phragmites* (Chen 2003). According to field observations, *Spartina* and the two native species differ in a number of phenological and morphological traits (e.g., shoot height and culm diameter) (Liao 2007). The dead shoots of *Spartina* and *Phragmites* remain standing in aerial positions for a long period. Interestingly, *Phragmites* is also an invasive species and has rapidly expanded into *Spartina* marshlands along the east coast of the USA. Past studies have shown that *Phragmites* significantly differs from *Spartina* in the USA in plant N concentration (Roman and Daiber 1984), plant biomass and N stock (Windham et al. 2003), but not in the decomposition rate of surficial litter (Windham et al. 2004). However, there is no information in the literature on whether *Spartina* differs in litter C and N dynamics from *Scirpus* and *Phragmites* along the east coast of China.

This study was designed to examine the effects of *Spartina* invasion on litter pool sizes, decomposition rates, and N dynamics during the decomposition of aerial, surficial, and belowground litter and to compare these with those found in *Scirpus* and *Phragmites* ecosystems in the coastal marshlands of the Yangtze Estuary. We measured aerial and surficial litter of the three species once a month and belowground litter once every 2 months in the Jiuduansha marshlands of the Yangtze Estuary. Using the litterbag method, we quantified litter decomposition rates and N immobilization and mineralization rates of these three species during decomposition at the aerial, surficial and belowground positions.

Materials and methods

Sites

Our study was conducted in the Jiuduansha marshlands, which are alluvial wetlands located in the Yangtze Estuary (30°10′N, 122°01′E) with a surface area of 3294 ha (Wang et al. 2006; Liao 2007; Liao et al. 2007). The mean annual air temperature is 15.7°C, with a monthly minimum of 4.2°C in January and a monthly maximum of 27.3°C in July. The mean annual precipitation is 1145 mm, with most of it concentrating in the summer. The mean annual salinity of the sea water is 11.7‰. The Jiuduansha marshlands have been rarely disturbed by human activities, and the plant communities in the marshlands are relatively simple. Before *Spartina* invaded, the two dominant native plant species in the marshlands were *Scirpus* and *Phragmites*. *Scirpus* is a species endemic to the Yangtze Estuary, and *Phragmites* is a cosmopolitan species widely distributed in freshwater and coastal marshlands throughout the world. All three species are perennials with overwintering belowground organs (rhizomes for *Spartina* and *Phragmites*, and rhizomes and corms for *Scirpus*). In the marshlands, *Spartina*, *Scirpus*, and *Phragmites* each build pure stands with clear boundaries separating them. The pure stands made it possible to quantify the changes in the pool size of belowground litter and assess the vertical patterns of litter mass caused by *Spartina* invasion. The major ecophysiological traits of the three species are listed in Table 1.

A 3-km transect was established in 2003 in the marshlands that intersected the monocultures of *Spartina*, *Scirpus* and *Phragmites*. Eight sites at the same elevation (measured by a theodolite), with intervals of approximately 300 m between sites, were selected along the transect. Due to the harsh working conditions in the estuarine wetlands, only four of the eight sites were used for sampling litter mass; the remaining four were used for decomposition experiments (Liao et al. 2007). At each of the eight sites,

Table 1 Key characteristics of *Spartina*, *Scirpus* and *Phragmites* (data are from Liao 2007)

Characteristics	*Spartina*	*Scirpus*	*Phragmites*
Stem height (cm)	143.3 b	40.4 c	212.9 a
Culm diameter (cm)	1.06 a	0.19 c	0.65 b
Shoot density (ramets m^{-2})	86 b	3735 a	49 c
Area per leaf (cm^2)	76.5 a	11.7 b	65.6 c
Yearly averaged leaf area index (m^2 m^{-2})	4.40 a	2.95 b	2.11 c
Yearly averaged net photosynthetic rate (μmol CO_2 m^2 S^{-1})	24.44 a	6.72 c	15.85 b
Season of ramet sprouting	End of February	Middle of April	End of March
Season of ramet senescence (partly yellow)	End of November	End of October	Beginning of November
Live aboveground plant N (%)	0.71 c	1.85 a	0.87 b
Live belowground plant N (%)	0.55 b	1.18 a	0.99 a
Net primary production (kg C m^{-2} $year^{-1}$)	2.16 a	0.72 c	1.69 b
Soil moisture (m %)	65 a	55 a	49 b
Soil bulk density (g cm^{-3})	1.14	1.18	1.18
Total soil C content (kg C m^{-3})	16.94 a	16.35 b	16.40 b
Total soil N content (g N m^{-3})	643.3 a	584.8 b	504.9 c

Most measurements were made in September 2004. Net primary production, soil bulk density, and total soil C and N contents were measured in soils to a depth of 100 cm

Values followed by different letters indicate significant differences among species within the row at $P < 0.05$

there were pure stands of all three species, which were adjacent to each other. Each pure stand had an area of about 4 ha. We used these adjacent stands at the same site to reduce the effects of environmental heterogeneities on litter pool sizes and litter decomposition (Delaune et al. 1983; Day et al. 1988).

Litter sampling

Aerial and surficial litter was collected in November 2003 and February, March, April, May, July, August, September, and December 2004. In each sampling area, we collected aerial and surficial litter within three quadrats of 1 × 1 m. Belowground litter was collected in November 2003 and February, April, July, September, and December 2004—after the aboveground litter had been removed—down to a depth of 100 cm, using a steel auger (inner diameter 14.2 cm). All samples were washed with clean water using a sieve (mesh size 0.45 mm) immediately after collection. Live plant tissues in the collected litter were separated by color and texture (Valiela et al. 1976). All samples were then oven-dried at 50°C to a constant weight and weighed.

