Oecologia (2011) 165:797–807
DOI 10.1007/s00442-010-1887-7

ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Spartina alterniflora invasion increases soil inorganic nitrogen pools through interactions with tidal subsidies in the Yangtze Estuary, China

Rong Hao Peng · Chang Ming Fang · Bo Li · Jia Kuan Chen

Received: 2 November 2009 / Accepted: 9 December 2010 / Published online: 4 January 2011

Abstract Invasive alien plants increase both plant N and soil inorganic N pools in many terrestrial ecosystems. This is believed to be the result of altered plant–soil–microbe feedbacks that accelerate N cycling. However, it may also be due to the greater ability of invasive species to uptake lateral N subsidies that can modify ecosystem N dynamics. We conducted manipulative field experiments to determine the impact of smooth cordgrass (*Spartina alterniflora*) invasion on the N cycling of salt marsh ecosystems in the Yangtze Estuary, China. The results showed that the aboveground plant N and soil inorganic N pools in *S. alterniflora* marshes, 14.39 and 3.16 g N m^{-2}, were significantly higher than those in native common reed (*Phragmites australis*) marshes, 11.61 and 2.29 g N m^{-2}. These increases after invasion were explained by a significantly higher uptake of dissolved inorganic N (DIN) from tidal subsidies in *S. alterniflora* marshes (6.59 g N m^{-2}) than from those in *P. australis* marshes (1.61 g N m^{-2}), and not by soil organic N mineralization, which was not significantly different between *S. alterniflora* (6.45 g N m^{-2}) and *P. australis* marshes (6.84 g N m^{-2}) during the growing season. Our study indicated that the ecosystem engineering effects of *S. alterniflora*, which increases the interception of external N input, can be an alternative mechanism that increases plant N and soil inorganic N pools—especially in ecosystems with ample anthropogenic N subsidies, such as the coastal wetlands of China.

Keywords Chongming Island · Ecosystem engineering · Nitrogen cycling · Plant invasion · *Spartina alterniflora*

Communicated by Pascal Niklaus.

R. H. Peng · C. M. Fang · B. Li · J. K. Chen (✉)
Coastal Ecosystems Research Station of the Yangtze River Estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, The Institute of Biodiversity Science, Fudan University, Shanghai 200433, China
e-mail: jkchen@fudan.edu.cn

B. Li · J. K. Chen
Center for Watershed Ecology, Institute of Life Science and Key Laboratory of Poyang Lake Environment and Resource Utilization, Nanchang University, Nanchang 330031, China

Introduction

Biological invasion is one of the three most pressing environmental problems, along with global change and habitat fragmentation (Sala et al. 2000); indeed, it has been regarded as being an important component of global change (Lovel 1997). Besides presenting a threat to the biodiversity of native ecosystems, it has also exerted profound effects on ecosystem functioning and processes (Ehrenfeld 2003; Seabloom et al. 2006). Such changes that are caused at the ecosystem level by biological invasion can be viewed as "an experiment in nature" in which invasive alien species are treated as model organisms, and can thus lead to a better understanding of fundamental ecological and evolutionary issues (Sax et al. 2007). In this approach, phenomena that contradict classical theories may trigger new issues and controversies in ecology (Rout and Callaway 2009), and are therefore highly valuable.

In terrestrial ecosystems, nitrogen is normally the first limiting factor influencing net primary production (NPP) (Vitousek and Howarth 1991). Raised NPP usually causes depletions in soil inorganic N and other soil nutrient pools in the short-term (Rout and Callaway 2009). However, in the case of biological invasion, alien plants may increase plant N stocks as well as soil NH_4 and NO_3 pools

(Ehrenfeld 2003; Liao et al. 2008b). Since their impact on nutrient pools and supply rates is one of the most important ecological effects of invaders (Parker et al. 1999; Levine et al. 2003), such a phenomenon is considered to be a "plant invasion paradox" (Rout and Callaway 2009). Altered plant–soil–microbe feedbacks during invasion have been found to contribute to increases in the ecosystem N (Liao et al. 2008b; Rout and Callaway 2009). There are two kinds of mechanisms that may cause plant species (both alien and native) to affect ecosystem nitrogen cycling: plant feedbacks and N input/output changes (Knops et al. 2002). It has been suggested that in grassland ecosystems, most nitrogen is retained in decomposing litter or soil organic matter that prevents immediate feedback, and plant C input into the soil may provide a negative feedback that immobilizes N rather than a positive feedback that accelerates N mineralization (Knops et al. 2002). That means that altered ecosystem N input/output during invasion can be another important mechanism for increasing the N pool, especially in ecosystems with high lateral subsidies of nutrients, such as tidal marshes. Ample subsidies make wetland ecosystems more vulnerable to biological invasions (Zedler and Kercher 2004), and enhanced N cycling may further accelerate the range expansion of alien plants. Except for several nitrogen-fixing invasive plants, such as the *Myrica faya* (Ait.) Wilbur invasion in Hawaii (Vitousek and Walker 1989) and the *Acacia* species invasion in South Africa (Stock et al. 1995), there are limited studies on the potentially positive feedbacks driven by accelerated N input/output exchanges: the changes in the fire regimes in Hawaii resulting from C_4 grass invasion (Mack et al. 2001), and the altered nitrate leaching of *Bromus tectorum* L. invasion in arid and semiarid ecosystems (Sperry et al. 2006).

The means by which plants alter N inputs include symbiotic and asymbiotic nitrogen fixation, interception of atmospheric nitrogen deposition, or other lateral N subsidies, such as dissolved inorganic N (DIN) in tidal water. Plants can also change N losses from ecosystems by altering fire regimes, through animal movement, or by tidal transportation (Knops et al. 2002). All of the above mechanisms are physical and chemical environmental modifications by organisms, independent of their own assimilatory or dissimilatory processes, and can be identified as ecosystem engineering effects (Wright and Jones 2006). The roles of ecosystem engineers have been recognized in relation to many ecosystem-level consequences of biological invasions, including the impact on the availability and flow of nutrients (Crooks 2002). Thus, besides plant–soil feedbacks, ecosystem engineering effects are an alternative explanation for the plant invasion paradox of N pool accumulation.

