Plant-mediated methane and nitrous oxide fluxes from a *Carex* meadow in Poyang Lake during drawdown periods

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Abstract

Aims Plants have been suggested to have significant effects on methane (CH₄) and nitrous oxide (N₂O) fluxes from littoral wetlands, but it remains unclear in subtropical lakes.

Methods We conducted *in situ* measurement of CH₄ and N₂O fluxes for two years. To distinguish between the effects of shoots and roots, three treatments (i.e., intact plants as control, shoot clipping, and root exclusion) were used. Effects of plant biomass, temperature, and soil moisture on CH₄ and N₂O fluxes were analyzed.

Results The mean ecosystem CH₄ emission rate was 36 µg CH₄ m⁻² h⁻¹ for drying periods, but 8219 µg CH₄ m⁻² h⁻¹ for drying-wetting transition periods. CH₄

fluxes were positively correlated with below-ground and total biomass, but not with above-ground biomass. Clipping did not significantly alter CH₄ flux rate, but root exclusion decreased the CH₄ flux by 116 % as compared to the control. N₂O emissions were similar for both the drying and drying-wetting transition periods, with a mean rate of 20 µg N₂O m⁻² h⁻¹. Both clipping and root exclusion significantly increased N₂O fluxes as compared to the control.

Conclusions There was no significant correlation between CH₄ and N₂O fluxes. Roots dominated plant-mediated enhancement in CH₄ fluxes, but played almost an equal role as shoots in plant-regulated suppression on N₂O fluxes in this *Carex* meadow during drawdown periods.

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Introduction

Atmospheric concentrations of methane (CH₄) and nitrous oxide (N₂O) have increased by 150 % and 20 %, respectively, since pre-industrial times, contributing to more than 25 % of anthropogenic global warming (Forster et al. 2007; IPCC 2013). Global wetlands were estimated to account for a third of the current annual CH₄ emissions, and they are the dominant natural source of atmospheric CH₄ fluxes and their inter-annual variability (Bridgman et al. 2013; IPCC 2013). Meanwhile, wetlands are recognized as considerable

N₂O emitters with an annual rate of 0.36 kg N₂O-N ha⁻¹ yr⁻¹ (Zhuang et al. 2012). Although high productivity and water-logged conditions make many wetlands significant carbon (C) sinks (Bernal and Mitsch 2012), strong CH₄ and N₂O emissions from wetlands could largely offset these C sinks. For example, considering CH₄ emission, a wetland in the southern Rocky Mountains acted as C source in each of the testing years from 1996 to 1998 (Wickland et al. 2001). The same results were observed in a subarctic peatland in Northern Sweden (Bäckstrand et al. 2010). Moreover, if the global warming potential (GWP) of CH₄ and N₂O is taken into account, many other wetlands could turn into sources of atmospheric radiative forcing (Whiting and Chanton 2001; Friberg et al. 2003). Hence, it is necessary to integrate both CH₄ and N₂O into assessments for the net greenhouse gas (GHGs) effect from wetlands.

CH₄ and N₂O emissions from wetlands are subjected to a number of biotic and abiotic controls (Jørgensen and Elberling 2012; Bridgman et al. 2013), among which plants are considered to be the major one because they can strongly affect CH₄ and N₂O production, consumption, and transportation (Rückauf et al. 2004; Laanbroek 2010). Plant presence can increase soil CH₄ flux by enhancing substrate availability. There is strong evidence showing that CH₄ emission is favored by photosynthates in the form of root exudates (King and Reeburgh 2002; Dorodnikov et al. 2011; Ström et al. 2012). The transport of oxygen from shoots to the rhizosphere via aerenchyma can lead to the suppression of methanogenesis and oxidation of CH₄ to CO₂. Additionally, transport through vascular plants is one of the most available pathways for CH₄ emissions from wetlands (Schimel 1995; Bellisario et al. 1999; Ding et al. 2005). Although nitrification and denitrification are the major processes leading to N₂O emission from soils (Conrad 1996), plants also affect these processes through competition with microbes for mineral N (Cavieres and Badano 2009). In addition, plants can supply microbes with labile substrates and serve as a transport pathway, which may increase N₂O emissions (Rückauf et al. 2004; Jørgensen et al. 2012). Previous studies have reported increases (Bellisario et al. 1999; Laanbroek 2010) or decreases (Kao-kniffin et al. 2010; Sutton-Grier and Megonigal 2011) of CH₄ emission in response to an increase in plant biomass or productivity. The contribution of plant-mediated CH₄ flux varied substantially among species and wetland types (Whiting and Chanton 1992; Ding et al. 2005; Dorodnikov et al. 2011). Similarly, lower (Johansson et al. 2003; Maltais-Landry

et al. 2009) and higher (Rückauf et al. 2004; Wang et al. 2008) N₂O emissions have been reported in artificial wetlands with plants, as compared to those without plants. Therefore, the mechanisms describing the effects of plants on CH₄ and N₂O fluxes from wetlands remain unclear. In addition, a full understanding of wetland CH₄ and N₂O emissions requires knowledge about how above- and below-ground compartments of plant community individually affect the fluxes. Distinguishing the specific influence of above- and below-ground parts is a way to better understand the effect of plants on CH₄ and N₂O fluxes.

