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CH$_4$ and N$_2$O emissions from *Spartina alterniflora* and *Phragmites australis* in experimental mesocosms

Xiaoli Cheng [a,b,c], Ronghao Peng [a], Jiquan Chen [a,c], Yiqi Luo [a,d], Quanfa Zhang [b], Shuqing An [e], Jiakuan Chen [a], Bo Li [a,*]

[a] *Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, 220 Handan Road, Shanghai 200433, PR China*
[b] *Wuhan Botanical Garden, CAS, Wuhan 430074, PR China*
[c] *Department of Earth, Ecological and Environmental Sciences, University of Toledo, Toledo, OH 43606, USA*
[d] *Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA*
[e] *School of Life Science, Nanjing University, Nanjing 210093, PR China*

Abstract

Spartina alterniflora, a perennial grass with C$_4$-photosynthesis, shows great invading potential in the coastal ecosystems in the east of China. We compared trace gas emissions from *S. alterniflora* with those from a native C$_3$ plant, *Phragmites australis*, by establishing brackish marsh mesocosms to experimentally assess the effects of plant species (*S. alterniflora* vs. *P. australis*), flooding status (submerged vs. non-submerged), and clipping (plants clipped or not) on trace gas emissions. The results show that trace gas emission rates were higher in *S. alterniflora* than *P. australis* mesocosms due to the higher biomass and density of the former, which could fix more available substrates to the soil and potentially emit more trace gases. Meanwhile, trace gas emission rates were higher in non-submerged than submerged soils, suggesting that water might act as a diffusion barrier in the brackish marsh mesocosms. Interestingly, methane (CH$_4$) emission rates were lower in clipped non-submerged mesocosms than in non-clipped submerged mesocosms, but nitrous oxide (N$_2$O) emissions were enhanced. CH$_4$ emissions were significantly correlated with the plant biomass and stem density ($R^2 > 0.48$, $P < 0.05$) for both species, suggesting that both the two species might play important roles in CH$_4$ production and transport and also act as suppliers of easily available substrates for the methanogenic bacteria in wetland ecosystems. N$_2$O emissions, however, were not significantly correlated with plant biomass and density ($P > 0.05$).
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1. Introduction

Wetlands cover large areas of land surface (Busch and Lösch, 1999). Because of the wet and submerged soils, wetlands are significant sources of greenhouse gases, such as methane (CH$_4$) and nitrous oxide (N$_2$O) that make an important contribution to the atmospheric content of these trace gases on local, regional and global scales (Busch and Lösch, 1999; IPCC, 2001). On a 100-year time frame, these gases are, respectively, 20 and 300 times more effective than CO$_2$ (on a mass basis) at absorbing infrared radiation (Rodhe, 1990). It has been shown that atmospheric concentrations of CH$_4$ and N$_2$O are increasing at approximately 0.8% and 0.25% per year, respectively (Kang et al., 1998), with various natural and anthropogenic factors determining the change and its magnitude of the emissions through regulating associated biological and ecological processes in wetlands (Kang et al., 1998).

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* Corresponding author. Tel.: +86 21 65642178; fax: +86 21 65642468.
 E-mail address: bool@fudan.edu.cn (B. Li).

It is widely recognized that submergence is the major factor regulating wetland biogeochemistry (Freeman et al., 1997). Water submergence very often results in observable changes in physics and chemistry of soil (Busch and Lösch, 1999). Thus, gas production and transport are, to a large extent, regulated by water submergence and constitute an indirect positive feedback to gas emissions (Vann and Megonigal, 2003). Meanwhile, vegetation type, and species composition collectively affect gas emissions by controlling production and transport in tidal marshes (Van der Nat and Middelburg, 2000). Wetland plants possess aerenchyma mechanisms dealing with the specific conditions of submerged habitats (Busch and Lösch, 1999; Van der Nat and Middelburg, 2000), which can affect CH_4 production and emissions (Van der Nat and Middelburg, 2000). For example, several studies have found that the gases escaping into the atmosphere via aerenchyma of wetland plants are CH_4 (e.g., Schimel, 1995), N_2O (Mosier et al., 1990), and CO_2 (e.g., Thomas et al., 1996). This 'plant pathway' may account for 80–90% of the CH_4 emitted from many wetlands through aerchymous tissues (Chanton et al., 2002). In addition, exotic-species invasions induced by human activities are among the most important factors affecting the vegetation structure of wetland ecosystems (Windham and Ehrenfeld, 2003). The change in vegetation structure as a result of plant invasions would change soil properties, especially the input of organic matter to soil (Ehrenfeld et al., 2001). This change may potentially affect trace gas transport and production in wetlands, where plants act as pathways for gas emissions and provide a soil substrate for gas production.