Quantification of litter decomposition

The litter decomposition was quantified by the litterbag method. This method is associated with a number of limitations: (1) it may underestimate the decomposition rates due to an oven-dried-litter process that kills some of colonized microorganisms before collection due to the exclusion of detritivores from the consumption of litter (e.g., Dornbush et al. 2002); (2) the collection of litter may cut off nutrient retranslocations of plant tissues during senescence (Newell and Fallon 1989; Gessner 2001); (3) the decomposition rates quantified solely by this method may not provide reliable predictions of litter dynamics in the real world. However, this method does enable the decomposition rates obtained to be compared among species and with other decomposition studies (e.g., Austin and Vitousek 2000).

At the end of the 2003 growing season, plant litter for each of the three species was collected just before it fell on the ground. *Spartina* and *Phragmites* shoot litter was separated into leaf, sheath, and stem litter, and their belowground litter into rhizome and root litter to account for any differences in initial litter quality of various tissues that might influence decomposition (Hackney and Cruz 1980; Windham et al. 2004). *Scirpus* litter was separated only into aboveground and belowground litter because of their relative simple structures (Chen 2003). The separated litter tissues were oven-dried at 50°C (Eviner 2004) and placed into 20 × 20-cm litterbags. Ten grams of either leaf or sheath litter and 20 g of either stem or rhizome litter were put into litterbags with a mesh size of 1.0 × 0.7 mm, and 5 g of root litter was placed into litterbags with a small mesh size of 0.2 × 0.2 mm. We employed the small mesh bags for root litter because the diameter of the roots was less than 0.5 mm. Filled litterbags were sealed shut with fiberglass thread. Subsamples were analyzed for initial C, N, and lignin concentrations of the litter. Seven litterbags for stem, sheath, leaf, and rhizome litter and four litterbags for root litter were placed at each site within their respective community of each species in January 2004 for a total of 496 litterbags. Litterbags were either hung from PVC pipes with string at a height of 1.3 m (aerial decomposition), placed on the soil surface (surficial decomposition) or buried below the ground at a depth of 20 cm (belowground decomposition) (Romero et al. 2005). One litterbag of each plant tissue for each species was randomly retrieved from each of the four sites after 29, 60, 101, 168, 257, 300 and 359 days (aerial decomposition), after 29, 60, 101, 136, 168, 208, 257 days (surficial litter decomposition and for rhizome litter decomposition of *Spartina* and *Phragmites*), or after 29, 60, 101, 168 days (root litter decomposition). Retrieved materials were rinsed clean in water, and the remaining litter was oven-dried at 50°C for 10 days before being weighed.

Analysis of chemical composition of litter

All litter samples were ground to powder in a Wiley mill and then analyzed for litter C and N concentrations with a NC Soil Analyzer (Flash EA 1112 Series; Thermo Finnigan, Elk Grove Village, IL). The remainder of the sample powder was used to determine the acid detergent lignin (lignin) concentration following the method of van Soest (1963) using a raw fiber extractor (model Fiwe; VELP Scientifica, Milan, Italy).

Statistical analysis

Litter decomposition is usually described by a negative exponential equation as

$$y = ae^{-k_1 t} \tag{1}$$

where y is the percentage of litter mass remaining at time t (year), k_1 (year^{-1}) is the exponential decomposition constant, and a is a coefficient. The litter decomposition data are also fit by a linearized equation (Austin and Vivanco 2006) as:

$$\mathrm{Ln}(y) = -k_2 t + b \tag{2}$$

Conceptually, k_2 is identical to k_1. They could be different when one data set was fitted by the nonlinear versus linearized equations (i.e., Eqs. 1 vs. 2). In addition, our litter decomposition study was conducted in the field with seasonal variations in temperature. To correct for temperature effects on little decomposition, we assumed that the decomposition constant is a function of temperature as:

$$k_3 = de^{cT} \tag{3}$$

where d and c are coefficients, T is the average of air temperature (°C) in the month before the litterbags were removed from the fields for analysis. The substitution of Eq. 3 into Eq. 1 leads to:

$$y = ae^{(-de^{cT})t} \tag{4}$$

We used Eqs. 1, 2, and 4 to fit decomposition data. Data on the air temperature were obtained from the eddy fluxes towers in Chongming islands (Bin Zhao, unpublished data), which are about 35 km away from our experimental sites. The decomposition constant (k_2) obtained with Eq. 2 was used for comparison among litter positions and species and with other decomposition studies (Austin and Vitousek 2000). The k_2 values estimated using Eq. 2 were integrated for different plant tissues at each position and weighed by their respective litter mass in order to estimate the averaged k values for *Spartina* and *Phragmites*. This averaging method is statistically valid because our data sets satisfied the criteria of normality and homogeneity.

To meet the assumption of normalities for statistical analysis, data of litter mass and litter N stocks in stands were cubic-root transformed. Interactive effects of plant tissue (or species), position, and sampling date on decomposition rates were analyzed by the homogeneity of the slope of a general linear models. Repeated-measures ANOVA was used: (1) to test the effects of species and sampling dates on the total litter mass and the total litter N stocks in stands of the three species; (2) to examine differences between two species or among the three species in terms of litter N remaining, lignin concentration, and lignin:N and C:N ratios of litter when they were sampled at the same time during decomposition. One-way ANOVA was used to examine the differences in initial litter N concentration and the litter C:N ratio for a given plant tissue between two species or among the three species. Nested ANOVA was used to test the site effects on the yearly averaged total litter mass and N stock, and on the averaged k values at each position across species. Tukey's post hoc tests were applied to examine the differences between the three species after ANOVA, which were considered to be significant at the level of $P < 0.05$. Student's t tests were used to examine the differences in the overall k value between the three species. STATISTICA ver. 6.0 software (StatSoft, Tulsa, OK; http://www.statsoft.com) was used to conduct all statistical analyses.