There are increasing concerns on the relations between GHGs, because these relations could be used to predict one GHG flux based on measurement of another. For instance, significant correlations between N₂O and CO₂ fluxes are observed in many terrestrial ecosystems (Garcia-Montiel et al. 2002; Xu et al. 2008), but little attention has been paid to GHG relations in wetlands. CH₄ is produced in anaerobic conditions, whereas N₂O can also be derived from aerobic nitrification and anaerobic denitrification. Theoretically, denitrification is energetically more favorable as compared to methanogenesis (Conrad 1996; Hedin et al. 1998). Therefore, when N₂O flux increases, CH₄ emission should decrease, and vice versa. This indicates a negative correlation between N₂O and CH₄ might be expected if denitrification is a dominant source of N₂O. The expected correlation between CH₄ and N₂O in the above-ground efflux needs to be proved by profiling below-ground measurements in relation to numerous environmental parameters.

The littoral zones of lakes comprise a biogeochemically active terrestrial-aquatic interface, where organic matter is transferred to the associated lakes, and GHGs are exchanged with the atmosphere (Larmola et al. 2003). Studies have demonstrated that littoral wetlands were 'hot spots' for CH₄ and N₂O emissions (Juutinen et al. 2003a; Wang et al. 2006a, 2006b; Chen et al. 2009). However, most of these studies were concentrated in boreal or cold regions (Larmola et al. 2003; Juutinen et al. 2003a, 2003b; Chen et al. 2009, 2011). Although lake areas in low latitudes are much smaller than in high latitudes, the estimated sediment GHG productions from low latitude lakes were substantially higher than boreal lakes (Marotta et al. 2014). Consequently, the knowledge of CH₄ and N₂O emissions from various littoral wetlands, especially in largely unexplored tropical and subtropical lakes, will help reduce the uncertainty in global wetland CH₄ and N₂O estimation.

Poyang Lake is the largest subtropical shallow water lake in China. It is characterized by drastic annual and inter-annual water level fluctuation affected by the tributary rivers in the watershed as well as the quantity of water in the Yangtze River. During drawdown periods, the littoral wetlands are dominated by wet *Carex* meadows that account for approximately 30 % of the total lake area (Hu et al. 2010). *Carex* meadows experience two growing seasons that occur in the spring and in autumn after the summer flooding (Hu et al. 2010). In recent years, climate change and the operation of the Three Gorges Dam (since 2003) have largely altered the hydrological regime of Poyang Lake, resulting in a reduction of the summer flooding duration and extension of drawdown periods (Zhang et al. 2012). Quantifying GHG fluxes from *Carex* meadows during drawdown periods will help to advance the understanding of biogeochemical processes in response to ongoing climate warming and hydrological change in this large subtropical lake. We have reported ecosystem respiration and its components in a *Carex* meadow during the drawdown period in a recent study (Hu et al. 2015). In this study, we evaluated CH₄ and N₂O emissions during drawdown periods, and aimed to determine the effects of above-ground and below-ground compartments of *Carex* on CH₄ and N₂O fluxes through shoot clipping and root exclusion. We also intended to test the following two hypotheses: (1) there is a negative correlation between CH₄ and N₂O fluxes based on thermodynamics of denitrification and methanogenesis, and (2) the presence of *Carex* should enhance emissions of CH₄ and N₂O because plants can provide root exudates for microorganisms living in the rhizosphere and increase their activities.

Materials and methods

Study area

This study was conducted in the Nanji Wetlands National Nature Reserve in the south of Poyang Lake in China. The experimental site is located at latitude 28° 53'35"N, longitude 116° 19'11"E and at an altitude of 15 m above sea level in Xinjian County, Jiangxi Province, China in the subtropical monsoon climate. The mean annual air temperature is 17.6 °C, with mean January temperature of 5.1 °C and July temperature of 29.5 °C. The annual precipitation ranges from 1450 mm

to 1550 mm and most falls from April to June. In the summer rainy season, the *Carex* meadows are completely inundated, and become part of the large water body of the lake. When the flood recedes in autumn, the *Carex* meadow emerges. Annual drawdown periods are largely dependent on both local precipitation and the hydrologic regime of the Yangtze River, ranging from 165 to 271 days (Liu et al. 2006; Hu et al. 2010). The drawdown periods could be further separated into drying and drying-wetting transition periods, respectively. For example, the total drawdown duration lasted 195 d in 2010, where the drying and drying-wetting transition periods were 180 d and 15 d, respectively. *Carex* meadows are widely distributed in the Nanji Wetlands National Nature Reserve, and the dominant plant is *Carex cinerascens*, which covers over 95 % of the meadows, leaving negligible amounts of plant-free soil areas. Other accompanying species include *Potentilla limprichtii*, *Cardamine lyrata*, and *Polygonum hydropiper*. Characterized as meadow soil, the organic horizon is about 15 cm in depth, and soil horizon (under 15 cm) is recognized as the mineral layer. The mean soil organic carbon and total nitrogen at a depth of 0–15 cm are 1.97 ± 0.22 % and 0.173 ± 0.017 %, respectively. The pH at a soil depth of 0–30 cm averaged 5.4 ± 0.6 . During drawdown periods the soil redox potential (Eh) at a depth of 0–30 cm averaged 171.7 ± 16.6 mV. Mean water table depth ranged from –30 to –50 cm below the soil surface (Hu et al. 2010). More details of this *Carex* meadow are described in Hu et al. (2015).