Although many studies have been conducted to investigate the effects of vegetation features on CH_4 emissions from wetland ecosystems worldwide (e.g., Schimel, 1995; Kutzbach et al., 2004), the emissions of N_2O transported by plants have so far been studied for only a few species e.g., such as rice, *Oryza sativa* L. (Reddy et al., 1989; Mosier et al., 1990). Previous studies have also shown that plant pathways may or may not contribute to the total gas emissions in wetland ecosystems (Rusch and Rennenberg, 1998). Recently, increasing attention has been paid to the roles of wetlands in the global trace gas budget because of their radiative force and significant contribution to global warming (e.g., Myhre et al., 1998). However, trace gas emissions within individual wetlands are temporally and spatially variable because of spatial and temporal changes in biophysical variables (Van der Nat and Middelburg, 2000). Because natural wetlands are permanently or temporarily flooded, the flooding regime (intensity and frequency) and vegetation type in the marshes offer a good opportunity to examine the factors influencing the emission of trace gases from wetland ecosystems (Vann and Megonigal, 2003). For example, previous field-oriented studies have demonstrated that the drainage management of flooded rice fields can reduce CH_4 emissions, but this drainage practice may increase N_2O emissions (Ratering and Conrad, 1998). However, for many natural tidal salt marsh

ecosystems, the effects of plants and water submergence on gas emissions are not well understood. Finally, it is equally important to understand how anthropogenic factors alter gas emissions in wetland ecosystems.

Since 1979, an invasive species *Spartina alterniflora* has been transplanted into the tidal marshes to stabilize the sediment along the eastern coast of China (Qin and Zhong, 1992). The ecological impacts are characterized by the displacement of native species including *Scirpus mariqueter* (Chen et al., 2004) and *Phragmites australis* (Wang et al., 2006b), changes in sedimentation and disturbance to the upper marshes (e.g., Qin and Zhong, 1992). Currently, *S. alterniflora* has become one of the dominant salt marsh plants in the eastern coast of China due to its faster growth rate compared to native species (Qin and Zhong, 1992; Wang et al., 2006b). Thus, understanding the expansion of *S. alterniflora* and its consequences on ecosystem functioning and services is of significance to the sustainable management of coastal lands. Previous studies have focused mainly on its biology, control and management (e.g., Qin and Zhong, 1992; Silliman and Zieman, 2001; Wang et al., 2006a). In this study, we designed mesocosm experiments to examine how the *S. alterniflora* introduction and other variables affected the gas emissions in the tidal marshes. Specifically, our objectives were to: (1) examine the emissions of CH_4 and N_2O from exotic *S. alterniflora* and native *P. australis* by conducting a mesocosm experiment; (2) quantify effects of water submergence and plant clipping on CH_4 and N_2O production and transport; (3) explore the relationships between trace gas emissions and plant characteristics (i.e., total biomass and density).

2. Materials and methods

2.1. Experimental design

We studied the CH_4 and N_2O emissions from brackish marsh mesocosms affected by species (*S. alterniflora* vs. *P. australis*), flooding status (submerged vs. non-submerged), and clipping treatment (plants clipped or not) in a full factorial design. The mesocosm experiment was conducted outside on the Fudan University campus in Shanghai (31°03′ – 31°17′N, and 121°46′ – 122°15′E), China, from early April to October, 2004. We constructed the brackish marsh mesocosms using large plastic containers (0.6 m × 0.8 m × 0.8 m in volume), and the plants and the soils from the Jiuduansha salt marsh in the Yangtze River estuary (see Table 1 for the soil properties), which were measured as previously described by Cheng et al. (2006). Each mesocosm was filled with soil to a depth of 60 cm, and planted with 15 young ramets of *S. alterniflora* or *P. australis*. Plants of approximately equal size with six true leaves were selected for this study. Two transplanted ramets that died within one week were replaced with those of similar size. Saltwater of 8–10 cm deep was maintained to create the submerged growing conditions by adding saltwater to compensate for evapotranspiration (ET) or only

Table 1
Soil properties of the mesocosms used in this study

Soil properties	*S. alterniflora* (C_4) mesocosms	*P. australis* (C_3) mesocosms
Soil total carbon (mg g^{-1})	13.9–15.2	11.4–14.4
Soil total nitrogen (mg g^{-1})	0.53–0.64	0.31–0.46
Soil organic carbon (mg g^{-1})	4.6–5.7	3.7–4.9
Dissolved organic carbon (mg g^{-1})	1.8–2.2	1.5–1.9
Recalcitrant carbon (mg g^{-1})	2.8–3.5	2.2–2.9

salt to maintain an approximate 5‰ water salinity for rain input. Approximately 2 months after transplanting, when these plants reached a height of approximately 40 cm, all measurements (next section) were started in the brackish marsh mesocosms.