Results

Litter mass and N stock

The yearly averaged litter mass was 1.01, 0.13, and 0.85 kg m^{-2}, respectively, for the aerial (Fig. 1a), surficial (Fig. 1b) and belowground litter (Fig. 1c) in *Spartina*

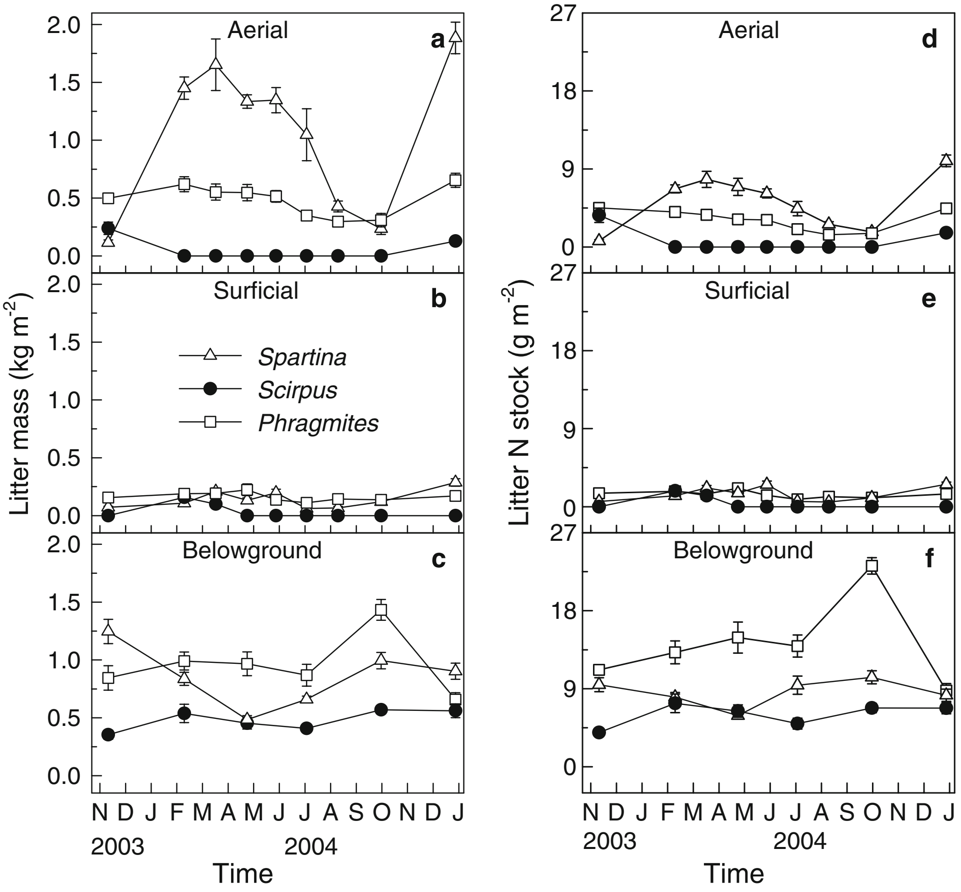

Fig. 1 Seasonal dynamics of litter mass (**a**–**c**) and litter N stock (**d**–**f**) of the invasive species *Spartina* and the two native species *Scirpus* and *Phragmites* at the aerial (**a**, **d**), surficial (**b**, **e**), and belowground positions (**c**, **f**). *Vertical bars* represent standard errors ($n = 12$)

stands; 0.06, 0.03, and 0.48 kg m^{-2} for the corresponding components of litter in *Scirpus* stands; 0.50, 0.16, and 0.96 kg m^{-2} for corresponding components of litter in *Phragmites* stands. The total litter mass in *Spartina* stands was 250 and 22.8% higher than that in *Scirpus* and *Phragmites* stands, respectively ($F_{2,\ 33} = 103$, $P < 0.001$). Litter in *Spartina* stands was primarily distributed in the air (45 ± 3%; mean ± SE) and belowground (48 ± 3%), with a small fraction (7%) at soil surfaces. Similarly, the *Phragmites* litter was primarily allocated to the air (31 ± 1%) and belowground (59 ± 2%). In contrast, *Scirpus* litter was mainly allocated belowground (88 ± 2%). The aerial litter mass of *Spartina* displayed a strongly seasonal variation—high in winter and spring and low in summer and autumn—while the litter mass of the other two species did not show a clear seasonality.

The yearly averaged litter N stock was 5.1, 1.3 and 8.6 g m^{-2}, respectively, for the aerial (Fig. 1d), surficial (Fig. 1e) and belowground litter (Fig. 1f) in *Spartina* stands, with a total of 15.0 g m^{-2}. The total litter N stock in *Spartina* stands was 7.3 g m^{-2} higher than that in *Scirpus* stands but 4.1 g m^{-2} lower than that in *Phragmites* stands ($F_{2,\ 33} = 54$, $P < 0.001$) (Fig. 1d–f). In particular, *Spartina* stands had a greater allocation (31 ± 2%) of litter N stock to the air than *Scirpus* (11 ± 2%) and *Phragmites* stands (19 ± 1%). The seasonal dynamics of litter N stock differed significantly between *Spartina* and the two native species at the aerial ($F_{16,\ 264} = 22$, $P < 0.001$) and belowground ($F_{10,\ 165} = 11$, $P < 0.001$) positions.

Litter decomposition

Litter decomposition for the three species was regulated by air temperature, particularly for aerial decomposition, as reflected by the patterns of mass remaining (Fig. 2). In terms of aerial decomposition for all three species, litter mass declined slowly from January to April and quickly from May to September (Fig. 2a–c). The slow mass loss from January to April was due to low temperature. This was reflected by the correlation coefficient (R), which was higher when Eq. 4 and not Eq. 1 or 2 was used to fit the data of aerial litter decomposition for a specific litter tissue (Table 2) because Eq. 4 considered monthly variations in air temperature over the year. Nevertheless, the data of litter decomposition were well fit by all three equations in our study (for all regressions, $P < 0.001$). The decomposition constants estimated by the three equations were very similar (Table 2).