Experimental design

Three treatments were set in a typical *Carex* meadow (> 200 m²). The plots with intact plants were used as a control treatment (IP). The plots where the above-ground vegetation was removed were referred to as a shoot clipping treatment (SC). Finally, the root exclusion (RE) treatment was where whole plants were removed in several stages in order to minimize soil disturbance. The distance between plots was approximately 10 m. Plots were initially isolated by trenching a plot boundary, and a square-based stainless steel frame (0.5-m length × 0.5-m width × 0.4-m depth) was inserted into the soil to prevent encroachment of new roots. Shoots inside the frame were frequently cut at the soil surface and removed until they did not grow again within a two-month period. There was no new shoot regrowth in the frame after the summer flooding in 2009. With the

above three treatments we attempted to separate the specific influence of above-ground vegetation (shoots) and roots on CH₄ and N₂O fluxes. The difference between IP and SC treatment represents the effect of above-ground vegetation on CH₄ and N₂O fluxes, while the difference between SC and RE treatment indicates the effects of living roots. The decomposition of new dead roots inside the RE plots should contribute to methane production and N transformation, but these impacts might be less important with time (Hanson et al. 2000; Kuzyakov 2006). Therefore, we used CH₄ and N₂O flux data from the RE treatment measured after February 2010 to determine the effects of root exclusion on the fluxes, because we found the effects of decomposing roots could be negligible after about 9 months when the trenching plots were completed. The CO₂ efflux rate ratio of the RE treatment to the SC treatment declined substantially from the previous average of 0.86 to 0.60 in March 2010, and the latter ratio (i.e., the contribution of soil microbial respiration to total soil respiration) was consistent with previous studies and was maintained in the following flux measurement days (Hu et al. 2015).

We clipped above-ground vegetation for the SC treatment one day before each flux measurement. After clipping, plants were allowed to grow until the next clipping. The frames were maintained during the entire flux measurements for IP and RE, but replaced in each growing season to ensure survival of below-ground roots for the SC treatment. The area of each sampling plot was 0.25 m² and triplicate plots were randomly located for each treatment. Measurements of CH₄ and N₂O fluxes started several days after installation of the base-frame to minimize soil disturbance.

Gas sampling and analysis

CH₄ and N₂O fluxes were measured using static closed chamber techniques during the drawdown periods from May 18, 2009 to June 12, 2011, including 5 plant growing periods: May 18 to June 24, 2009; September 27, 2009 to January 20, 2010; February 20 to April 10, 2010; October 9, 2010 to January 20, 2011; and February 20 to June 12, 2011.

The sample chambers were made of thin stainless steel, with a chamber and a base-frame component. The chamber (0.5 m × 0.5 m × 0.5 m) was equipped with two fans inside the top, powered by a 12-V battery. The base-frame had a groove on the upper side that was

filled with water to avoid leakage during sampling. Chamber air was sampled using a 100 ml syringe at time intervals of 0-min, 10-min, 20-min and 30-min. Samples were taken between 9:00 and 11:00 h, two to three times per month. Gas samples were transferred to sampling air bags (Polymer film and aluminum foil) and brought to the laboratory for CH₄ and N₂O analysis using a gas chromatograph (GC; Agilent 4890D, Agilent Technologies). The GC was equipped with a flame-ionization detector (FID) and an electron capture detector (ECD). CH₄ was separated from other gases using a 2 m stainless-steel (inner diameter of 2 mm) 13XMS column (60/80 mesh) and was detected by FID. N₂O was separated using a 1 m stainless-steel (inner diameter of 2 mm) Porapak Q (80/100 mesh) column and was detected by ECD. The FID, ECD and column temperatures were maintained at 200 °C, 330 °C and 55 °C, respectively. High purity nitrogen was used as a carrier gas for FID and ECD systems at a flow rate of 30 and 35 ml/min, respectively. The GC configurations for analyzing CH₄ and N₂O concentrations were according to the method outlined in Wang and Wang (2003), and the flux calculations followed the description of Song et al. (2008). Negative fluxes indicated an uptake of the gas from the atmosphere and positive indicated a release from the ecosystem.