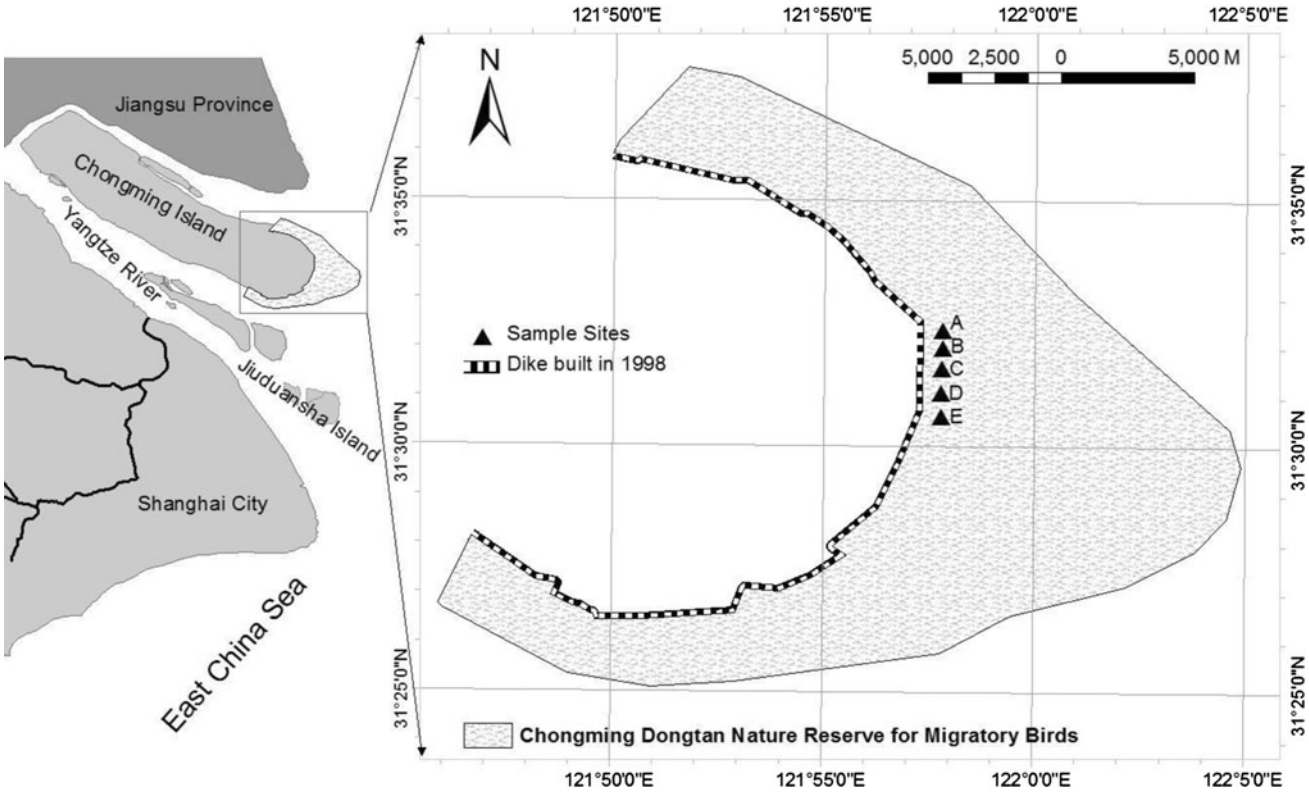

Fig. 1 Locations of sampling sites in the Dongtan wetland, Chongming Island, the Yangtze Estuary

Spartina alterniflora Loisel. (smooth cordgrass) is native to the Atlantic and Gulf Coasts of North America, and was intentionally introduced to China in 1979 to accentuate sediment accumulation and land formation (Chung 2006). Subsequently, *S. alterniflora* has rapidly become a dominant invasive plant in the coastal salt marshes of China, including the Yangtze estuarine marshlands, such as Jiuduansha and Dongtan marshlands (Li et al. 2009, Fig. 1). It has been documented that *S. alterniflora* has dramatically enhanced the total N stocks in plant tissue and the soil in less than seven years at Jiuduansha Island in the Yangtze Estuary, China (Liao et al. 2007). Accelerated decomposition and epiphytic N fixation on the surface of standing dead litter of *S. alterniflora* were believed to be the major reason for the rapid increase in ecosystem N pools after *S. alterniflora* invasion (Liao et al. 2007; 2008a). It is still not known if there are other complementary mechanisms for the increase in N in *S. alterniflora* marshes, since the N cycling process is closely related to the ecosystem engineering effect of sedimentation acceleration by *S. alterniflora*, while tidal wetlands in the Yangtze Estuary have more abundant sediment supplies than most other wetlands in the world (Chen et al. 1985).

Dongtan is a marshland at the east end of Chongming Island, the largest alluvial island in the world, with a high progradation rate (averaging 150–200 m in distance or 4.06 km^2 in area per year; Xu and Zhao 2005). Dongtan was recognized as a Wetland of International Importance in 2001 by the Ramsar Wetlands Convention, and accepted as a National Nature Reserve in 2005. The Dongtan wetland is composed of salt marshes and bare mudflats. *Phragmites australis* (Cav.) Trin. ex Steud. (common reed) grows near the dike, while *Scirpus* × *mariqueter* Tang et Wang (sea bulrush) is the dominant native plant in the low salt marshes. In 2001, *S. alterniflora* was intentionally introduced to the northern Dongtan as an ecosystem engineer species to accelerate sedimentation. In a few years, *S. alterniflora* has expanded rapidly to cover the entire area; it has become a dominant species, outcompeting *P. australis* and *S. mariqueter* and having a profound impact on the native ecosystems (Li et al. 2009). Manipulative field experiments were conducted to investigate how *S. alterniflora* influences the nitrogen cycle in the Dongtan salt marshes, what the major mechanism of the impacts of invasion on nitrogen cycling is, and to establish the relationship between these impacts of *S. alterniflora* and its success as an invasive species. We aimed to examine if *S. alterniflora* could take up DIN in tidal subsidies more efficiently than the native plants, thus leading to increases in the plant N pool and soil inorganic N pool.

