



# Influence of plant communities and soil properties on trace gas fluxes in riparian northern hardwood forests

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## ABSTRACT

Wetlands contribute significant amounts of greenhouse gases to the atmosphere, yet little is known about what variables control gas emissions from these ecosystems. There is particular uncertainty about forested riparian wetlands, which have high variation in plant and soil properties due to their location at the interface between land and water. We investigated the fluxes of carbon dioxide (CO<sub>2</sub>), nitrous oxide (N<sub>2</sub>O), and methane (CH<sub>4</sub>) and associated understory vegetation and soil parameters at five northern hardwood riparian sites in the Adirondack Park, NY, USA. Gas fluxes were measured in field chambers 4 times throughout the summer of 2008. CO<sub>2</sub> flux rates ranged from 0.01 to 0.10 g C m<sup>-2</sup> h<sup>-1</sup>, N<sub>2</sub>O fluxes ranged from -0.27 to 0.65 ng N cm<sup>-2</sup> h<sup>-1</sup> and CH<sub>4</sub> flux rates ranged from -1.44 to 3.64 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup>. Because we observed both production and consumption of N<sub>2</sub>O and CH<sub>4</sub>, it was difficult to discern relationships between flux and environmental parameters such as soil moisture and pH. However, there were strong relationships between ecosystem-scale variables and flux. For example, CO<sub>2</sub> and N<sub>2</sub>O flux rates were most strongly related to percent plant cover, i.e., the site with the lowest vegetation cover had the lowest CO<sub>2</sub> and highest N<sub>2</sub>O emissions. These ecosystem-scale predictive relationships suggest that there may be prospects for scaling information on trace gas fluxes up to landscape and regional scales using information on the distribution of ecosystem or soil types from remote sensing or geographic information system data.

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## 1. Introduction

Wetlands are considered to be important sources of the greenhouse gases carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O), to the atmosphere. While wetland ecosystems are often net carbon sinks, they can be a net source of CO<sub>2</sub> when soils dry and decomposition and total soil respiration rates increase (Armentano and Menges, 1986; Gorham, 1991; Silvola et al., 1996). In addition, wetlands contribute an estimated  $110 \times 10^{12}$  g CH<sub>4</sub> year<sup>-1</sup> to the atmosphere from anaerobic processes (Matthews and Fung, 1987; Denmen and Brasseur, 2007) and are the second largest natural source of nitrous oxide (N<sub>2</sub>O) to the atmosphere, behind oceans (Bowden, 1986; Prather et al., 1995). These gases significantly impact atmospheric chemistry; in a 100-year period CH<sub>4</sub> is 25 times and N<sub>2</sub>O is 298 times more potent than CO<sub>2</sub> as a greenhouse gas (Solomon et al., 2007). Greenhouse gas emissions from northern temperate wetlands are predicted to increase with temperature, thereby creating a positive feedback loop (Gedney et al., 2004). At the same time, increased

temperature may decrease soil moisture, which could result in a decrease of some greenhouse gas emissions. With either response to temperature, there is considerable uncertainty about just what ecosystem variables control greenhouse gas fluxes in these wetlands and how these variables will respond to climate change. These controls are particularly dynamic in riparian wetlands that sit at the interface between terrestrial and aquatic components of the landscape (Naiman and Decamps, 1997).

Much research has investigated how water table position and temperature indirectly influence CO<sub>2</sub>, N<sub>2</sub>O, and CH<sub>4</sub> production (Davidson and Swank, 1986; Bubier et al., 1993; Dunfield et al., 1993; Willems et al., 1997; Kiese and Butterbach-Bahl, 2002; McLain and Martens, 2006) by controlling the reduction–oxidation (redox) reactions responsible for greenhouse gas flux. Water table position, or water depth, fluctuates regularly in riparian areas with flooding and drying events, and this fluctuation dictates the amount of oxygen in the substrate (i.e., which redox reactions will occur). While CO<sub>2</sub> is produced under both aerobic and anaerobic conditions, in aerobic soil zones CH<sub>4</sub> is oxidized to CO<sub>2</sub> (Altor and Mitsch, 2006), while in anaerobic zones CO<sub>2</sub> is reduced to CH<sub>4</sub> through the process of methanogenesis (Whalen, 2005). Similarly, N<sub>2</sub>O can be produced and consumed under both aerobic and anaerobic conditions. Wetlands with variable water levels have

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been found to have particular potential for high  $\text{N}_2\text{O}$  flux (Hernandez and Mitsch, 2006, 2007a).