Environmental factors

During gas sampling, ambient air temperature, soil temperature at a depth of 5 cm, and headspace air temperature of sample chambers were measured simultaneously using a portable thermometer (JM624, JinMing Instruments, China). Soil water content at a depth of 10 cm was determined using a moisture meter (TDR300, Spectrum Technologies, USA). An automatic air temperature meter (HOBO Pro, Onset Company, USA) was employed at the sampling site to record daily air temperature at an interval of 2 h.

Plant biomass was measured by clipping vegetation samples from three representative 0.25-m² areas about every 30 days during the drawdown periods. The first biomass measurements in spring and autumn were conducted in early February and 10 days after the drawdown area emergence, respectively. Plant materials were divided into living and dead parts before they were oven dried at 70 °C for 48 h and then weighed. Root biomass was measured by collecting soil samples from depths of 0–40 cm from three 0.25-m × 0.25-m plots, which were

co-located with the plot of the above-ground biomass measurement. The main parameters for distinguishing live from dead roots were the root color, the elasticity of the roots, and the presence of cortex and lateral roots (Dong 1997; Robertson et al. 1999). We combined the above parameters to decide whether a root should be regarded as live or dead. We collected all live roots with a diameter less than 2 mm. Following this standard procedure, the accuracy of root biomass differentiation reached a confidence level of 95 % and the expected error probability of the end values was less than $P < 0.05$. However, it is difficult to completely distinguish between live and dead roots and minor errors may have occurred for small-sized roots.

Data analysis

We excluded outliers when building correlations between CH_4 and N_2O fluxes and for the comparison of CH_4 flux among the three treatments. NPP was estimated as the sum of the above-ground and below-ground NPP, and NEP was calculated as the difference between NPP and the total soil C emission as heterotrophic respiration, which was published in Hu et al. (2015) (Table 1). To correlate with plant biomass, GHG fluxes measured at the dates of plant samplings ($n = 18$) were used.

Statistical analysis

One-way ANOVA and paired-t tests were used to test CH_4 and N_2O flux differences among the three treatments. Linear regression models were used to describe the relations between fluxes and temperature, moisture and plant biomass. Data analysis and plotting were processed using SigmaPlot 10.0 (SPSS Inc., Chicago, USA). All statistical analysis was performed using SPSS 11.5 (SPSS Inc., Chicago, USA). All differences were considered statistically significant when $P < 0.05$.

Results

CH_4 and N_2O fluxes

During the drying periods of 2009 to 2011, CH_4 fluxes from IP, SC and RE treatments showed similar temporal variability. Fluxes reached the maximum at the peak of growing periods and the minimum occurred in January

when plants were nearly dormant (Fig. 1b). Over the entire measurement period, CH_4 emissions prevailed. CH_4 uptakes were observed in all three treatments from the end of November to January when air temperature was lower than 10 °C and soil moisture content was about 55 %. The CH_4 flux rates ranged from -128 to $230 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for the IP treatment, but -81 to $154 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for the SC treatment and -174 to $233 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for the RE treatment, respectively. Two extreme CH_4 emission events were observed during the soil drying-wetting transition periods. The flux rates were 16,961, 19,157 and 10,925 $\mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for IP, SC and RE treatments, respectively, on June 14, 2009 before summer flooding. Similarly, the counterparts were 3287, 3074 and 1708 $\mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ on October 9, 2010 after summer flooding. CH_4 fluxes showed no significant difference among the three treatments ($P > 0.05$). On average, the ecosystem CH_4 emission rate was 36 $\mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for drying periods, but 8219 $\mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for drying-wetting transition periods.

N_2O fluxes from the three treatments also showed clear temporal variability, with higher flux rates occurring in soil drying-wetting transition periods after flooding (Fig. 1c). The flux rates varied from 2 to 66 $\mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$ for the IP treatment, but -9 to 132 $\mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$ for the SC treatment and 1 to 395 $\mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$ for the RE treatment, respectively. The mean ecosystem N_2O emission rate was 20 $\mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$ during the drawdown periods. N_2O flux rates significantly differed among the three treatments ($F = 24.1$, $P < 0.01$). The mean N_2O flux rate of the RE treatment was almost five times higher than the IP treatment, and more than two times higher than the SC treatment. There were no significant correlations between CH_4 and N_2O fluxes from the three treatments (Fig. 2).