In this experiment, three treatments to simulate three types of habitats in tidal ecosystems were used as follows. (1) SP (submerged with plants), the soil in this treatment was submerged with plants by using artificial seawater with approximately 5‰ salinity which was maintained at 10 cm above the soil surface. (2) AP (aerial with plants), the soil was non-submerged, but stayed water-saturated. In this treatment, we removed the flooded water from the three containers for each species one day prior to gas measurement to allow the soil to begin drying up by the time we measured gas fluxes in the AP mesocosms. (3) AC (aerial with clipped plants), all the plants were removed at soil surface, and the flooded water was depleted from the three containers for each species one day prior to gas sampling to prepare for the measurements of gas fluxes in the AC mesocosms.

Totally, we created 42 mesocosms in this experiment, i.e., 21 mesocosms for each species. Of the 21 mesocosms for each species, three mesocosms were allocated to SP, three to AP, and the rest 15 to AC. Monthly measurements, a total of five times, were conducted in continuous 3-day time period from June to October in 2004. The same three SP and AP mesocosms were sampled every month. For the AC mesocosms, the plants were allowed to grow normally until 24 h before the start of a monthly flux measurement. At that time, three of the AC mesocosms were chosen and clipped. Once gas flux measurements were made, the clipped mesocosms were not used again. Another three AC mesocosms were chosen for clipping and sampling next month.

2.2. Measurement of gas fluxes

The static closed chambers were used to measure CH_4 and N_2O emissions from *S. alterniflora* and *P. australis* containers. Stainless-steel collars were inserted into the soil to a depth of 50 mm one day prior to gas sampling. Every care was taken to minimize disturbance to the soil, particularly inside the chamber, during insertion. The transparent acrylic resin chambers covered an area of 50×40 cm, but the chamber height varied, depending on the height of plants. The small transparent acrylic resin chambers covering an area of 10×10 cm with a height of 10 cm were used to measure CH_4 and N_2O emissions from the aerial soil with no plants covered, which is abbreviated as AN thereafter. During the measurement, the chambers were placed on the notch collars, and airtight closure was ensured by water-filled sealing (Zhu et al., 2005). Air inside the chambers was circulated with battery-driven fans during the measurement in order to ensure gas samples to be well-mixed. To minimize any effects of diurnal variation in emissions, samples were taken at the same time of the day between 8:00 and 10:00 h on each occasion. The gas fluxes of CH_4 and N_2O in all treatments were measured simultaneously. Generally, five gas samples of chamber air were pulled into 100 ml polypropylene syringes at 0, 10, 20, 30, and 40 min after enclosure. Samples were injected into pre-evacuated vials for laboratory analysis. The air temperature inside the chamber was taken simultaneously for each measurement. These gas samples were analyzed in the Laboratory of Material Cycling in Pedosphere, Institute of Soil Science, Chinese Academy of Sciences, Nanjing. Since high vacuum inside the vial is changed little within a year (Zhu et al., 2005), the quality of the gases in the vials would not be affected during transport and storage period. The CH_4 concentrations in the gas samples were determined by using a gas chromatography (GC/FID Shimadzu 14 B), with a unibead-C column. Column, injection, and FID temperatures were set at 100 °C, 120 °C, and 300 °C, respectively, with a carrier gas (N_2) flow rate of 65 ml min^{-1}, and an injection volume of 0.5 ml (Towprayoon et al., 2005). N_2O concentrations in the gas samples were measured by using a gas chromatography unit (HP5890 IIGC) that is equipped with a ^{63}Ni electron capture detector (ECD). Compressed air was used as the standard gas with the value of 303 ppbv, and the response of GC was linear within 200–5000 ppbv. The coefficient of variation for the standard samples ranged from 0.1% to 0.3% in 10 h. Porapak-Q column, injection, and ECD detector temperatures were set at 65 °C, 50 °C, and 300 °C, respectively, with a carrier gas (N_2) flow rate of 60 ml min^{-1}, and an injection volume of 1 ml (Towprayoon et al., 2005; Zhu et al., 2005). The CH_4 and N_2O fluxes were then calculated by linear model from the change of gas concentration in the mixed chamber with time over a 40-minute period ($n = 5$) with an average chamber temperature (Rolston, 1986):

$$F = \frac{M}{V} \times \frac{\mathrm{d}c}{\mathrm{d}t} \times H \times \left(\frac{273}{273 + T} \right)$$

where F is the gas flux (mg m^{-2} h^{-1}), M the gas molecular weight, V the volume of the gas in standard condition, $\frac{\mathrm{d}c}{\mathrm{d}t}$ the ratio of gas concentration, H the height of the chamber, and T the air temperature inside the chamber. The regression coefficients from linear regressions were rejected when

r^2 was less than 0.9. Positive values indicate flux to the atmosphere (efflux), and negative values consumption of atmospheric gases (influx).