Few studies have examined the linkages between understory plant communities and greenhouse gas emissions in riparian ecosystems even though plants can influence emissions in several ways. Plant  $\text{CO}_2$  production by respiration and consumption via photosynthesis vary markedly with species and environmental conditions (Welsch and Yavitt, 2007). Plants influence soil  $\text{CH}_4$  emissions by plant ventilation and plant-mediated diffusion through aerenchymous tissue (Joabsson et al., 1999), which can be responsible for more than 90% of  $\text{CH}_4$  flux from a wetland (Holzapfel-Pschorn et al., 1986; MacDonald et al., 1998). Plants also mediate  $\text{CH}_4$  and  $\text{CO}_2$  production through the release of oxygen and root exudates (e.g., labile carbon) into the rhizosphere. Exudation of labile carbon may facilitate  $\text{CH}_4$  and  $\text{CO}_2$  production, whereas oxygen released from the plant roots can inhibit  $\text{CH}_4$  production and promote production of  $\text{CO}_2$  (Frenzel, 2000; Conrad, 2002; Hernandez and Mitsch, 2007b). Plants influence nitrogen availability and  $\text{N}_2\text{O}$  flux through variation in root N uptake, and nitrogen content and its subsequent effects on inorganic nitrogen release during decomposition (Reddy and DeBusk, 1987; Welsch and Yavitt, 2007).

Several soil variables can affect greenhouse gas fluxes from riparian systems. In addition to the effects of water table on soil moisture discussed above, soil texture may influence greenhouse gas fluxes by altering the permeability, porosity, and water-holding capacity of soils, which in turn can alter soil moisture (Pinay et al., 2000). There are complex relationships between soil pH and gas fluxes. While some studies have found low soil pH to decrease methane production by inhibiting methanogenesis (Dunfield et al., 1993; Valentine et al., 1994), others have found no relationships between pH and  $\text{CH}_4$  production (Bubier et al., 1993; Chang and Yang, 2003). Low pH can inhibit nitrification, an important source of  $\text{N}_2\text{O}$ , but can also increase the  $\text{N}_2\text{O}$  yield during denitrification (Robertson and Groffman, 2007). There is great interest in understanding how atmospheric deposition of nitrogen

and acid alters soil conditions that influence greenhouse gas fluxes (Venterea et al., 2003a,b).

In this study, we examined how multiple plant community and soil processes and parameters affect greenhouse gas flux rates in riparian areas in northern hardwood forests in the Adirondack Mountains of New York. The two novel aspects of our study are that we (1) explored links between understory plant communities and trace gas fluxes and (2) in an important and understudied ecosystem type. Understory plant communities are dynamic and very few studies have addressed their effects on trace gas fluxes. While several studies have addressed  $\text{N}_2\text{O}$  fluxes in riparian zones in agricultural landscapes, there have been almost no analyses of trace gas fluxes (including methane) in riparian zones in forested landscapes. These zones are particularly important in forested regions subject to high rates of atmospheric deposition of N and S such as our study region. Our specific objectives were to (1) determine if riparian wetlands are significant sources or sinks of  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  in this region and (2) evaluate the plant and soil riparian factors influence these fluxes.

## 2. Materials and methods

### 2.1. Site description and experimental design

The study area was located in Adirondack Park, near Old Forge, NY, along a 5350 m stretch of Big Moose Road, with a northern terminus at Pancake Hall Creek on the northern edge of Big Moose Lake (43° 83'N, 74° 87'W) and a southern terminus at Cascade Lake Outlet (Fig. 1). Temperature averages 18 °C in July and –11 °C in January, and mean annual precipitation is 1280 mm (TWC, 2008). The soils in the region are dominated by acidic Spodosols that developed on glacial sediments (R. April, personal communication). Dominant tree species included American beech (*Fagus grandiflora*), sugar and mountain maple (*Acer saccharum* and *Acer spicatum*), spruce spp. (*Picea*), and eastern hemlock (*Tsuga canadensis*). Five riparian sites were sampled to obtain a