Materials and methods

Study site

Experiments were conducted in the Dongtan marshland, which is located at the eastern end of Chongming Island in the Yangtze Estuary, Shanghai, China (31°25′–31°38′N, 121°50′–122°05′E). The island has a northern subtropical monsoon climate. The mean annual precipitation is 1,022 mm, with the majority (60%) of rainfall occurring between May and September. The mean annual temperature is 15.3°C, and the average humidity is 82% (Xu and Zhao 2005). The growing season at the study site lasts about seven months (April to October).

Sampling transect

In April 2007, a 3.2 km long north–south transect was established in a salt marsh zone at Dongtan (Fig. 1). The transect was approximately along the boundary between *S. alterniflora* and *P. australis* monocultures, and parallel to the dike built in 1998. Five sites were randomly selected on the transect, and two adjacent patches of *S. alterniflora* and *P. australis* were chosen at each site. All patches were homogeneous and larger than 10 m in diameter. This pairwise design was used to avoid pseudo-replication and to minimize the effects of heterogeneities in the background environment (Liao et al. 2007).

Measurements of total N in plant aboveground tissues and inorganic N in soil

Aboveground biomass and soil cores from *S. alterniflora* and *P. australis* marshes at each site were sampled in April, July, and September 2007 and April 2008.

Five samples of aboveground biomass and five soil cores from each of the five sites were obtained for both species at each time. In each patch, aboveground biomass was collected by harvesting four randomly selected quadrats of 0.5 × 0.5 m^2, and this biomass was then combined and sorted into live ramets and dead litter. All samples were oven-dried at 50°C to constant weight before weighing. The dry biomass was ground to powder in a Wiley mill and passed through a sieve of 100 meshes per square inch. The total C and N concentrations of plant samples were analyzed using an NC analyzer (FlashEA 1112 Series, Thermo Inc., Milan, Italy) (Liao et al. 2007).

Using a stainless steel auger with an inner diameter of 5 cm, soil cores were sampled down to a depth of 20 cm at the centers of the four quadrats after harvesting. Each soil core was divided into 0–10 and 10–20 cm subsamples, and subsamples from the same depth in the four quadrats were

combined. Roots and rhizomes were immediately picked out before the pooled soil samples were freshly weighed. Twenty grams of wet soil in each sample were added to 200 mL of 2 M KCl solution. After oscillation at 200 rpm for 1 h, the KCl extract was used to determine the soil inorganic N concentration (Keeney and Nelson 1982). Extracted NH_4 and NO_3 were measured using a UV spectrophotometer (Unico2100, Unico Inc., Shanghai, PRC). The NH_4 concentration was determined by the indophenol blue method (Ivancic and Degobbis 1984). The NO_3 concentration was determined by a dual-wavelength UV spectrophotometer (Norman et al. 1985). The soil inorganic N (SIN) pool was calculated against the soil wet weight.

Measurements of SON mineralization rate and tidal inorganic N exchanges

An in situ incubation method, modified from Raison et al. (1987) and Stenger et al. (1996), was used to separate the input to the SIN pool from soil organic N (SON) mineralization and tidal subsidies in *S. alterniflora* and *P. australis* marshes. Five undisturbed soil cores of depth 0–10 cm were taken in both marshes at each site in March and September 2007. One of them was brought back to the laboratory to measure the original SIN concentration (method described above). The residual cores were put into four polyvinyl chloride (PVC) tubes of 10 cm long and 5 cm in inner diameter. The bottoms of all of the tubes were sealed with PVC lids and sealing tape to avoid plant uptake and leaching. Polytetrafluoroethylene (ePTFE) films and sealing tape were used to seal the tops of two randomly selected tubes, so all gases but no liquids could be exchanged with the soil within the tube. The tops of the other two tubes were kept open. One sealed tube and one open-top tube were buried back into the holes at their original positions (in situ). The other two holes were filled with soil from adjacent marshes. In total, there were $2 \times 2 \times 2 = 8$ treatments at each site: tube top (sealed vs. open-top) × soil source (from *S. alterniflora* marsh vs. from *P. australis* marsh) × buried habitat (in *S. alterniflora* marsh vs. from *P. australis* marsh) (Fig. 2). The aboveground shoots were removed where the tubes were

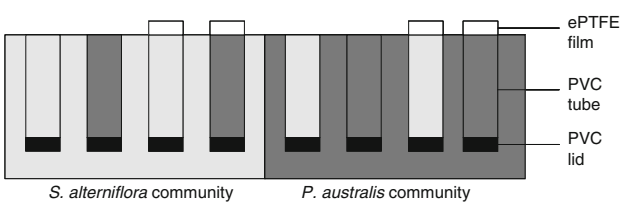

Fig. 2 Design of the treatments at each site of the in situ incubation experiment

buried, leaving a bare patch about 15×15 cm^2 in size in the vegetation. All 40 tubes (8 treatments × 5 sites) were incubated in the field for 30 days and then taken out in April and October 2007 to determine the SIN concentration. All plots were regularly maintained by removing plant litter every week over a period of 30 days. Rates of net ammonification and nitrification were calculated as the difference between the NH_4 and NO_3 concentrations of sealed tubes and the original soil cores (Windham and Ehrenfeld 2003). The differences between the open-top and sealed tubes were regarded as the tidal subsidy rates of NH_4 and NO_3.