2.3. Plant biomass and density

We also obtained aboveground biomass (AGB) by harvesting all plants to the soil level for clipping treatment at each time. We estimated the belowground biomass (BGB) in these containers after the measurements of trace gas flux were made. Plant samples were oven-dried to constant weight at 65 °C. The samples were then weighed for AGB and BGB, from which the total biomass (TB) was obtained. Stem density were also recorded.

2.4. Data analysis

The means of AGB, BGB, and density were obtained from the three replicates for each treatment. A two-way ANOVA was used to analyze the differences in AGB, BGB and density between the two species. By comparing the experimental treatments, the relative change in gas emission due to non-submergence was calculated as: $([r(AP) - r(SP)]/r(SP))$ for AP vs. SP, and clipping $([r(AC) - r(AP)]/r(AP))$ for AC vs. AP, where $r(X)$ is the rate of CH_4 or N_2O emission from the SP, AP, or AC mesocosms. The proportions of methane and N_2O emitted through the plants were similarly calculated as $[r(AP) - r(AN)]/r(AP)$; and the emission rates per unit dry weight of total biomass (TB) as $[r(AP) - r(AN)]/TB$. For each plant species, the differences in trace gas emissions among SP, AP, AC and AN mesocosms were tested with repeated measures ANOVA, where multiple measurements on a given plant species through time represented the repeated variables. The differences in trace gas emissions between the two species were analyzed with a nested ANOVA, where multiple treatments nested in a given plant species through time represented the repeated variables. Furthermore, the repeated measures ANOVA was separately performed for trace gas emissions from each treatment event (SP, AP, AC and AN mesocosms). The relationships of trace gas emissions to plant characteristics (total biomass and density) from June through September were investigated with simple linear regression analysis. All the analyses were performed using Stat Soft's Statistica, statistical software for Windows (Version 6.0, StatSoft Inc., 2001) and Microsoft Excel software.

3. Results

3.1. Plant growth

The plant density in the S. alterniflora mesocosms was significantly higher than that in P. australis mesocosms ($P < 0.001$) (Fig. 1a). The biomass of S. alterniflora was also significantly higher than that of P. australis ($P < 0.001$). AGB of S. alterniflora ranged from 158.2 to 4470.0 g m^{-2},
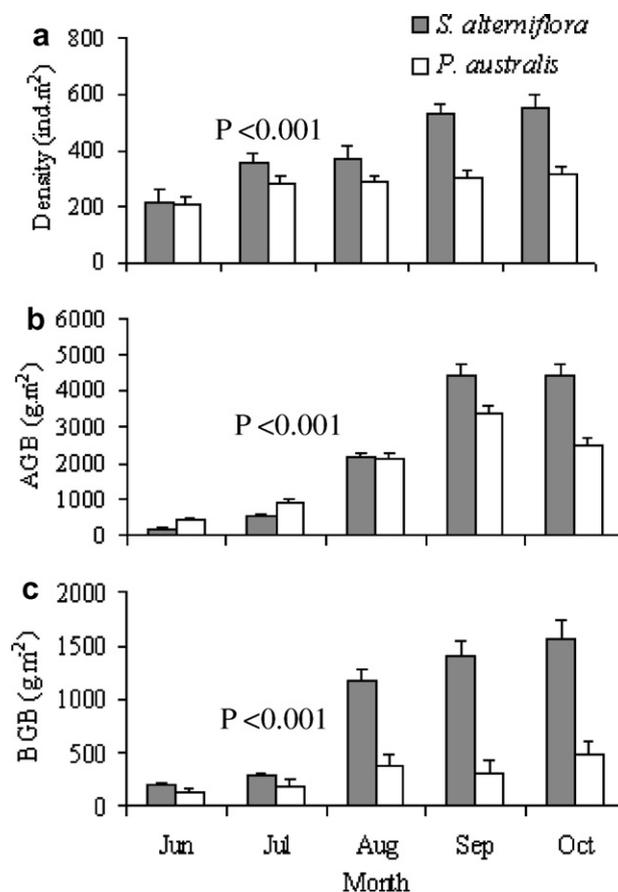

Fig. 1. Seasonal changes of biomass and density of Spartina alterniflora and Phragmites australis. Error bars represent standard errors (SE) of the mean values ($n = 3$). Note: AGB – Aboveground Biomass; BGB – Belowground Biomass.

and that of P. australis from 441.6 to 3380.0 g m^{-2} (Fig. 1b), while BGB of S. alterniflora ranged from 186.8 to 1566.7 g m^{-2}, and that of P. australis from 133.3 to 485.0 g m^{-2} in a growing season (Fig. 1c).