Effects of temperature and soil moisture on CH_4 and N_2O fluxes

During drying periods, CH_4 flux rates of the three treatments were positively correlated with both air and soil temperatures (Fig. S1). Changes in air temperature could explain 42 % to 44 % of the variation in CH_4 fluxes (Fig. S1A-C). By comparison, 43–47 % of CH_4 flux variability could be explained by changes in soil temperature at a depth of 5 cm (Fig. S1D-F). N_2O fluxes from all three treatments were not correlated with air

Table 1 Comparison of CH₄ and N₂O flux rates among different littoral zones of various lakes

Location	Dominant vegetation	Sampling period	CH ₄ (μg CH ₄ m ⁻² h ⁻¹)	N ₂ O (μg N ₂ O m ⁻² h ⁻¹)	Reference
Subtropical Poyang Lake, China (28° 53'35" N, 116° 19'11"E)	<i>Carex cinerascens</i>	Drawdown periods	2276 – 16961 ^a	46 – 104 ^a	This study
Lake Mochou, east Antarctica (69°23'–69°56' S, 76°20'–76°45' E)	Alga	Summer	–128–230 ^b 145	2 – 38 ^b 5	Zhu et al. 2010; Liu et al. 2011
Lake Tuanjie, east Antarctica (69°23'–69°56' S, 76°20'–76°45' E)	Alga	Summer	110	4	
Boreal Lake Alinen Raujärvi, Finland (61°11' N; 25°6' E)	<i>Schoenoplectus lacustris</i> zone <i>Phragmites australis</i> zone	Summer	1280–2240 1600–3840		Kankaala et al. 2005
Boreal Lake Ekojärvi, Finland (61°12' N; 24°58' E)	<i>Equisetum fluviatile</i> zone <i>Phragmites australis</i> zone	Summer	4160–9920 320–4480		
Boreal Lake Kevätön, Finland (63°06' N, 27°37' E)	<i>Calamagrostis canescens</i> , <i>Calla palustris</i> L, <i>Carex aquatilis</i>	Summer		6–24	Huttunen et al. 2003
Huahu Lake, Tibetan plateau, China (33°56' N, 102°52' E)	<i>Hippuris vulgaris</i> , <i>Carex multensis</i> <i>Glyceria maxima</i> , <i>Kobresia tibetica</i> <i>Polygonum amphibium</i>	Summer	–100 – 90,000	110–550	Chen et al. 2009, 2011
Subtropical Taihu Lake, China (31°24'– 31°32' N, 120°04'–120°14' E)	<i>Phragmites australis</i> <i>Miscanthus saccharifloous</i>	Annual	–1700 – 13,100	–278 – 2101	Wang et al. 2006a, 2006b

^a The flux rate range during the drying-wetting transition period^b The flux rate range during the drying period

Fig. 1 Temporal variations of air temperature (*AT*) and soil moisture (*SM*) (a), CH_4 fluxes (b), N_2O fluxes (c) from the control treatment, intact plants (*IP*), removal of the aboveground vegetation by clipping (*SC*) and root exclusion (*RE*) treatments in the *Carex* meadow. The flux values are presented as mean $\pm$ SD of three replicates

temperature or soil temperature (Fig. S2). In addition, there was no significant correlation between soil moisture at the top 0–10 cm and CH_4 and N_2O flux rates from the three treatments (Fig. S3).

Effects of plant biomass on CH_4 and N_2O fluxes

CH_4 fluxes from *IP* and *SC* treatments were positively correlated to below-ground and total biomass, but not to

above-ground biomass (Fig. 3a–c). Changes in below-ground biomass could explain 37 % and 44 % of the variation in CH_4 fluxes from *IP* and *SC* treatments, respectively (Fig. 3b). By contrast, negative correlations were observed between N_2O fluxes and above-ground and total biomass in the same two treatments (Fig. 3d, f). Changes in above-ground biomass accounted for 28 % and 30 % of N_2O flux variability from *IP* and *SC* treatments, respectively (Fig. 3d).

Fig. 2 The relationship between CH₄ and N₂O fluxes from the control treatment, intact plants (IP), removal of the above-ground vegetation by clipping (SC) and root exclusion (RE) treatments in the *Carex* meadow. The long dash, dotted and solid regression lines were used for IP, SC and RE treatments, respectively

Discussion

Impact of shoot clipping and root exclusion on CH₄ fluxes

The effects of clipping on CH₄ emissions have been reported to vary with water table depth and clipping height above the surface, and are largely species dependent (Schimel 1995; Kelker and Chanton 1997; Ding et al. 2005; Askaer et al. 2011). For example, Askaer et al. (2011) found that clipping all above-ground vegetation decreased CH₄ flux by about 70 % as compared to the intact plant system in a *Phalaris arundinacea* dominated temperate wetland in Denmark. In contrast, Schimel (1995) found that clipping leaf blades significantly increased CH₄ flux from a *Carex aquatilis* site, but not from an *Eriophorum angustifolium* site in a wet meadow of Alaska. However, we did not find significant difference of CH₄ flux rates between shoot clipping and control treatment, which was not consistent with other studies (Ding et al. 2005; Askaer et al. 2011).