Measurements of the diurnal course of the inorganic N exchange rate at the monthly high tide at each site were conducted in March and May 2008. Soil cores of depth 0–10 cm were sampled before and after the inundation period, and overlying tidal water was sampled at the beginning and end of the slack tide period to minimize the disturbance of lateral turbulence. Water samples (15 ml each) were taken at the water's surface (about 20–30 cm above the soil surface), the subsurface (about 10–15 cm above the soil surface) and near the ground, using syringes and tubes. The water samples from the three depths were mixed and stabilized by 0.1 ml L M HCl. All samples of soil and water were immediately taken back to the laboratory to determine SIN concentrations (using the same method as in the soil extract determination). The rate of exchange of inorganic N between the soil and tidal water was estimated by calculating the changes in the inorganic N concentrations in the soil and water during a tidal cycle.

Data analyses

Repeated-measures ANOVA was used to analyze the differences between adjacent *P. australis* and *S. alterniflora* marshes at different times and sites in traits such as aboveground plant biomass, plant tissue N concentration, aboveground plant nitrogen (PAN) pool, SIN pool, exchange between the soil and tidal water, tidal inorganic N subsidies in the SIN pool, net ammonification, net nitrification, and ΔN pools (ΔPAN pool and ΔSIN pool). ΔN pools were calculated as the increases in these pools in the *S. alterniflora* marshes compared to the adjacent *P. australis* marshes.

A simple budget of N demand for plant growth and available N sources was calculated to determine the relative importance of the impact of invasion on each component (Windham and Ehrenfeld 2003). Plant N uptake was estimated via the increase in the PAN pool of fresh shoots during the growing season (N stocks of fresh shoots in September minus those in April). The inputs included SON mineralization, tidal subsidies, and SIN depletion. The first two components were the results from the in situ incubation

experiment (the average of SON mineralization rate in April and September multiplied by six months, the time duration from April to September; and the calculation of tidal subsidies used the same method). The SIN depletion was estimated from the decrease in the SIN pool during the growing season (SIN pool in April minus that in September).

Levene's test was performed to ensure that the raw data sets achieved normality and homogeneity of variance. Post hoc Duncan's tests were performed to examine differences between means ($P < 0.05$). All data are reported as means ± 1 SE. Statistical analyses were performed using STATISTICA 6.0 (StatSoft Inc. 2001).

Results

Aboveground plant N pool and soil inorganic N pool

There was significantly higher aboveground biomass in *S. alterniflora* marshes than in *P. australis* marshes ($F_{1,32} = 56.86$, Fig. 3a) (if not specified, all F values are significant at $P < 0.05$). The N concentration of fresh shoots of *S. alterniflora* was significantly lower than that of fresh shoots of *P. australis* ($F_{1,32} = 172.41$). However, there was no significant difference in the N concentration of aboveground litter between *S. alterniflora* and *P. australis* ($F_{1,32} = 0.00$, $P = 0.99$, Fig. 3b). The PAN pool in *S. alterniflora* marshes (14.39 ± 1.22 g N m^{-2}) was significantly higher than that in *P. australis* marshes (11.61 ± 0.71 g N m^{-2}, $F_{1,32} = 10.00$).

The SIN pool at a depth of 0–20 cm in *S. alterniflora* marshes (3.16 ± 0.35 g m^{-2}) was significantly higher than that in *P. australis* marshes (2.29 ± 0.24 g m^{-2}, $F_{1,32} = 22.30$). The difference in the SIN pool between the two marshes was mainly caused by a significantly higher NO_3–N pool in *S. alterniflora* marshes ($F_{1,32} = 177.22$, Fig. 4a), while the NH_4–N pool showed no significant difference between the two types of marshes ($F_{1,32} = 1.03$, $P = 0.32$, Fig. 4b).

In both marshes, the SIN pool in 0–10 cm surface soil (1.58 ± 0.13 g m^{-2}) was significantly higher than that in 10–20 cm subsoil (1.15 ± 0.09 g m^{-2}, $F_{1,64} = 111.76$). This was also true for the soil NO_3–N pool ($F_{1,64} = 41.00$, Fig. 4a) and the NH_4–N pool ($F_{1,64} = 49.90$, Fig. 4b). These pools decreased gradually over the growing season, and were significantly higher at the beginning of the growing season in 2008 than at the same time in 2007 (Fig. 4a, b).

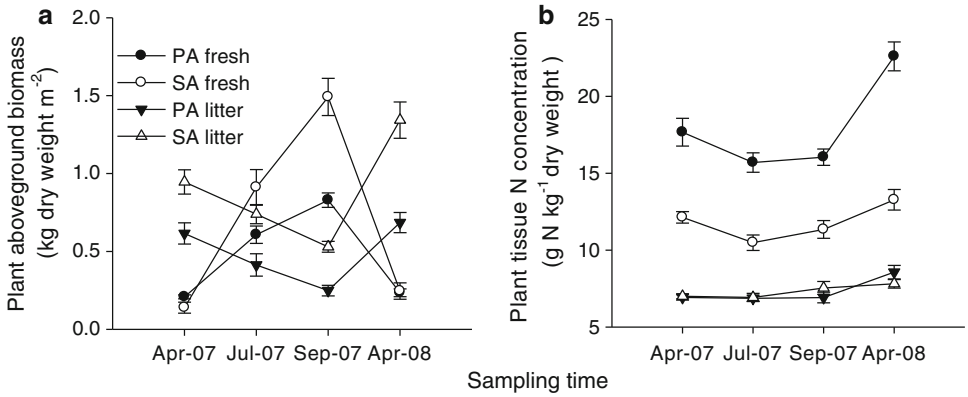

Fig. 3 Temporal dynamics of **a** plant aboveground biomass and **b** plant tissue N concentration (mean ± SE, $n = 5$) in fresh shoots (*circles*) and litter (*triangles*) of *Spartina alterniflora* (SA, *open symbols*) and *Phragmites australis* (PA, *filled symbols*)