3.2. CH_4 and N_2O emissions

The flux rate of CH_4 emissions from the S. alterniflora mesocosms was significantly different from that from the P. australis mesocosms (Table 2), ranging from 0.16 to

Table 2
P-values from the nested ANOVA and repeated ANOVA of CH_4 and N_2O fluxes in S. alterniflora and P. australis brackish marsh mesocosms

Source of variation	CH_4	N_2O
Species	0.005	<0.0001
Species × Treatments	0.001	<0.0001
Species × SP	0.196	0.0007
Species × AP	0.018	0.013
Species × AC	0.066	0.076
Species × AN	0.059	0.063

Note: SP: submerged with plants; AP: aerial with plants; AC: aerial with clipped plants; AN: aerial soil with no plants covered. See text for detailed explanations.
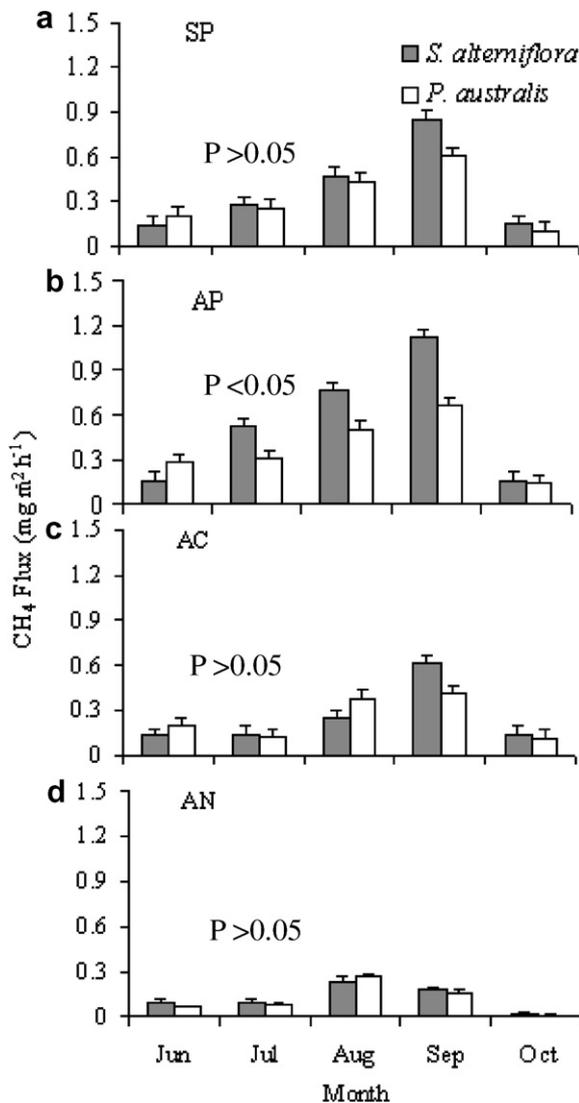
Fig. 2. CH₄ emissions from brackish marsh mesocosms planted with *Spartina alterniflora* and *Phragmites australis* in different treatments, Error bars represent standard errors (SE) of the mean values ($n = 3$).
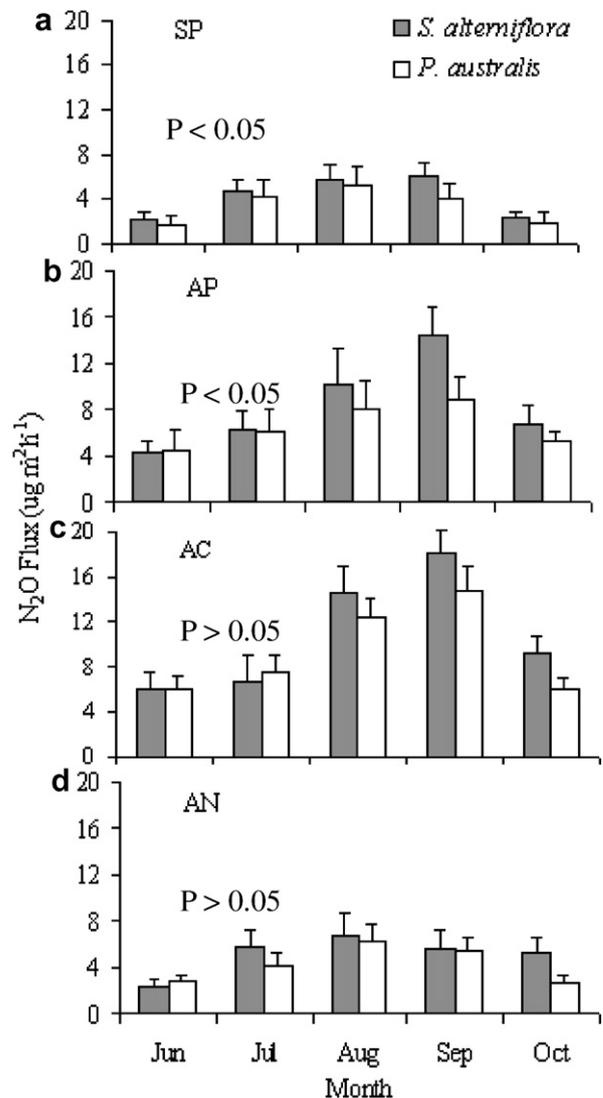