CH₄ flux depends on the balance between CH₄ production, oxidation and transport. Above-ground shoot clippings not only reduced the labile C into the soil (King and Reeburgh 2002; Ström et al. 2012), but also simultaneously influenced plant mediated CH₄ transport and oxidation. For instance, increased CH₄ flux due to clipping of *Carex aquatilis* was attributed to the removal of the resistance to CH₄ flow within plant tissues (Schimel 1995). Ding et al. (2005) concluded that *Carex lasiocarpa*

clippings mainly decreased CH₄ oxidation, rather than CH₄ production, whereas *Carex meyeriana* clippings led to almost the same effects on CH₄ oxidation and production. Although above-ground shoot clipping inevitably decreased the substrate availability for methanogenesis, clipping probably enhanced CH₄ transport because the main plant compartment limiting CH₄ emissions may not be in the stem of plants, but located at the root-shoot boundary (Kelker and Chanton 1997; Ding et al. 2005). In addition, clipping largely decreased plant photosynthetic activity, leading to less O₂ transporting into the rhizosphere and further decreased CH₄ oxidation (Ding et al. 2005; Sutton-Grier and Megonigal 2011). Consequently, positive and negative shoot clipping effects on CH₄ flux were in balance, resulting in similar CH₄ flux rates of shoot clippings and control treatments. This balance may only be relevant for conditions without standing water, as CH₄ emissions significantly decreased when shoots were clipped below the water surface (Kelker and Chanton 1997; Ding et al. 2005). Additionally, when no standing water occurs and there is a relatively low water table depth and low soil moisture, typical gas diffusion is not hindered and may prevail over plant-mediated transport. In other words, the role of the plant-mediated gas transport pathway might be weakened under these conditions. This may be another possible reason for the non-significant difference of CH₄ fluxes between shoot clippings and control treatments.

In this study, significant positive correlations between CH₄ flux and total plant biomass supported our hypothesis that the presence of *Carex* could enhance CH₄ flux in this subtropical wetland. However, CH₄ flux was not significantly related to the above-ground biomass, likely because shoot clippings did not significantly alter the CH₄ flux rate (Fig. 3a). This suggests that below-ground roots mainly contributed to the plant mediated enhancement in CH₄ fluxes during drawdown periods. This was further confirmed by the relationship between CH₄ flux and below-ground biomass (Fig. 3b). Both control and shoot clipping treatments showed significant positive correlations between CH₄ flux and below-ground biomass, (rather than total biomass) and changes in below-ground biomass could explain 37 % and 44 % of the variation in CH₄ fluxes from control and shoot clipping treatments, respectively (Fig. 3b). Owing to the restriction of the trenching method, dead roots were certainly inside the root exclusion plots, and may have contributed to CH₄ production. To our knowledge, previous studies have not assessed this impact. Although the effect of

Fig. 3 Effects of biomass on CH_4 (a, b, c) and N_2O (d, e, f) fluxes. The relation between biomass and fluxes was described using $Y = aX + b$ for intact plants treatments (IP) and $y = ax + b$ for

shoot clipping treatments (SC), respectively. The values are presented as mean $\pm$ SD of three replicates

decomposing roots may not be eliminated, it should be less important with time (Ewel et al. 1987; Bowden et al. 1993; Hanson et al. 2000; Zhou et al. 2007). According to our previous study (Hu et al. 2015), the effects of decomposing roots on soil CO_2 efflux are almost negligible after 9 months when the trenching plots were completed. Thus, root exclusion significantly decreased the CH_4 flux rate compared to the control treatment ($t = 3.0$, $P < 0.01$) when flux data measured after February 2010 was used for the comparison. This result was consistent

with previous observations from a vegetation removal study in Alaska (King et al. 1998). When the enormously high flux measured on October 9, 2010 (Fig. 1) was excluded, the mean flux rate of the root exclusion treatment was $-5 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$, and decreased by 116 % in contrast to the control treatment ($32 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$). Root exclusion may have stopped the translocation of labile photosynthates, in the form of root exudates, into the rhizosphere, and completely damaged the plant mediated CH_4 transport conduit.

Impact of shoot clipping and root exclusion on N₂O fluxes

Shoot clippings significantly increased N₂O fluxes compared to intact plant systems, and the mean N₂O flux rate of the shoot clipping treatment was double that of the control treatment. With respect to the root exclusion treatment, the mean N₂O flux rate was almost five times greater than the control treatment. The increased N₂O emission in the root exclusion treatment might be partly explained by the decomposition of dead roots (Kaiser et al. 1996). However, as mentioned above, it is reasonable to assume that the effect of decomposing roots on N transformation should gradually decrease. Ross et al. (2001) suggested soil mineral-N concentrations and gross nitrification rates were initially higher in trenched-plots than controls, but were similar in trenched and control treatments after incubation of the soil samples at 25 °C for 57 days. We found the mean N₂O flux rate of the root exclusion treatment was still more than five times higher than the control treatment when flux data were measured after February 2010. This indicates that the presence of plants could suppress N₂O emissions from the *Carex* meadow, which did not support our hypothesis. This suppression was further demonstrated by the negative correlations between N₂O fluxes and the above-ground and total biomass (Fig. 3d, f). Contrasting results have been reported on how the presence of plants potentially influences N₂O fluxes. For instance, no significant alterations on N₂O emissions by *Phalaris arundinacea* was reported by Rückauf et al. (2004), whereas the presence of the *Phalaris arundinacea* increased the annual N₂O emissions from approximately 65 to 650 g N₂O-N ha⁻¹ yr⁻¹ compared to unplanted peat soil in Finland (Hyvoenen et al. 2009). Similar to our study, decreased N₂O fluxes compared to unplanted controls were also observed in artificial wetlands of Sweden and Canada (Johansson et al. 2003; Maltais-Landry et al. 2009).