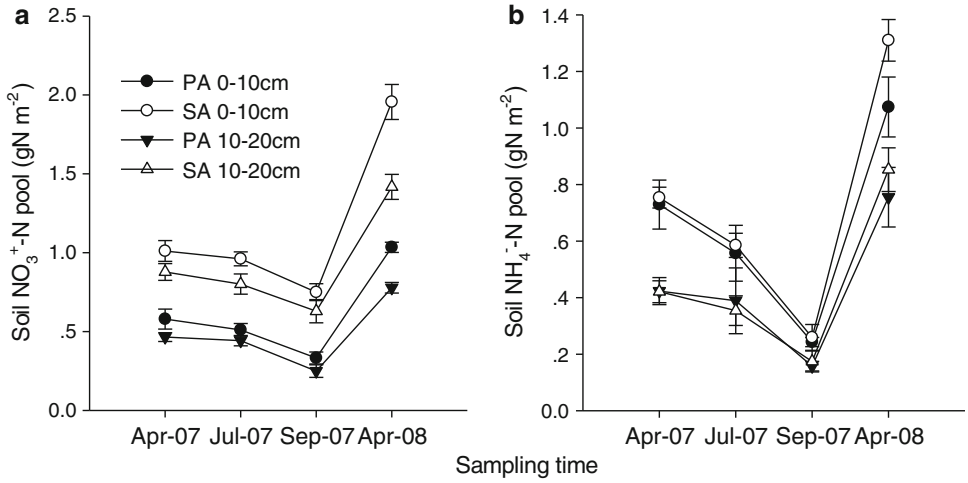

Fig. 4 Temporal dynamics of **a** the NO_3–N pools and **b** the NH_4–N pools (mean ± SE, $n = 5$) in surface (0–10 cm depth, *circles*) and subsurface (10–20 cm depth, *triangles*) soils of *S. alterniflora* (SA, *open symbols*) and *P. australis* (PA, *filled symbols*) marshes

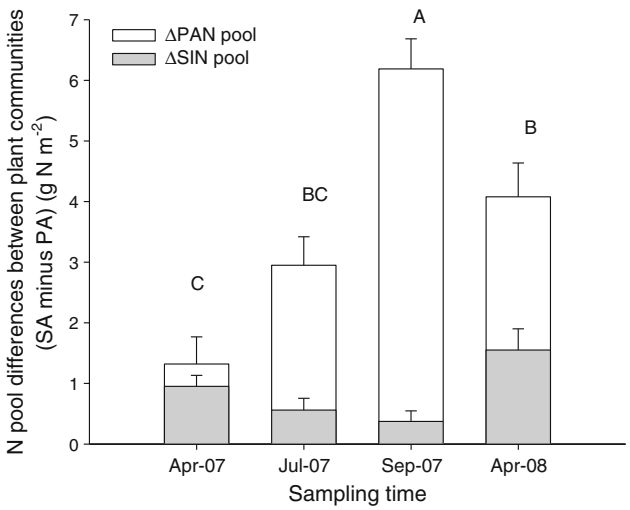

Fig. 5 Temporal dynamics of the plant aboveground N (PAN, *open bars*) pool and the soil inorganic N (SIN, *filled bars*) pool (mean ± SE, $n = 5$) for *S. alterniflora* (SA) marshes and adjacent *P. australis* (PA) marshes. Results of post hoc comparisons are shown via *uppercase letters* for the sum of ΔPAN pool and ΔSIN pool (bars labeled with different letters are significantly different at the $P < 0.05$ level)

The sum of ΔSIN pool + ΔPAN pool increased gradually during the growing season, and was significantly higher in April 2008 than in April 2007 (Fig. 5). During the growing season, ΔPAN pool gradually increased but ΔSIN pool gradually decreased (Fig. 5).

SON mineralization and tidal inorganic N subsidies

The results of field incubation experiments showed abundant DIN subsidies from tidal water to the soil in the salt marshes, and *S. alterniflora* had an enhanced ability to intercept and take up this source of nitrogen. The mean increase in SIN concentration (Δ[SIN]) after incubation was significantly higher in open-top tubes (22.78 ± 1.24 mg N kg^{-1} dry soil $month^{-1}$) than that in sealed tubes (13.87 ± 0.48 mg kg^{-1} $month^{-1}$, $F_{1,64} = 149.38$). In open-top tubes, Δ[SIN] was significantly higher when buried in *S. alterniflora* marshes (28.99 ± 1.28 mg kg^{-1} $month^{-1}$) than in *P. australis* marshes (16.56 ± 0.81 mg kg^{-1} $month^{-1}$, $F_{1,32} = 102.15$), with no significant difference between soil sources ($F_{1,32} = 3.73$, $P = 0.06$). In sealed tubes, Δ[SIN] showed no significant difference between habitats ($F_{1,32} = 0.51$, $P = 0.48$). Although the soil from *S. alterniflora* marshes had significantly higher Δ[SIN] than that from *P. australis* marshes ($F_{1,32} = 4.77$, $P = 0.04$), the difference in the means was rather small (14.72 ± 0.68 vs. 13.02 ± 0.64 mg kg^{-1} $month^{-1}$). The mean increase in NO_3–N concentration after field incubation (Δ[NO_3]) was significantly higher than that in NH_4–N (Δ[NH_4], $F_{1,128} = 1152.07$, $P = 0.00$, Fig. 6), which was consistent with the results shown above that the SIN pool was mainly raised by the increased NO_3–N pool.