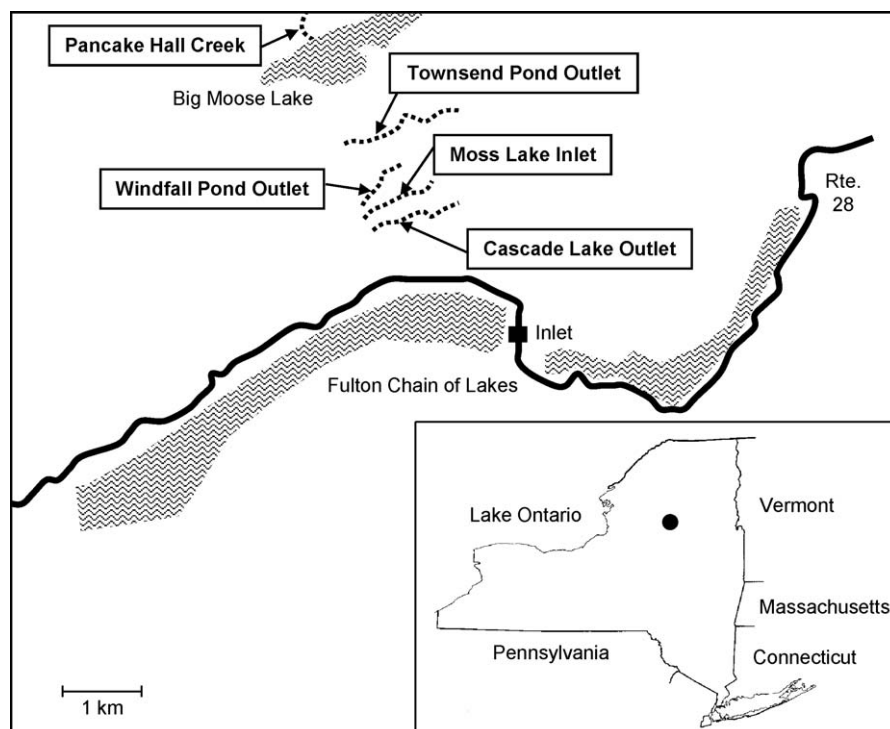


Fig. 1. Location of the five riparian study sites in Adirondack Park, NY, USA.

representative sampling of the study area: Pancake Hall Creek (Pancake), Townsend Pond Outlet (Townsend), Windfall Pond Outlet (Windfall), Moss Lake Inlet (Moss), and Cascade Lake Outlet (Cascade). Three, 1 m<sup>2</sup> plots were randomly placed along the stream bank at each of the five riparian areas.

## 2.2. Trace gas fluxes between soil and the atmosphere

Trace gas fluxes were measured 4 times at two-week intervals in the summer of 2008 (May 20, June 3, June 19, and July 2) using an in situ chamber design identical to that used by Bowden et al. (1990, 1991). Opaque chambers were placed in the center of the three, 1 m<sup>2</sup> plots at each of the five riparian sites ( $N = 15$ ). Chambers consisted of 287 mm (inner diameter) by 40 mm high polyvinyl chloride (PVC) cylinders (chamber top) that were placed securely on a permanently installed PVC base ring of the same diameter. On each sampling day, 9 ml gas samples were collected from gas sampling ports in the center of the chamber top using fine-needle polypropylene syringes at sampling intervals of 0, 10, 20, and 30 min after placement of the chamber top on the base. Gas samples were immediately transferred to an evacuated glass vial, and all vials were stored at room temperature prior to analysis. Gas samples were analyzed using gas chromatography with electron capture (N<sub>2</sub>O), thermal conductivity (CO<sub>2</sub> efflux), or flame ionization (CH<sub>4</sub>) detection. Fluxes were calculated from the linear rate of change in gas concentration, the chamber internal volume, and soil surface area.

## 2.3. Vegetation and soil parameters and processes

Vegetation was analyzed on June 19, 2008. We recorded percent cover (Braun-Blanquet, 1964) of each species and species richness for each plot to assess the herbaceous composition of the riparian areas. We also recorded the abundance (number of stems per chamber) of each species and species richness within each sampling chamber.