Fig. 3. N₂O emissions from brackish marsh mesocosms planted with *Spartina alterniflora* and *Phragmites australis* in different treatments, Error bars represent standard errors (SE) of the mean values ($n = 3$).

$1.12 \, \text{mg m}^{-2} \, \text{h}^{-1}$ for the former, and from 0.21 to $0.66 \, \text{mg m}^{-2} \, \text{h}^{-1}$ for the latter (Fig. 2). AP treatment increased CH₄ emissions by 6.7–85.7% and 4.8–40.0% in the *S. alterniflora*, and *P. australis* mesocosms, respectively (Fig. 2a vs. b). AC treatment significantly decreased CH₄ emissions of both the *S. alterniflora* and *P. australis* mesocosms (Fig. 2b vs. c; $P < 0.001$). CH₄ emissions from the *S. alterniflora* and *P. australis* mesocosms decreased by 18.8–73.1% and 21.4–61.2%, respectively, after the plants were clipped (Fig. 2b vs. c). Meanwhile, CH₄ emissions transported by plants accounted for 39.7–90.0% in the *S. alterniflora* mesocosms, and 48.8–90.0% in the *P. australis* mesocosms (Fig. 2b vs. d). Finally, CH₄ emission rates per unit dry weight were 2.0×10^{-5} to $5.0 \times 10^{-4} \, \mu\text{g g}^{-1} \, \text{h}^{-1}$ from *S. alterniflora*, and 4.0×10^{-5} to $4.0 \times 10^{-4} \, \mu\text{g g}^{-1} \, \text{h}^{-1}$ from *P. australis* (Fig. 1b, c vs. Fig. 2b, d).

Similarly, the flux rate of N₂O emissions from the *S. alterniflora* mesocosms was significantly different from that

from the *P. australis* mesocosms (Table 2), being 2.17–$18.10 \, \mu\text{g m}^{-2} \, \text{h}^{-1}$ and $1.69–14.77 \, \mu\text{g m}^{-2} \, \text{h}^{-1}$, respectively (Fig. 3). AP treatment significantly increased the rate of N₂O emissions by 67.0–192.2% and 41.2–178.6% from the *S. alterniflora* and *P. australis* mesocosms, respectively (Fig. 3a vs. b; $P < 0.001$). AC treatment significantly increased N₂O emissions from both the mesocosms (Fig. 3b vs. c; $P < 0.001$). N₂O emissions from the *S. alterniflora* and *P. australis* mesocosms increased, on average, by 29.3% and 37.3%, respectively, after plants were clipped (Fig. 3b vs. c). While N₂O emissions transported by plant accounted for an average of 43.4% from *S. alterniflora* and 38.7% from *P. australis* (Fig. 3b vs. d). N₂O emission rates per unit dry weight were 2.4×10^{-7} to $5.6 \times 10^{-6} \, \mu\text{g g}^{-1} \, \text{h}^{-1}$ for *S. alterniflora* and 8.6×10^{-7} to $3.2 \times 10^{-6} \, \mu\text{g g}^{-1} \, \text{h}^{-1}$ for *P. australis* (Fig. 1b, c vs. Fig. 3b, d).