The results from direct measurements of tidal exchange between water and soil also demonstrated similar patterns. In the soil, the mean increase in SIN concentration ($\Delta[SIN]_{tide}$) was significantly higher in *S. alterniflora* marshes (8.46 ± 0.96 mg N kg^{-1} dry soil) than in *P. australis* marshes after inundation in one tidal cycle (4.58 ± 0.39 mg kg^{-1}, $F_{1,16} = 103.51$). For the components of $\Delta[SIN]_{tide}$, the mean increase in soil NO_3–N concentration ($\Delta[NO_3]_{tide}$) was significantly higher than that in NH_4–N ($\Delta[NH_4]_{tide}$, $F_{1,128} = 262.81$, Fig. 7a). Meanwhile, in the overlying tidal water, the mean decrease in dissolved inorganic N concentration (Δ[DIN]) was significantly higher in *S. alterniflora* marshes (3.56 ± 0.43 mg N L^{-1}) than in *P. australis* marshes (2.74 ± 0.26 mg L^{-1}, $F_{1,16} = 17.98$). For the components of Δ[DIN], the mean decrease in NO_3–N concentration ($\Delta[NO_3]_{water}$) was significantly higher than that in NH_4–N ($\Delta[NH_4]_{water}$, $F_{1,128} = 301.67$, Fig. 7b).

N budget in plant growth

During the growing season, plant uptake in *S. alterniflora* marshes was higher by 5.51 g N m^{-2} than that in *P. australis* ($F_{1,8} = 85.35$). SON mineralization showed no significant difference between the two types of marshes. SIN depletion was significantly higher in *S. alterniflora* marshes than in *P. australis* ($F_{1,8} = 28.68$), but the difference in the means was small (0.58 g N m^{-2}). Thus, the increased N demand for *S. alterniflora* growth was met mainly by additional N input from tidal DIN subsidies, which was 4.98 g N m^{-2} higher in *S. alterniflora* marshes than in *P. australis* marshes ($F_{1,8} = 551.56$, Fig. 8).

Discussion

It is difficult to analyze the uncertainties when the impacts of plant invasions on tidal marshes are assessed due to the high spatial and temporal variations in this system (Weinstein and Kreeger 2002). In our experiments, pairwise design and repeated measures were used to reduce the effect of soil heterogeneities that might have existed before invasion (Liao et al. 2008a). However, the observed difference between *S. alterniflora* and *P. australis* marshes may be the effect of selective invasion into a fine-scale resource hotspot instead of an impact of invasion on nitrogen pools. Therefore, the changes ΔSIN pool and ΔPAN pool were calculated to determine the differences caused by invasion and to minimize selective invasion effects. In our manipulative experiments, tidal subsidies were estimated by comparing soil cores in sealed tubes

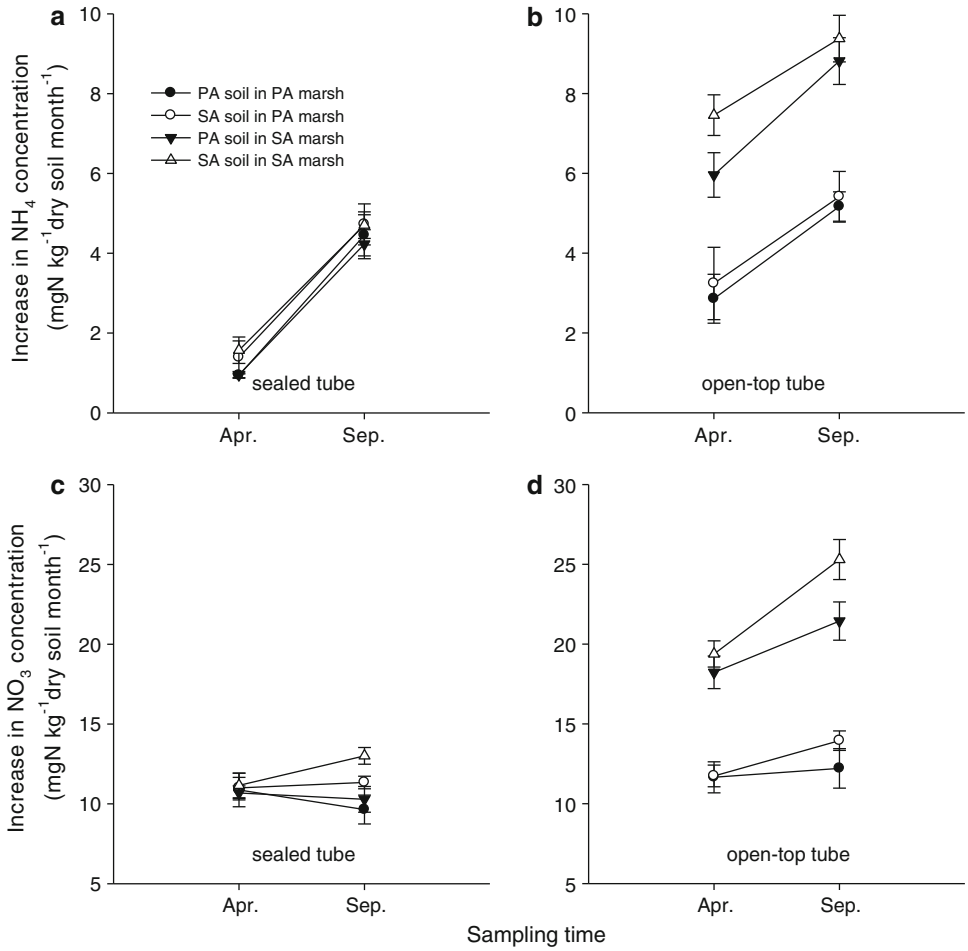

Fig. 6 Increase of **a** the NH_4–N pool in sealed PVC tubes, **b** the NH_4–N pool in open-top tubes, **c** the NO_3–N pool in sealed tubes, and **d** the NO_3–N pool in open-top tubes (mean ± SE, $n = 5$) containing soil cores from *S. alterniflora* (SA, *open symbols*) and *P. australis* (PA, *filled symbols*) marshes that were buried in PA (*circles*) and SA marshes (*triangles*) during the field incubation