Soil parameters measured included soil pH, texture, moisture, organic matter and C:N. Soil from each plot was sampled and measured for pH after every gas sampling event following the protocol of Robertson et al. (1999b). Soil from each plot was analyzed for particle size (texture) using the hydrometer method (Gee and Bauder, 1986). Three soil cores, 10 cm length by 5 cm diameter, were collected from each plot, large roots and rhizomes were removed, and homogenized samples were sieved through a 2 mm mesh sieve ( $N = 15$ ). Samples were dried at 70 °C to a constant weight and then pulverized using a ball mill. Organic matter of each soil core was obtained using the loss on ignition technique (Nelson and Sommers, 1996). Soil samples were analyzed for total carbon and nitrogen with a Leco TruSpec instrument.

Potential net N mineralization and nitrification were measured following the laboratory incubation protocol described by Robertson et al. (1999a). At each plot within a riparian site, three

soil cores (10 cm length by 5 cm diameter) were collected on June 3, 2008. Soil samples were combined and homogenized by plot ( $N = 15$ ), and 10 g subsamples were placed into six, 125-ml flasks. Three of the six samples were immediately extracted with 2 M KCl. The other three flasks were incubated at 20 °C for 28 days and then extracted with 2 M KCl. Pre- and post-incubation soil extracts were stored at 4 °C prior to analysis. Extracts were analyzed for ammonium-N (NH<sub>4</sub><sup>+</sup>-N) (phenate method), and nitrite-N (NO<sub>2</sub><sup>-</sup>-N) and nitrate-N (NO<sub>3</sub><sup>-</sup>-N) (automated cadmium reduction method) using flow injection analysis (Lachat QuikChem Automated Flow Injection Analysis System; APHA, 1998; USEPA, 1999).

Potential denitrification rates were measured using the denitrification enzyme assay (DEA) (Smith and Tiedje, 1979). Three soil cores (10 cm length by 5 cm diameter) were taken from each plot on July 2, 2008. Large roots were removed by hand and samples were homogenized and held at field moisture for analysis ( $N = 15$ ). All samples were amended with potassium nitrate (KNO<sub>3</sub>), glucose, chloramphenicol, and acetylene, and incubated under anaerobic conditions for 90 min (similar to Groffman et al., 1999). Gas samples were collected at 30 and 90 min, stored in evacuated glass vials, and analyzed for N<sub>2</sub>O by electron capture gas chromatography.

## 2.4. Statistical analyses

One-way analysis of variance (ANOVA) with Tukey's HSD was used to determine differences in soil processes and soil and vegetation parameters among the five riparian sites. Repeated measures ANOVAs (RMANOVA) were used to determine if the response variables (pH and the gas flux rates) varied among the riparian sites and sampling dates. Spearman correlation analysis was used to investigate relationships among all variables (gas flux rates, soil processes, and soil and vegetation parameters). Gas flux rates for each plot were averaged among all sampling dates for Spearman correlation analysis. To conform to the ANOVA assumption of normality, soil moisture was log + 1 transformed. All statistical analyses were performed in the SAS system for Windows (SAS Institute v8). Significance was determined at  $\alpha = 0.05$ .

## 3. Results

The five riparian sites varied greatly in many plant community and soil variables (Table 1). All four plant community variables (percent cover and number of species per plot and number of stems and species per sampling chamber) were correlated and differed among riparian sites (% plant cover m<sup>-2</sup>:  $F = 17.8$ ,  $P < 0.01$ ). Moss had the highest species richness per plot ( $10.0 \pm 0.6\%$ ), and Pancake had the lowest means for all four plant variables. Within the sampling rings, Pancake had the lowest stem count, while significant ground covering moss was found at the Windfall, Moss, and Cascade sites (Table 2). Soil C:N was highest at Townsend and lowest at Pancake ( $F = 3.7$ ,  $P = 0.04$ ), while percent clay was also lowest at Pancake but

**Table 1**

Vegetation and soil process and parameter means  $\pm 1$  standard error for five riparian wetland sites in the Adirondack Mountains.