Soil N₂O flux was also linked to its production, consumption and gas transport (Jørgensen et al. 2012). Little is known about the effects of shoot clipping and root exclusion on plant-mediated N₂O transport, although a few studies have suggested the importance of this transport conduit (Jørgensen et al. 2012; Jørgensen and Elberling 2012). In this study, the role of this gas transport pathway might be weakened due to the relative low water table depth and soil moisture because this

mechanism of N₂O release is generally characterized by high soil water content or saturated soil (Chang et al. 1998). In the *Carex* meadow of Poyang Lake however, the water table varied from -30 to -50 cm in most of the drawdown periods (Hu et al. 2010), and the soil volumetric moisture in the meadow site ranged from 48 % to 65 % (mean of 55 %). Hence, diffusive transport via soil matrix might out-compete plant-mediated transport in this meadow. More importantly, shoot clipping and root exclusion probably enhanced the availability of mineral N for microbes because plants cease to take up NH₄⁺-N and NO₃⁻-N after cutting (Neftel et al. 2000). Therefore, microbe-related N₂O production prevailed. Similar clipping or cutting effects were also observed in other studies (Rafique et al. 2012; Lavoie et al. 2013).

Both shoot clipping and root exclusion approximately increased N₂O emissions to the same extent, suggesting shoots and roots might play an equal role in affecting N₂O flux from the *Carex* meadow during drawdown periods.

Relations among CH₄, N₂O and CO₂

In this study, we found that CH₄ flux was not significantly related to N₂O for any of the three treatments (Fig. 2). Hence, our hypothesis on the negative relation between CH₄ and N₂O fluxes was not supported. Several possible explanations exist. CH₄ is produced only from anaerobic processes, but N₂O can result from both aerobic and anaerobic processes (Conrad 1996). Most of the N₂O emitted into the atmosphere is produced in the upper-most soil layer, whereas CH₄ is produced in deeper horizons (Conrad et al. 1983; Conrad 1996). However, we did not measure below-ground gas in this study. Furthermore, CH₄ and N₂O can be disproportionately consumed in the soil (Lavoie et al. 2013), and CH₄ and N₂O fluxes can be influenced by numerous environmental variables, including various biotic and abiotic factors (e.g., plant biomass, net primary productivity, water table depth and temperature). Each of them may differ in their roles in CH₄ and N₂O production, consumption and transport. For example, in this study, plants enhanced the CH₄ flux, but suppressed the N₂O flux.

Unlike the CH₄-N₂O relation, significant positive CH₄-CO₂ correlations were observed in all three treatments (CO₂ data was published in Hu et al. 2015) (Fig. 4), which was consistent with reported studies (Song et al. 2008; Kato et al. 2011). Changes in CO₂

Fig. 4 Relationship between CH_4 and CO_2 fluxes from intact plants (*IP*), shoot clipping (*SC*) and root exclusion (*RE*) treatments. CH_4 flux data on June 14, 2009 and October 9, 2010 were not shown in this figure

emission could explain 35 % of CH_4 variability. This was mainly due to temperature and plant biomass being identical controls of CO_2 and CH_4 fluxes, and both environmental variables were positively related to them. Although a significant positive N_2O - CO_2 relation was reported in most terrestrial ecosystems (Garcia-Montiel et al. 2002; Xu et al. 2008), no studies have observed the same relation in wetlands. This indicates that distinct microbial processes could be responsible for N_2O production in terrestrial ecosystems and wetlands. Significant positive N_2O - CO_2 relations reflect that nitrification could be a dominant pathway to produce N_2O in terrestrial ecosystems where there is high O_2 availability. On the contrary, O_2 availability is very low in wetlands due to high water contents. Consequently, denitrification is a dominant pathway to produce N_2O in wetlands, probably leading to insignificant N_2O - CO_2 correlations. Such insignificant correlations were also

observed at our meadow site due to high soil moisture. However, this still needs further investigations.