Table 3
Summary of regression analyses between trace gas emissions (CH_4 and N_2O) and plant characteristics

Trace gas	Species	Water treatment	Independent variable	Regression equation	R^2 value	P value
CH_4	S. alterniflora	SP	Biomass	$Y = 0.0001x + 0.13$	0.83	0.003
			Density	$Y = 0.001x - 0.10$	0.48	0.01
		AP	Biomass	$Y = 0.0002x + 0.19$	0.84	0.007
			Density	$Y = 0.002x - 0.24$	0.61	0.003
	P. australis	SP	Biomass	$Y = 0.0003x + 0.09$	0.86	0.004
			Density	$Y = 0.003x - 0.41$	0.71	0.009
		AP	Biomass	$Y = 0.0003x + 0.16$	0.71	0.006
			Density	$Y = 0.003x - 0.33$	0.55	0.005
N_2O	S. alterniflora	SP	Biomass	$Y = 0.0002x + 3.70$	0.05	0.71
			Density	$Y = 0.003x + 2.84$	0.06	0.68
		AP	Biomass	$Y = 0.001x + 5.18$	0.43	0.22
			Density	$Y = 0.02x + 1.40$	0.35	0.29
	P. australis	SP	Biomass	$Y = 0.001x + 2.76$	0.03	0.80
			Density	$Y = 0.02x - 0.81$	0.15	0.39
		AP	Biomass	$Y = 0.001x + 4.82$	0.14	0.54
			Density	$Y = 0.02x - 0.34$	0.29	0.34

3.3. Relationship between gas emission and plant characteristics

Overall, CH_4 emissions increased from June through September and decreased in September and October (Fig. 2); and the highest N_2O emissions occurred in August and September over the sampling period (Fig. 3). In both SP and AP treatments, CH_4 emissions were positively correlated with plant TB and density for S. alterniflora from June through September (submergence: r^2 ranged from 0.48 to 0.83, $P < 0.05$; non-submergence: r^2 from 0.61 to 0.84, $P < 0.01$) and P. australis (submergence: r^2 ranged from 0.71 to 0.86, $P < 0.01$; non-submergence: r^2 from 0.55 to 0.71, $P < 0.01$) (Table 3). In contrast, N_2O emissions were not significantly correlated with plant characteristics for either S. alterniflora or P. australis in both SP and AP ($P > 0.05$) (Table 3).

4. Discussion

4.1. Effects of plant and clipping on trace gas emissions

In this study, we compared the trace gas emissions from invasive S. alterniflora and native P. australis in brackish marsh mesocosms. We found that CH_4 and N_2O emissions from the S. alterniflora mesocosms were higher than those from the P. australis mesocosms (Figs. 2 and 3). Ding et al. (2003) have reported that vegetation types and nutrient supplies are important factors in field investigations of trace gas emissions. Previous studies have also found that invasive S. alterniflora has great biomass production in the east coast of China (e.g., Qin and Zhong, 1992). In our brackish marsh mesocosms, S. alterniflora had significantly greater biomass than P. australis (Fig. 1), suggesting that S. alterniflora could fix more carbon and allocate more carbon (photosynthesis followed by leaching, root turnover, and detritus inputs) to the soil (Table 1), implying a potential to emit more trace gases.

Previous studies have indicated that increased CH_4 emissions from vegetated areas are primarily attributable to the plant-mediated transport of trace gas produced through the plant aerenchyma tissues and an increase in rhizodeposition by root exudation and/or rapid fine root turnover (e.g., Rusch and Rennenberg, 1998; Storm et al., 2003). As might be expected, we found that CH_4 emissions transported by plants accounted for 39.7–90.0%, and 48.8–90.0% of the total emissions, respectively, from the S. alterniflora and P. australis mesocosms, while the CH_4 emissions decreased by 18.8–73.1% from S. alterniflora, and 21.4–61.2% from P. australis 24 h after the plants were clipped in the brackish marsh mesocosms (Fig. 2). These responses suggested that plant aerenchyma might act as a pathway of plant-mediated CH_4 transport in wetlands (Rusch and Rennenberg, 1998), and plants may lead to a high input of root exudates associated with recent production and to a stimulation of methanogesis (e.g. Christensen et al., 2001). Several studies have demonstrated that the relationships between CH_4 emission and plant biomass or density varied substantially (Schimel, 1995; Kutzbach et al., 2004). Our results indicated that CH_4 emission rates ranged from 2.0×10^{-5} to 5.0×10^{-4} µg g^{-1} h^{-1} for S. alterniflora mesocosms, and 4.0×10^{-5} to 4.0×10^{-4} µg g^{-1} h^{-1} for P. australis mesocosms and were strongly correlated with plant biomass and

density (Table 3 and Fig. 2). CH$_4$ production might be enhanced because of the increase in rhizodeposition (i.e., root exudation and/or rapid fine root turnover), and increased plant biomass might have increased the rate that soil CH$_4$ is ventilated through plants (Rusch and Rennenberg, 1998). Thus, our results, together with those of other wetland studies, further suggest that wetland vascular plant species may play important roles in CH$_4$ production and transport, and can be envisaged as suppliers of easily available substrates for the methanogenic bacteria in wetland ecosystems (e.g., Joabsson et al., 1999; Storm et al., 2003).