	Pancake	Townsend	Windfall	Moss	Cascade
% Plant cover (% cover m <sup>-2</sup> )	21.3 $\pm$ 3.8	31.3 $\pm$ 1.9	42.0 $\pm$ 1.2	47.3 $\pm$ 4.3	35.7 $\pm$ 0.7
Soil C:N	8.9 $\pm$ 6.6	25.4 $\pm$ 2.8	24.5 $\pm$ 0.6	23.3 $\pm$ 0.4	24.2 $\pm$ 3.3
% Clay	5.8 $\pm$ 0.8	11.5 $\pm$ 2.3	12.3 $\pm$ 1.8	8.1 $\pm$ 0.3	9.2 $\pm$ 0.3
Soil pH	4.7 $\pm$ 0.2	4.5 $\pm$ 0.1	4.4 $\pm$ 0.1	4.4 $\pm$ 0.1	4.4 $\pm$ 0.1
Soil OM (%)	0.27 $\pm$ 0.01	0.32 $\pm$ 0.03	0.12 $\pm$ 0.01	0.22 $\pm$ 0.001	0.17 $\pm$ 0.05
Soil moisture (g H <sub>2</sub> O/g dry soil <sup>-1</sup> )	1.60 $\pm$ 0.06	0.93 $\pm$ 0.03	0.67 $\pm$ 0.03	2.00 $\pm$ 0.58	2.80 $\pm$ 1.10
N mineralization rate (mg N kg <sup>-1</sup> d <sup>-1</sup> )	0.14 $\pm$ 0.02	0.18 $\pm$ 0.02	0.05 $\pm$ 0.01	0.11 $\pm$ 0.03	0.12 $\pm$ 0.03
Denitrification rate (ng N/g dry soil <sup>-1</sup> h <sup>-1</sup> )	362 $\pm$ 177	201 $\pm$ 18	45 $\pm$ 33	557 $\pm$ 192	933 $\pm$ 260

All variables, except pH, differed significantly among the sites,  $\alpha = 0.05$ .

**Table 2**

Number of individual stems per species found in each ring sampled on June 19, 2008 (3 rings per site).

Species	P1	P2	P3	T1	T2	T3	W1	W2	W3	M1	M2	M3	C1	C2	C3
<i>Acer rubrum</i> L.												2			
<i>Acer spicatum</i> Lam.										1					
<i>Clintonia borealis</i> (Aiton) Raf.				1											
<i>Cornus canadensis</i> L.										3			1		
<i>Onoclea sensibilis</i> L.										1	1				
<i>Oxalis corniculata</i> L.										7					
<i>Rubus odoratus</i> L.		1													
<i>Rubus pubescens</i> Raf.										5	4	5			
<i>Trientalis borealis</i> Raf.							2	3							
Unknown fern					8	1				2		14		8	11
Unknown herb													1		
Unknown grass							16	15	26	7	2		1	5	
Unknown sedge														1	
<i>Viola renifolia</i> A. Gray									5						
<sup>a</sup> <i>Sphagnum</i> spp. L.							100	90				100		100	
<sup>a</sup> Unknown moss									4				2		60