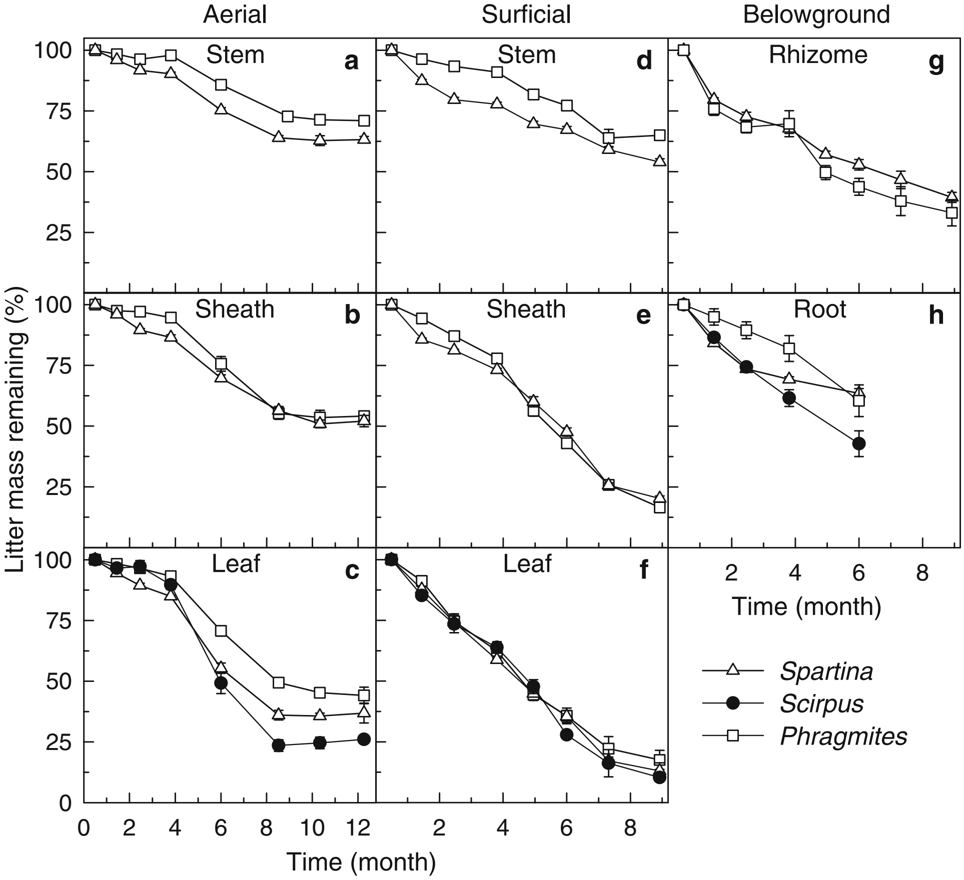

Fig. 2 Litter mass remaining of stem (**a**, **d**), sheath (**b**, **e**), leaf (**c**, **f**), rhizome (**g**), and root litter (**h**) of *Spartina, Scirpus* and *Phragmites* during decomposition at the aerial (**a**–**c**), surficial (**d**–**f**), and belowground positions (**g**, **h**). *Vertical bars* represent standard errors ($n = 4$)

Litter decomposition differed between *Spartina* and the two natives at each of the three positions (for all analyses, $P < 0.05$; Table 3, Fig. 2). Overall, litter decomposition rates (k_2) at the aerial, surficial, and belowground positions, respectively, were 0.82, 1.83 and 1.27 year^{-1} for *Spartina* (Table 3), which were, respectively, 158, 144 and 78% of those for *Phragmites*, and 52, 62 and 69% of those for *Scirpus*. For both *Spartina* and *Phragmites*, the aerial decomposition was significantly slower than the surficial and belowground decomposition (for all, $P < 0.001$). For *Scirpus*, the decomposition of aerial litter was significantly slower than that of surficial litter ($F_{1,\,60} = 44$, $P < 0.001$) but not different from that of the belowground litter ($F_{1,\,48} = 1.8$, $P = 0.18$). Site did not affect decomposition rate at any positions across species (for all, $P > 0.05$).

Litter quality

The initial N concentrations in the litter of *Spartina* stem, sheath, and root were significantly lower than those of the corresponding litter components of *Phragmites* (for all, $P < 0.001$), but they were similar in the leaf and rhizome litter (Table 3). Both the aboveground and belowground litter of *Scirpus* had higher initial N concentrations than *Spartina* and *Phragmites* (for all, $P < 0.001$).

The litter N content of *Spartina* differed significantly, at all three positions, from that of *Scirpus* and *Phragmites* during decomposition (for all, $P < 0.001$; Fig. 3). The N content significantly increased to 290% of the initial value for *Spartina* stem litter after 6 months of aerial decomposition (Fig. 3a) and to 150% for sheath litter after 2 months (Fig. 3b). Based on the amount of increased N content and the litter mass in November 2003, the net N input into the litter from the aerial decomposition was estimated to be at least 4.8 g N m^{-2} year^{-1} in *Spartina*. The N contents of *Spartina* stem, sheath, and root litter also increased slightly during decomposition at soil surfaces and belowground (Fig. 3d, e, h). However, no similar increase in N contents was observed during decomposition for the litter of the two native species. The N contents of leaf litter continuously decreased during aerial or surficial decomposition for all three species (Fig. 3c, f).

Lignin concentrations of *Spartina* litter were significantly lower than those of corresponding components of *Scirpus* and *Phragmites* litter at each position during the decomposition period of nearly 1 year (for all, $P < 0.001$; Fig. 4). However, the lignin:N ratio of rhizome litter and the C:N ratios of rhizome and root litter of *Spartina* were higher than those of the corresponding components of *Scirpus* and *Phragmites* litter during decomposition (for all, $P < 0.001$).