Interestingly, we found that N$_2$O emissions transported by plants accounted for an average of 43.4%, and 38.7% of the total emissions respectively from *S. alterniflora* and *P. australis* in the mesocosms (Fig. 3), while N$_2$O emission rates per unit total dry biomass were 2.4×10^{-7} to 5.6×10^{-6} µg g^{-1} h^{-1} for *S. alterniflora* and 8.6×10^{-7} to 3.2×10^{-6} µg g^{-1} h^{-1} for *P. australis* mesocosms (Fig. 1b, c vs. Fig. 3b, d), which were consistent with the finding that these gases are mainly transported through aerenchyma of plants (Colmer, 2003). However, few have studied N$_2$O emissions from plants although Mosier et al. (1990) have demonstrated that rice plants increase the flux of N$_2$O + N$_2$ from the soil to the atmosphere through their conduit transport. Chen et al. (1997) have shown that the N$_2$O emissions from plants are not directly correlated with plant photosynthetic activity. Our results showed that the N$_2$O emissions were uncorrelated with plant characteristics of *S. alterniflora* and *P. australis* in the marsh mesocosms. It is well-known that N$_2$O can originate from both the nitrification and denitrification processes (Towprayoon et al., 2005). More interestingly, the results from our clipping treatments showed that N$_2$O emissions increased after plants were clipped (Fig. 3), suggesting that plants might compete for NO$_3^-$ and NH$_4^-$ from soil for growth with microbes (nitrifers/denitrifier), and suppress N$_2$O emissions from nitrification and denitrification processes in the marshes.

4.2. Effects of water submergence on trace gas emissions

Water submergence plays a key role in trace gas emissions from wetland ecosystems (i.e., Bridgham et al., 1999; Grünfeld and Brix, 1999). Draining water from wetlands would suppress CH$_4$ emissions because of increased CH$_4$ oxidation activity in soil (Christensen et al., 2001). When water table falls below the soil surface, CH$_4$ oxidation increases drastically and hence CH$_4$ emissions are reduced (Kutzbach et al., 2004). Our results showed that non-submergence increased CH$_4$ emissions in both *S. alterniflora* and *P. australis* mesocosms (Fig. 2). There are two possible explanations for the increase in CH$_4$ emissions in response to non-submergence. First, water might have acted as a diffusion barrier (Rusch and Rennenberg, 1998) that suppresses CH$_4$ emissions. Second, the soils were not dried out to support significant CH$_4$ emissions in our

water-saturated soils which might have resulted in little O$_2$ getting into the soil to actually oxidize CH$_4$ (Vann and Megonigal, 2003).

Draining water may lead to relatively high rates of N$_2$O efflux during non-flooded periods (Chen et al., 1997; Bridgham et al., 1999). Our results also indicated that non-submerged status significantly increased N$_2$O emissions from *S. alterniflora* and *P. australis* mesocosms (Fig. 3a vs. b). Aerobic and anaerobic conditions resulted in production of N$_2$O (Towprayoon et al., 2005). In wetland soils, N$_2$O is excreted into the soil by anaerobic denitrifiers in considerable amount, but the release of gases from flooded wetlands was thought to be low (Martikainen et al., 1995). The low release may be caused by a tremendous reduction of nitrate to N$_2$ or by water acting as a diffusion barrier (Rusch and Rennenberg, 1998). This diffusion barrier would be circumvented by plant-mediated transport (Reddy et al., 1989; Mosier et al., 1990).

It is important to note that the emission of trace gases from wetlands is complex process that is controlled by multiple factors like hydrology, soil temperature, substrates, and vegetation (e.g., Kang et al., 1998; Rusch and Rennenberg, 1998; Fenner et al., 2006). Although both CH$_4$ and N$_2$O emissions seemed to be influenced by water submergence and clipping, we found that invasive *S. alterniflora* increased trace gas emission rates compared with native *P. australis* in our experimental mesocosms due to its larger biomass and higher density of *S. alterniflora* which could fix more available substrates to the soil and have the potential to emit more trace gases. However, more field studies and related modeling work are still necessary to extrapolate the effects of invasive plants like *S. alterniflora* at various spatial and temporal scales.

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