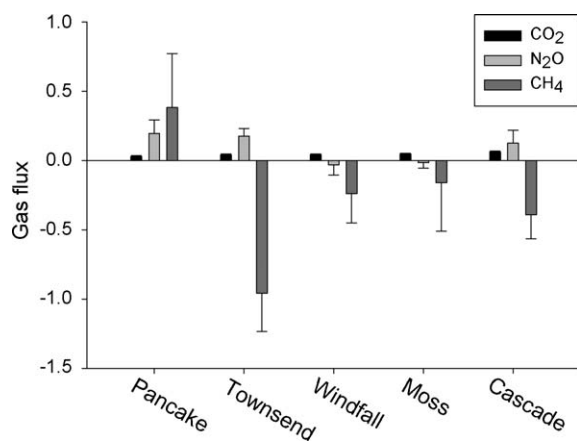
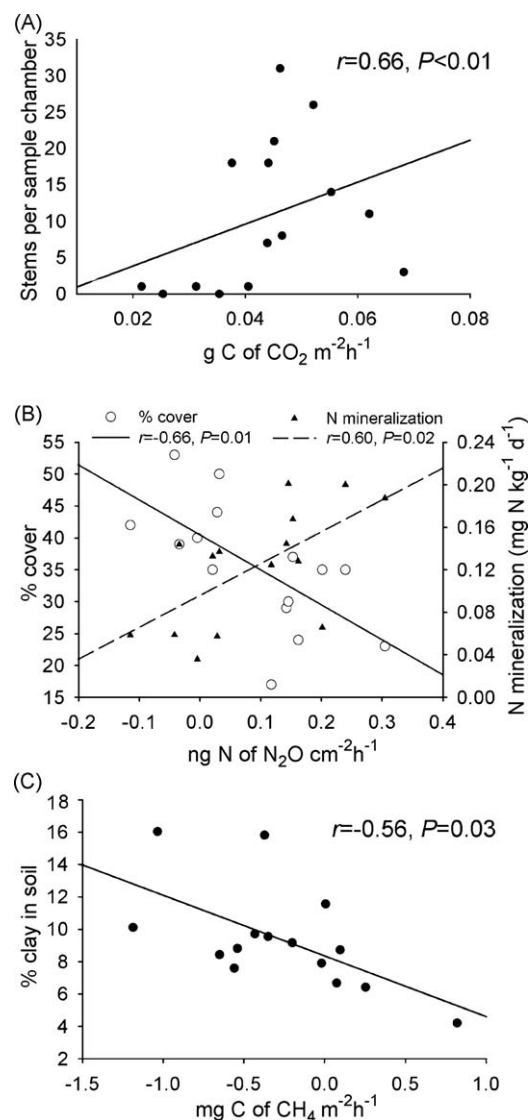
Locations sampled were Pancake Hall Creek (P), Townsend Pond Outlet (T), Windfall Pond Outlet (W), Moss Lake Inlet (M), and Cascade Pond Outlet (C).

<sup>a</sup> *Sphagnum* spp. and an unknown moss were recorded as the percent of ground coverage in each ring.

highest at Windfall ( $F = 3.7$ ,  $P = 0.04$ ). Windfall had the lowest soil organic matter ( $F = 7.2$ ,  $P = 0.01$ ), soil moisture ( $F = 4.3$ ,  $P = 0.03$ ), N mineralization rate ( $F = 4.8$ ,  $P = 0.02$ ), and denitrification potential ( $F = 4.3$ ,  $P = 0.03$ ). Soil pH and nitrification rates did not vary among riparian sites. Percent sand and percent clay were correlated ( $r = -0.67$ ,  $P = 0.001$ ) and all four vegetation variables were correlated with each other; however, soil moisture was not correlated with % sand or clay, or organic matter. Organic matter was correlated with percent cover of vegetation ( $r = -0.63$ ,  $P = 0.01$ ).

Riparian sites differed in all three gas fluxes measured,  $\text{CO}_2$ ,  $\text{N}_2\text{O}$ , and  $\text{CH}_4$  (Fig. 2). Cascade emitted the most  $\text{CO}_2$ , while Pancake produced the least  $\text{CO}_2$  ( $F = 53.7$ ,  $P < 0.01$ ). However, Pancake produced the most  $\text{N}_2\text{O}$  ( $F = 7.0$ ,  $P < 0.01$ ) and was the only site to emit  $\text{CH}_4$  ( $F = 4.4$ ,  $P < 0.01$ ) to the atmosphere. Townsend consumed the most  $\text{CH}_4$ . There were no significant differences in any gas flux rates through time, and no significant interactions between site and time for any of the gas flux rates.  $\text{CO}_2$  was produced at all riparian sites and average  $\text{CO}_2$  flux per plot was most strongly correlated with number of stems and species in the sampling chamber (Fig. 3A). No other soil processes or soil and vegetation parameters were correlated with average  $\text{CO}_2$  flux.

Average  $\text{N}_2\text{O}$  flux was negatively correlated with plot percent vegetation cover and positively correlated with N mineralization rates (Fig. 3B). No other soil parameters were correlated with average  $\text{N}_2\text{O}$  flux. Percent clay was the only variable measured that was correlated with average  $\text{CH}_4$  flux (Fig. 3C).