CH_4 and N_2O emissions during drawdown periods

The littoral zones of lakes have been regarded as hotspots of CH_4 and N_2O emissions (Juutinen et al. 2003a; Wang et al. 2006a, 2006b; Chen et al. 2009). For instance, in the boreal Lake Kevätön in Finland, the littoral zone occupied 26 % of the lake area but was estimated to account for most of the N_2O emissions from the lake (Huttunen et al. 2003). Similarly, in the subtropical Meiliang Bay, Taihu Lake, the littoral zones only accounted for 5.4 % of the total bay area, but contributed about 43.6 % of total N_2O emissions of the bay (Wang et al. 2006b). CH_4 and N_2O emissions from littoral zones of lakes are largely dependent on the vegetation zone and differ amongst climate zones

Table 2 Net primary productivity, net ecosystem production, soil CO_2 , CH_4 and N_2O from the *Carex* meadow of Poyang Lake during drawdown and flood periods in 2010. The values were presented as mean $\pm$ SD of three replicates

Properties	Drawdown periods (195 d)	Flood periods (170 d)	Total
CO_2 ($\text{g CO}_2 \text{ m}^{-2}$)	906 ± 403	320 ± 105	1226 ± 508
CH_4 ($\text{g CH}_4 \text{ m}^{-2}$)	3 ± 2	18 ± 4	21 ± 6
N_2O ($\text{mg N}_2\text{O m}^{-2}$)	100 ± 60	8 ± 25	108 ± 85
CH_4_e ($\text{g CO}_2_eq \text{ m}^{-2}$)	84 ± 56	504 ± 112	588 ± 168
N_2O_e ($\text{g CO}_2_eq \text{ m}^{-2}$)	27 ± 16	2 ± 7	29 ± 23
NPP (g C m^{-2})	2005 ± 375	0	2005 ± 375
NEP (g C m^{-2})	1758 ± 265	-87 ± 29	1671 ± 294

(Table 1). As shown in Table 1, CH₄ emissions from the littoral *Carex* meadow of Poyang Lake during drying-wetting transition periods were comparable to other littoral wetlands, but were much lower during drying periods. This was mainly due to that the drying periods in our site were characterized by no standing water and relatively low soil moisture. In addition, our N₂O flux rate was much lower than those of Tibetan Huahu Lake and subtropical Taihu Lake, likely because of lake trophic differences (Wang et al. 2006a; Chen et al. 2009).

In the same *Carex* meadow, CH₄ emissions during summer flood periods from 2009 to 2010 ranged from 2637 to 5625 $\mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ (mean of 4426 $\mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$) (Hu et al. 2011), and N₂O emission rate varied from -13 to 9 $\mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$ (mean of 2 $\mu\text{g N}_2\text{O m}^{-2} \text{ h}^{-1}$) (unpublished data). Meanwhile, the mean soil microbial respiration rate was 194 $\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ during drawdown periods (Hu et al. 2015), but 78 $\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ during flood periods (unpublished data). Therefore, we estimated annual greenhouse gas emissions from the *Carex* meadow in 2010 (Table 2). There were large annual variations of CH₄ and N₂O emissions. Drawdown periods accounted for about 14 % of the total CH₄ emission, and 93 % of total N₂O emission in 2010, whereas, the flood periods was 86 % and 7 %, respectively. Previous studies have suggested that about 3 % to 4 % of net ecosystem production (NEP) is emitted back to the atmosphere as CH₄ (Whiting and Chanton 1993; Bellisario et al. 1999). In this study, however, CH₄ emissions during drawdown periods were relatively low and accounted for less than 1 % of the annual carbon assimilation, which was consistent with Askaer et al. (2011). This could be partly explained by a strong C sink due to the double growing season of the *Carex* meadow during drawdown periods (Hu et al. 2015). In addition, the meadow soil was not covered by standing water during the drawdown periods, resulting in low CH₄ emissions.

CH₄ and N₂O have 28 and 265 times larger global warming potentials (GWP) than CO₂ over a 100-year timescale, respectively (IPCC 2013). When the GWP of CH₄ and N₂O are taken into account, many studies have suggested the wetland C sink could be largely offset, and potentially turn into sources of atmospheric radiative forcing (Whiting and Chanton 2001; Friborg et al. 2003; Ding et al. 2013). In the *Carex* meadow, soil CO₂ emission dominated the GHG emissions (Table 2). However, when the GWP was taken into account, CH₄ and N₂O accounted for 11 % of the overall GHG emissions during drawdown periods and 33 % for the whole

year in 2010. Hence, it is necessary to integrate CH₄ and N₂O emissions into the assessment of net greenhouse gas effects from the *Carex* meadow.

Conclusions

With two-year in situ measurements of CH₄ and N₂O fluxes from a *Carex* meadow of Poyang Lake during drawdown periods, we conclude that shoot clipping did not significantly alter CH₄ flux rates, but root exclusion decreased CH₄ flux by 116 % compared to the control. This suggests that roots, rather than shoots, dominated plant-mediated enhancement in CH₄ fluxes in this *Carex* meadow during drawdown periods. Both shoot clipping and root exclusion significantly increased N₂O fluxes compared to the control, likely due to the increase of mineral N available for soil microbes. Shoots played an almost equal role as roots in plant-regulated suppression on N₂O fluxes in this *Carex* meadow during drawdown periods. There were no significant correlations between CH₄ and N₂O fluxes. Considering GWP, CH₄ and N₂O accounted for 11 % of the overall GHG emissions in the *Carex* meadow during drawdown periods, but 33 % for the whole year in 2010. Therefore, CH₄ and N₂O fluxes should be considered when C sinks or sources are evaluated in such subtropical wetlands.

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