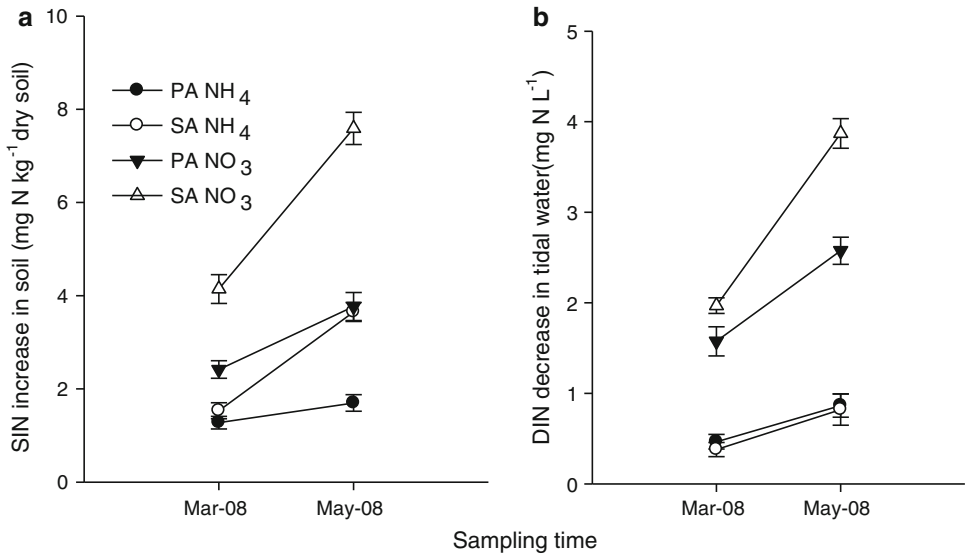

Fig. 7 **a** SIN increase in soil and **b** DIN decrease in tidal water (mean ± SE, $n = 5$) of the NO_3 (*triangles*) and NH_4 (*circles*) concentrations during inundation in *S. alterniflora* (SA, *open symbols*) and *P. australis* (PA, *filled symbols*) marshes

with those in open-top tubes. Direct measurements of soil–water exchange during the inundation period of a single tidal cycle confirmed the tube incubation results. Furthermore, the SIN pool was mainly enhanced by the accumulation of the NO_3–N pool, not the NH_4–N pool, which was consistent with the high NO_3:NH_4 ratio of DIN in tidal water in the Yangtze Estuary (Chai et al. 2009). The results from the field observations and the manipulative experiments matched up well in an integrated budget (Fig. 8), which made both datasets more credible.

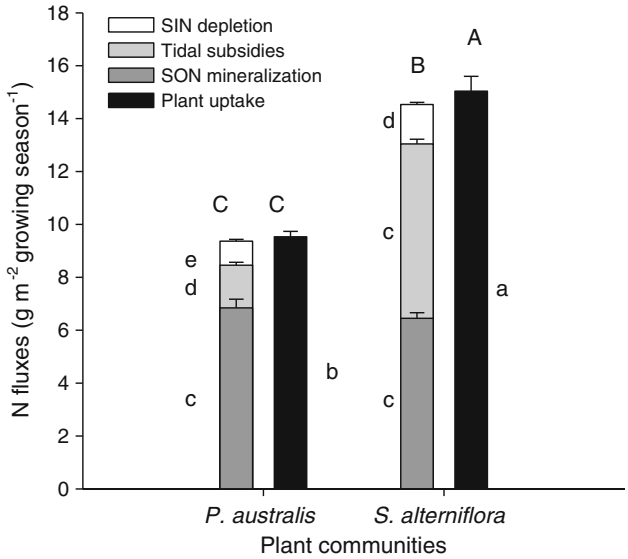

Fig. 8 Comparison of soil inorganic N fluxes (mean ± SE, $n = 5$) from different sources: SIN depletion (*open bars*), tidal subsidies (*gray bars*), SON mineralization (*dark gray bars*), and plant N uptake (*black bars*) during the growing season in *S. alterniflora* and *P. australis* marshes. Results of *post hoc* comparisons are shown in *lowercase letters* for each N flux and *uppercase letters* for plant uptake and the sum of other fluxes (bars labeled with different letters are significantly different at the $P < 0.05$ level)

Manipulative field experiments can separate ecosystem engineering effects from direct metabolic influences. For example, the changes that occurred to environmental factors after invasion accelerated the decomposition rate, along with the higher litter quality (lower C/N ratio) of invasive plants (Ashton et al. 2005). Our results from the soil cores exchanged between adjacent marshes showed that ecosystem engineering effects were the most important determinant of the increases in the PAN and SIN pools (*S. alterniflora* is denser and stouter than *P. australis*, and can intercept tidal N subsidies more efficiently), rather than the changes to SON mineralization and nitrification rate caused by plant invasion. Actually, ΔSIN pool decreased during the growing season, suggesting that *S. alterniflora* invasion might have caused SIN depletion in the same marsh without tidal exchange. On the eastern coast of North America, *P. australis* invasion led to SIN depletion in marshes dominated by native *S. alterniflora*. In that case, the greater N demand of the invasive *P. australis* species explained the low ammonium concentrations (Chambers 1997; Bart and Hartman 2000; Meyerson et al. 2000). Invasive *S. alterniflora*, which also had a greater N demand, was proven to increase the soil N pool in Jiangsu (Zhou et al. 2008) and Jiuduansha (Liao et al. 2007), in accord with our results on Chongming Island. The different patterns of invasion impacts suggest similar differences between *S. alterniflora* and *P. australis* in terms of interception of tidal subsidies in both China and America.