Table 2 Parameter values and correlation coefficient (*R*) derived from fitting decomposition data by Eq. 1: $y = ae^{-k_1 t}$, Eq. 2: Ln (y) = $-k_2 t + b$, and Eq. 4: $y = ae^{(-de^{cT})t}$, where y is percentage of mass remaining, t is time, and T is the monthly average of air temperature

Species	Tissue type	Position	Equation 1		Equation 2		Equation 4			
			k_1	R	k_2	R	d	c	k_3	R
Spartina	Stem	Aerial	0.54	0.97	0.54	0.97	0.41	0.017	0.54	0.99
		Surficial	0.93	0.97	0.91	0.97	1.33	−0.016	1.01	0.98
	Sheath	Aerial	0.74	0.98	0.74	0.97	0.60	0.012	0.74	0.99
		Surficial	1.72	0.96	2.00	0.95	0.84	0.033	1.58	0.98
	Leaf	Aerial	1.14	0.96	1.18	0.95	0.77	0.024	1.14	0.98
		Surficial	2.31	0.98	2.73	0.94	1.48	0.022	2.24	0.99
	Rhizome	Belowground	1.44	0.96	1.39	0.95	2.07	−0.017	1.55	0.97
	Root	Belowground	1.24	0.89	1.17	0.87	2.12	−0.032	1.40	0.99
Phragmites	Stem	Aerial	0.37	0.95	0.37	0.95	0.29	0.014	0.37	0.96
		Surficial	0.60	0.94	0.62	0.93	0.25	0.038	0.47	0.97
	Sheath	Aerial	0.66	0.94	0.69	0.94	0.49	0.018	0.66	0.95
		Surficial	1.73	0.94	2.15	0.93	0.53	0.055	1.56	0.99
	Leaf	Aerial	0.82	0.95	0.87	0.95	0.64	0.015	0.82	0.96
		Surficial	2.16	0.97	2.48	0.92	1.40	0.022	2.08	0.98
	Rhizome	Belowground	1.74	0.92	1.74	0.87	2.19	−0.011	1.82	0.92
	Root	Belowground	0.91	0.85	0.99	0.83	0.54	0.028	0.81	0.88
Scirpus	Leaf	Aerial	1.37	0.95	1.58	0.93	0.80	0.033	1.41	0.95
		Surficial	2.36	0.96	2.96	0.93	1.26	0.031	2.28	0.98
	Root	Belowground	1.80	0.97	1.85	0.94	1.76	0.002	1.80	0.97

k_3 was computed from d and c according to Eq. 3 in text. All R values are significant at $P < 0.001$

Coefficient a in Eqs. 1 and 4 was set to 100, and coefficient b in Eq. 2 was set to 4.60517 before k values were estimated since initial mass had been standardized to be 100%

Table 3 Initial litter N concentration and C:N ratio, mean lignin:N ratio during decomposition, and decomposition rate (k) estimated from the litterbag method for the invasive species *Spartina* and the two native species *Phragmites* and *Scirpus*

Species	Tissue	Initial N concentration (%)	Initial C:N ratio	Mean lignin:N ratio	k_2 (year^{-1})		
					Aerial	Surficial	Belowground
Spartina	Stem	0.24 ± 0.01	177.1 ± 6.67	40.85 ± 1.21	0.54 ± 0.01	0.91 ± 0.01	
	Sheath	0.34 ± 0.01	114.0 ± 1.86	31.19 ± 0.54	0.74 ± 0.04	2.01 ± 0.02	
	Leaf	1.40 ± 0.02	27.80 ± 0.41	6.26 ± 0.17	1.18 ± 0.05	2.73 ± 0.16	
	Rhizome	0.57 ± 0.03	64.80 ± 1.04	27.39 ± 1.38			1.39 ± 0.05
	Root	0.69 ± 0.00	53.32 ± 0.57	19.52 ± 0.70			1.17 ± 0.04
Average					0.82 ± 0.03	1.83 ± 0.07	1.27 ± 0.05
Phragmites	Stem	0.68 ± 0.02	64.12 ± 1.51	25.65 ± 1.41	0.37 ± 0.02	0.62 ± 0.03	
	Sheath	1.07 ± 0.02	34.24 ± 0.77	16.69 ± 0.15	0.69 ± 0.05	2.15 ± 0.07	
	Leaf	1.46 ± 0.02	26.52 ± 0.35	10.50 ± 0.11	0.87 ± 0.05	2.48 ± 0.27	
	Rhizome	0.51 ± 0.01	57.50 ± 0.30	21.72 ± 0.79			1.74 ± 0.15
	Root	0.83 ± 0.01	39.54 ± 0.20	18.19 ± 0.71			0.99 ± 0.18
Average					0.52 ± 0.03	1.27 ± 0.08	1.63 ± 0.15
Scirpus	Leaf	1.55 ± 0.02	23.07 ± 0.23	13.38 ± 0.24	1.58 ± 0.07	2.96 ± 0.18	
	Root	1.13 ± 0.03	31.25 ± 0.81	19.33 ± 0.69			1.85 ± 0.22

All values are given as the mean ± 1SE ($n = 4$). The average decomposition rates in each of the positions were obtained on the basis of the stem:sheath:leaf ratio of senescent litter mass, which was 40:24:36 and 61:24:15 in November 2003 for *Spartina* and *Phragmites*, respectively, and on the rhizome:root ratio of mean annual biomass, which was 74:26 and 85:15 from November 2003 to December 2004, respectively (Liao 2007)

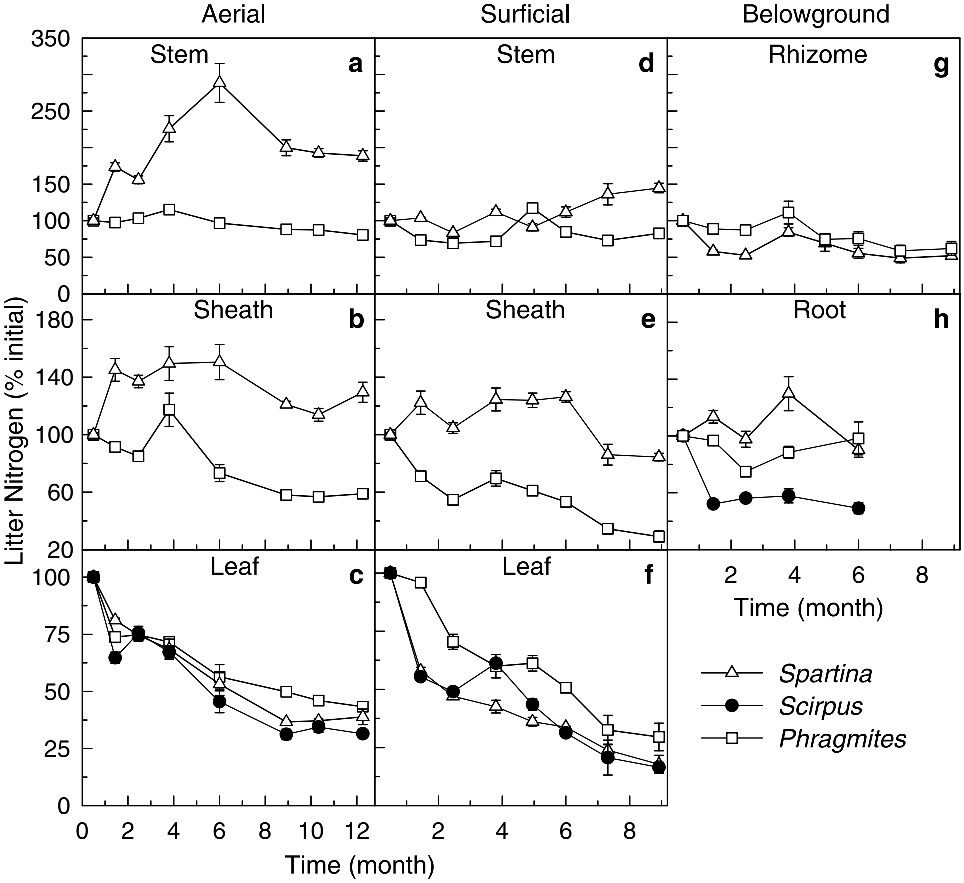

Fig. 3 Nitrogen dynamics (expressed as the percentage of initial content) of stem (**a**, **d**), sheath (**b**, **e**), leaf (**c**, **f**), rhizome (**g**), and root litter (**h**) of *Spartina, Scirpus* and *Phragmites* during decomposition at the aerial (**a**–**c**), surficial (**d**–**f**), and belowground positions (**g**, **h**). *Vertical bars* represent standard errors ($n = 4$)

Discussion

Impact of position on litter decomposition

Our results showed that large fractions of litter mass were distributed to the aerial position as standing litter for *Spartina* and *Phragmites* and to the belowground for all three species. Surficial litter mass accounted for a small fraction of the total litter (Fig. 1a–c). Several studies (e.g., Newell 1993; Kuehn et al. 2004; Schubauer and Hopkinson 1984) have shown that a considerable amount of aerial litter remains standing for an extended period in marshlands. Roman and Daiber (1984) demonstrated that a large fraction of net primary production is allocated belowground for many species in salt marshes. Belowground litter production is substantial (e.g., Schubauer and Hopkinson 1984; Gross et al. 1991; Netto and Lana 1999). Thus, it is essential to quantify decomposition rates of aerial and belowground litter for a comprehensive understanding of the effects of plant invasion on litter decomposition.

Litter decomposition rates were lower at the aerial than surficial positions (Table 3, Fig. 2), probably due to lower water availability at the former. Water availability is an important factor in regulating microbial activities during litter decomposition (Kuehn et al. 1998; Kuehn and Suberkropp 1998). The litterbags used for assessing aerial decomposition were hung at a height of 1.3 m; they were therefore beyond the reach of tidal water with the exception of extreme climatic events, such as typhoons. In contrast, tidal water submerged the surficial litter eight to ten times a month. Thus, water availability was likely lower for aerial than surficial litter decomposers.

The decomposition rates of aerial litter ranged from 0.37 to 1.58 year^{-1} in our study (Table 3). These values were higher than those ($k = 0.3 \sim 0.4$ year^{-1}) reported by Austin and Vivanco (2006). Their experiments of aerial decomposition were conducted in a semi-arid ecosystem, and photodegradation was the major mechanism underlying the mass loss of aerial litter. However, humidity in the stands of coastal marshlands is high. Microbial decomposers that have adapted to the moist conditions can relatively easily colonize the aerial litter (Kuehn and Suberkropp 1998; Kuehn et al. 2004).

Effects of *Spartina* invasion on C and N cycling

Spartina invasion increased the total litter pool size in comparison to the size of the litter pool produced by the two native species (Fig. 1a–c). Litter pool sizes are