Even within the same estuary that presents the invasion impact pattern described above, the relative importance of nutrient input control may vary. Epiphytic nitrogen fixation on the surfaces of standing dead shoots of *S. alterniflora*, which led to a much higher litter N pool in *S. alterniflora* marshes than in *P. australis* marshes, was considered to be an important mechanism for increasing ecosystem N stocks on Jiuduansha Island, about 40 km south of Chongming Island (Fig. 1, Liao et al. 2007; Liao et al. 2008a). In our study at Dongtan on Chongming Island, where SON mineralization and tidal DIN subsidies can meet most of the nitrogen demands of plants for growth, the potential effect of nitrogen fixation would be relatively small (Fig. 8). This is not an unexpected result. First, the field nitrogen fixation rate on *S. alterniflora* litter exhibited very large variations (0.47 g N m^{-2} $year^{-1}$, Hanson 1977; 0.66 g N m^{-2} $year^{-1}$, Casselman et al. 1981; 2.6 g N m^{-2} $year^{-1}$, Currin and Pearl 1998; 287 g N m^{-2} $year^{-1}$, Newell et al. 1992). Second, the amount of aboveground nitrogen fixation at Jiuduansha was estimated as a seasonal increase in *S. alterniflora* standing litter N (Liao et al. 2008a), while the chemical adsorption and microbial immobilization of DIN from tidal water can also lead to such an increase (Windham and Ehrenfeld 2003). In New Jersey, the N concentrations in standing dead shoots of both *S. alterniflora* and *P. australis* increased during decomposition (Frasco and Good 1982; Windham and Ehrenfeld 2003). At Jiuduansha, only dead shoots of *S. alterniflora* showed a rise in N content (Liao et al. 2007). At Dongtan on Chongming Island, there was no significant increase in the litter N pool (Fig. 3). Direct measurements of the nitrogen fixation rate and isotope analysis should be conducted in future studies in order to separate out the different sources of increased N in soil and *S. alterniflora* standing litter.

The mechanisms that enable plants to influence sediment transport have been well studied (Yang et al. 2008). Plants can reduce the sediment concentration in tidal water and induce sediment deposition through two mechanisms (Davidson-Arnott et al. 2002). First, plants attenuate wave height and flow velocity since they act as obstacles (Leonard et al. 2002); they then enhance flocculation and particle trapping of fine-grained silt and suppress its resuspension on the soil surface. Second, the suspended sediments can directly adhere to plant tissues, such as leaves and stems (Yang 1999). While most of the related literature has focused on particle materials in tidal waters, little attention has been paid to the effects of invasive plants on the interception and exploitation of dissolved nutrients during a tidal cycle. At the sediment–water interface of the unvegetated mudflats in the Yangtze Estuary, NH_4^+ diffuses mainly from sediments to the overlying water body, while NO_3^- diffuses in the reverse direction, from water to sediment (Liu et al. 2007). Our results showed that both

NH_4^+ and NO_3^- in the soil increased after tidal exchange (Fig. 7). This difference implies that the interception and utility of tidal N subsidies in *S. alterniflora*-invaded salt marshes involves a complex of processes affected by the influence of vegetation on sedimentation (mainly physical obstruction), DIN exchange in soil (chemical diffusion), and biologically active uptake and transport. Dissolved nutrient cycling in invaded marshes is entangled with the suspended silt sedimentation process. More efforts should be directed towards clarifying whether the vegetation assumes the same role in the impact of invasion on both SIN and ecosystem total N pools.

Successful invaders generally accrue more biomass than native competitors (Mack et al. 2000; Erhenfeld 2003; Liao et al. 2008b), and nitrogen limitation of primary production is common in temperate salt marshes (Mitsch and Gosselink 1993; Tyler et al. 2003). Thus, species-driven changes in nitrogen cycling can be a key factor determining positive feedbacks between the dispersal of invasive plants and its impact on the ecosystem. Invasive plants can maximize their productivity through two strategies: increasing N use efficiency or increasing the total plant N pool (Laungani and Knops 2009). In our study, *S. alterniflora* used both strategies during its invasion process. On the one hand, the lower tissue N concentration in *S. alterniflora* compared to *P. australis* enabled the invader to produce more biomass than the native with the same N input (Fig. 3b). On the other hand, *S. alterniflora* took up more tidal DIN subsidies than *P. australis*, held it as a ΔPAN pool in the growing season, and this finally led to an increased SIN pool during the next year through the decomposition process (Fig. 5). Additional N supplies amplified the differences in performance that led to *S. alterniflora* outcompeting *P. australis* in a pot transplant experiment (Wang et al. 2006). This effect may be more important in heterogeneous marshes than in the pots, where the nutrient levels were kept the same. First, invasive plants often occupy fine-scale resource hotspots in natural ecosystems (Knops et al. 2002). Second, as our study has shown, the ecosystem engineering effects of invaders can enhance or build up these resource hotspots. While "invasional meltdown" feedback based on invasive alterations of trophic interactions has become a research hotspot in invasion ecology (Simberloff 2006), more attention needs to be paid to the "invasive engineers" that create feedbacks though habitat modification and niche construction (Laland et al. 1999; Cuddington and Hastings 2004).

Conclusion

Spartina alterniflora invasion has significantly increased the aboveground plant N pool and the soil inorganic N pool in a salt marsh dominated by native *P. australis* in the Dongtan wetland of Chongming Island in the Yangtze Estuary. The higher interception and uptake of tidal N subsidies (mainly in the form of nitrate) by *S. alterniflora*, which is tightly coupled with the promotion of accretion, was one of the major causes of the great impact of the invader on nitrogen cycling. This process was an ecosystem engineering effect of invasive *S. alterniflora*. The increased nutrient levels resulting from the invasion can in turn accelerate the expansion of the invader and create positive feedbacks for the invasion process. Such mechanisms may be common in wetland ecosystems, and especially coastal and estuarine tidal marshes, where sufficient nitrogen subsidies are deposited and the rapid expansion of invasive plants often occurs.

Acknowledgments We are very grateful to Naishun Bu, Meng Lu, Chenghuan Wang, Long Tang and Jinqing Wang for their assistance, and Martin Wattenbach, Chengzhang Liao, Qing Wang, and Guanghui Lin for constructive comments on the earlier versions of this paper. This work was financially supported by National Basic Research Program of China (Grant No. 2009CB119201), National Science Foundation of China (Grant No. 30930019) and Science and Technology Commission of Shanghai (Grant Nos. 07JC14002, 07DZ12038 and 10JC1400700).

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