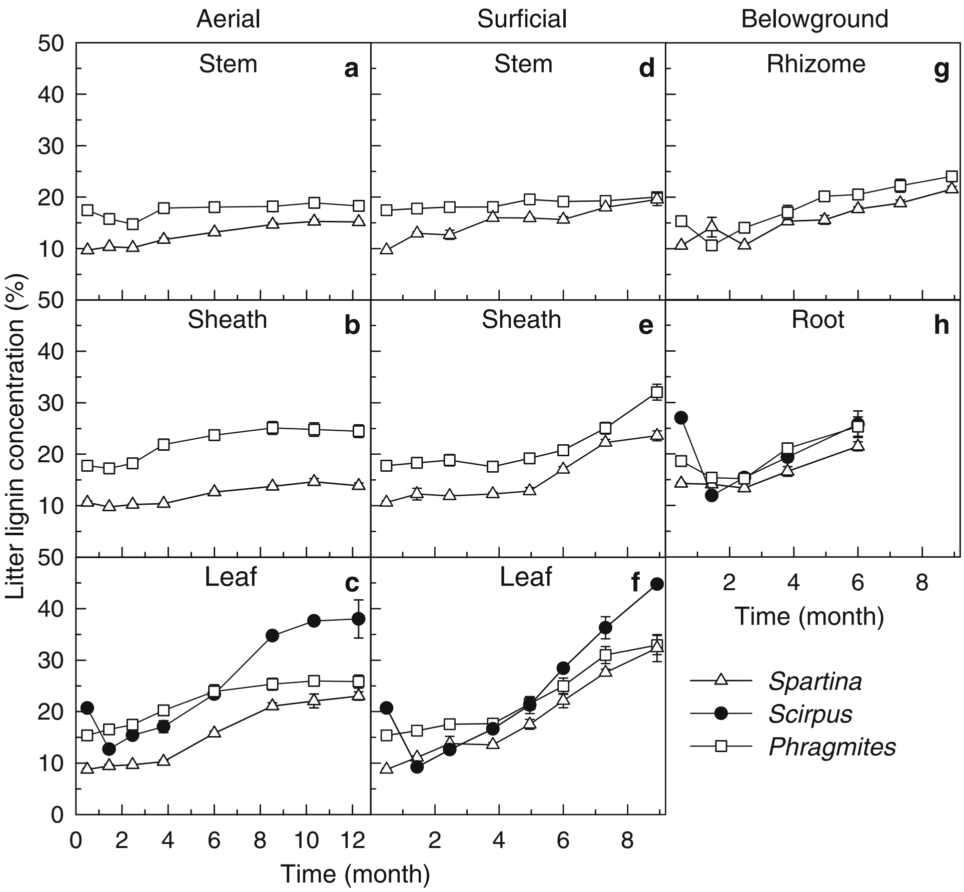

Fig. 4 Temporal changes in the lignin concentration of stem (**a**, **d**), sheath (**b**, **e**), leaf (**c**, **f**), rhizome (**g**), and root litter (**h**) of *Spartina, Scirpus* and *Phragmites* during decomposition at the aerial (**a**–**c**), surficial (**d**–**f**), and belowground positions (**g**, **h**). *Vertical bars* represent standard errors ($n = 4$)

controlled by both litter production and decomposition. Net primary production of *Spartina* stands was 200 and 28% greater than that of *Scirpus* and *Phragmites* stands, respectively (Table 1). In addition to a small fraction of plant biomass that may be consumed by herbivores in marshlands (Daehler and Strong 1995), the aboveground parts of all three species die annually, thereby producing litter. Thus, the litter production of *Spartina* was greater than that of *Scirpus* and *Phragmites*. Moreover, *Spartina* litter decomposed more slowly than *Scirpus* litter at all three positions and more slowly than *Phragmites* litter at the belowground position (Table 3), resulting in a high accumulation of litter mass in *Spartina* stands. Spatially, the area covered by *Spartina* stands was about 1080 ha (32.8% of the total marshland area) in Jiuduansha wetlands in 2003 (Wang et al. 2006), 4553 ha (21.4%) in the Yangtze Estuary in 2003 (Huang et al. 2005), and 1.12×10^5 ha along the east coast of China in 2002 (Wang et al. 2006). As *Spartina* is still spreading rapidly along the east coast of China (Huang et al. 2005; Wang et al. 2006), the size and allocation of litter C pools at the three positions will be altered in invaded ecosystems in comparison to native ecosystems.

Our litter decomposition results were inconsistent with those reported in previous studies in which, in most cases, invasive species had higher decomposition rates than native species at soil surfaces (e.g., Ehrenfeld 2003; Allison and Vitousek 2004). Variations in litter decomposition rates among *Spartina*, *Scirpus* and *Phragmites* can be explained by differences in their litter quality (Berg and McClaugherty 2003). Litter quality is commonly defined in terms of the initial N concentration, lignin concentration, or C:N and lignin:N ratios. The lower initial N concentration of *Spartina* litter may explain the lower decomposition rate relative to that of *Scirpus* at each position (Table 3) (e.g., Windham and Ehrenfeld 2003). The lower lignin concentration in the aboveground litter of *Spartina* could account for its aerial and surficial decomposition rates being higher than those of *Phragmites* (Fig. 4a–f) (e.g., Chimney and Pietro 2006). However, the higher ratios of the initial C:N and the mean lignin:N in *Spartina* belowground litter (Table 3) could largely explain the observed lower decomposition rates of *Spartina* belowground litter relative to that of *Phragmites* (e.g., Chimney and Pietro 2006; Vivanco and Austin 2006). The lower decomposition rate of belowground litter could result in an accumulation of soil organic matter (Berg and McClaugherty 2003), which can explain why we found higher total soil C content in *Spartina* ecosystems than in *Scirpus* and *Phragmites* ecosystems (Table 1).

Increases in the N content of *Spartina* stem and sheath litter during decomposition may result from the N_2 fixation of epiphytic microbial communities (Currin and Paerl 1998). The cyanobacteria are believed to be the microorganisms primarily responsible for N_2 fixation. The amount of additional N added into the invaded ecosystems was substantial when compared with other influxes of N (Currin and Paerl 1998). The increased litter N content can be incorporated into soil during decomposition (Knops et al. 2002), leading to higher soil N stock under *Spartina* stands than that under either *Scirpus* or *Phragmites* stands (Table 1). The loss of N from *Scirpus* and *Phragmites* litter during decomposition is likely a result of a higher initial N concentration and a lower initial C:N ratio than those found in *Spartina* litter (Table 3) (Parton et al. 2007). However, several other studies in the USA (Murkin et al. 1989; Findlay et al. 2002; Windham and Ehrenfeld 2003) have found increases in the N content of *Phragmites* litter during surficial decomposition. Findlay et al. (2002) and Windham and Ehrenfeld (2003) both pointed out that the increase in the N content of *Phragmites* litter during surficial decomposition was caused by exogenous N immobilization from soil into litter due to the low initial N concentration of the litter.

Environmental conditions that regulate litter decomposition could be potentially different among the three species stands in the Jiuduansha marshlands due to differences in canopy shading, as indicated by leaf area index (Table 1). However, our 45-day-long glasshouse experiment on aerial decomposition confirmed that the decomposition rate of *Spartina* stem litter was higher than that of *Phragmites* stem litter and that litter N content increased in *Spartina* stem litter, which did not occur in *Phragmites* litter (Liao 2007). Moreover, increased N concentrations of stem and sheath litter of *Spartina* were also observed after 1 year of aerial decomposition at six sites along the east coast of China (Liao 2007). Therefore, we conclude that our findings on the impacts of *Spartina* invasion on litter C and N cycling are robust despite the limitations of the litterbag method and potential differences in environmental conditions among the three species stands in the Jiuduansha marshlands. Underlying mechanisms and issues related to increases in N content during the decomposition of *Spartina* litter have to be examined in future studies. For example, why is the increase in N content of *Spartina* stem or sheath litter much greater during aerial than surficial decomposition (Fig. 3)?

Comparisons between China and the USA

Spartina and *Phragmites* are two reciprocal invasive species between China and the USA. *Spartina* is native to the east coasts of the USA but has invaded the east coasts of China. *Phragmites* is native to the east coasts of China but has invaded the east coasts of the USA. Table 4 shows that both *Spartina* and *Phragmites* in China had a larger peak total biomass and plant N stock and that the leaf litter had a higher surficial decomposition rate than their counterparts in the USA. *Phragmites* had larger total peak biomass and plant N stock but a lower shoot density and a lower mean concentration of N in aboveground litter than *Spartina* along the east coast of the USA. However, Windham et al. (2004) have shown that *Phragmites* did not differ from *Spartina* in surficial decomposition rates of leaf (0.95 year^{-1}) and stem litter (2.04 year^{-1}) in the USA. In the USA, the N content of the aboveground litter of both *Spartina* and *Phragmites* was observed to increase significantly during surficial decomposition (e.g., Frasco and Good 1982, Windham and Ehrenfeld 2003). These contrasting changes indicated that plant invasion had altered various components of litter C and N cycling processes in invaded ecosystems in both China and the USA.

At our study site, the changes in litter mass and decomposition caused by *Spartina* invasion could stem from its ecophysiological properties, which differ from those of the native *Scirpus* and *Phragmites*. For example, *Spartina* had a significantly higher leaf area index and net photosynthetic rate, longer growing season, larger net primary production (Table 1) and higher allocation of annual total litter mass to the aerial position (Fig. 2a–c) than *Scirpus* and *Phragmites*. Additionally, substantial epiphytic N_2 fixation occurred in standing dead shoots of *Spartina* (Fig. 3a–b), while this did not occur in those of *Scirpus* and *Phragmites*. These physiological properties give *Spartina* competitive advantages over *Scirpus* and *Phragmites*, and contribute to the rapid invasion of *Spartina* into the marshlands originally dominated by the two native species.

Studies conducted along the east coast of the USA (e.g., Frasco and Good 1982; Windham 2001; Windham and Ehrenfeld 2003; Windham et al. 2004) suggest that the differences in litter C and N cycling between the invasive *Phragmites* and the native *Spartina* result mainly from the fact that *Phragmites* has a greater plant production than *Spartina* (Table 4). This rapid growth and great plant production contribute to the success of *Phragmites* invasion. A study that simultaneously examines differences in the litter C and N pool sizes and their dynamics during decomposition between *Phragmites* and *Spartina* at the aerial, surficial, and belowground positions would provide additional information on the mechanisms underlying the reciprocal invasion of the two species in the USA and

Table 4 Comparison of *Spartina* and *Phragmites* grown in China (data from Liao 2007) and the USA

	China (based on this study)	USA		
		Values	Locations	References
Shoot density (ramets m^{-2})				
Spartina	86	289	Delaware (N)	Gratton and Denno (2005)
Phragmites	49	91	Delaware (I)	
Peak total biomass (kg C m^{-2})				
Spartina	3.83	0.42	New Jersey (N)	Windham et al. (2003)
Phragmites	2.94	0.63	New Jersey (I)	
Peak total N stock (g N m^{-2})				
Spartina	57.2	14.1	New Jersey (N)	Windham et al. (2003)
Phragmites	73.1	21.8	New Jersey (I)	
Initial N concentration of aboveground litter (%)				
Spartina	0.68	0.93	Massachusetts (N)	Hicks et al. (1991)
Phragmites	0.94	0.81	New Jersey (I)	Windham and Ehrenfeld (2003)
Initial C:N ratio of aboveground litter				
Spartina	62.8	28.6	New Jersey (N)	Frasco and Good (1982)
Surficial decomposition rate of stem litter ($year^{-1}$)				
Spartina	0.91	≈0.95	New Jersey (N)	Windham et al. (2004)
Phragmites	0.62	≈0.95	New Jersey (I)	
Surficial decomposition rate of leaf litter ($year^{-1}$)				
Spartina	2.73	≈2.04	New Jersey (N)	Windham et al. (2004)
Phragmites	2.48	≈2.04	New Jersey (I)	
Surficial decomposition rate of aboveground litter ($year^{-1}$)				
Phragmites	1.27	0.25	New Jersey (I)	Windham (2001)
Change in stem litter N content during surficial decomposition				
Spartina	Increase	Increase	New Jersey (N)	Frasco and Good (1982)
Phragmites	Decrease	Increase	New Jersey (I)	Windham and Ehrenfeld (2003)

N, Native species; I, invasive species

China. Our results suggest that litter C and N cycles at soil surfaces could considerably differ from those at aerial and belowground positions for both *Phragmites* and *Spartina* in the USA. In addition, comparative studies of conspecifics in both native and introduced ranges (biogeographical approach) would be able to shed light on their successful invasions and the consequences to the invaded ecosystems (Hierro et al. 2005).

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