**Fig. 2.** Average  $\text{CO}_2$  ( $\text{g C m}^{-2} \text{h}^{-1}$ ),  $\text{N}_2\text{O}$  ( $\text{ng N cm}^{-2} \text{h}^{-1}$ ), and  $\text{CH}_4$  ( $\text{mg C m}^{-2} \text{h}^{-1}$ ) flux rates + 1 standard error for each of the riparian study sites.**Fig. 3.** Dominant variables driving gas flux in our northern riparian study sites were (A) a positive relationship between  $\text{CO}_2$  and number of stems per sampling chamber; (B) a negative relationship between  $\text{N}_2\text{O}$  and percent plant cover and a positive relationship between  $\text{N}_2\text{O}$  and N mineralization; and (C) a negative relationship between  $\text{CH}_4$  and percent clay in the soil.  $\alpha = 0.05$ .



#### 4. Discussion

Our five riparian sites varied greatly in numerous soil and vegetation metrics even though they were in close proximity to one another. This variation led to marked differences in trace gas fluxes, suggesting that evaluating the importance of riparian zones to landscape and regional scale greenhouse gas budgets will be difficult. However, our results show promising relationships between ecosystem-scale variables such as plant cover and soil texture that may be useful for scaling site-specific data to larger areas.

Understory plant cover was a stronger predictor of CO<sub>2</sub> (positively) and N<sub>2</sub>O (negatively) fluxes than process-level variables in these forested riparian wetlands. Areas with high percent plant cover had the highest CO<sub>2</sub> fluxes. These areas likely had high root and microbial activity belowground, which led to increased CO<sub>2</sub> flux. Low N<sub>2</sub>O flux was found in areas with high percent plant cover likely because plant competition for nitrogen reduced the flow of nitrogen to microbes responsible for N<sub>2</sub>O production. This reasoning is supported by the strong correlation between organic matter and percent cover of vegetation and the negative correlation between plant cover and N mineralization rates. Some studies have attempted to link understory plant community dynamics to the production of N<sub>2</sub>O (Otto et al., 1999; Findlay et al., 2003; Hopfensperger et al., 2009), but the focus of these studies was more on differences in plant type than on cover per se. There was no relationship between plant cover and CH<sub>4</sub> flux because of a complex balance between production and consumption (discussed below).

CO<sub>2</sub> flux rates ranged from 0.01 to 0.10 g C m<sup>-2</sup> h<sup>-1</sup> with the lowest rates found in May at Pancake and the highest rates found in July. Our average CO<sub>2</sub> emission rates were similar to one riparian study in the Adirondacks (Yavitt et al., 1995), but less than rates from a nearby Adirondack beaver impoundment (Table 3; Yavitt and Fahey, 1994). In comparison to other riparian sites, our Adirondack CO<sub>2</sub> emission rates were similar to riparian rates in Europe (Teiter and Mander, 2005), but less than riparian rates in Tennessee (Jones and Mulholland, 1998). When comparing our CO<sub>2</sub> emission rates to other forests in the northeast, they were similar to those measured at Hubbard Brook Experimental Forest (HBEF; Groffman et al., 2006a), but lower than values reported from other northeastern hardwood forests (Crill, 1991; Lessard et al., 1994; Savage and Davidson, 2001).

We observed both production and consumption of CH<sub>4</sub> and N<sub>2</sub>O from our sites, which complicated analysis of relationships between flux and process-level measurements. Many studies have found chemical and physical variables (i.e., soil organic matter, pH, and anoxic microsites) to control N<sub>2</sub>O flux (Brumme et al., 1999; Barnard et al., 2005; Chapuis-Lardy et al., 2007). Soil moisture has often been found to be the dominant variable controlling N<sub>2</sub>O emissions associated with denitrification, as an increase in soil moisture creates the anaerobic conditions necessary for this process to occur. Anaerobic conditions, and pH and nitrate concentrations influence the reduction of N<sub>2</sub>O to N<sub>2</sub> during denitrification, further complicating relationships between N<sub>2</sub>O flux and process-level measurements. A final complication arises

from the fact that nitrification, an aerobic process, can also be a significant source of N<sub>2</sub>O. We did not find any relationship between soil moisture or potential net nitrification and N<sub>2</sub>O production, and only a weak correlation between denitrification potential and N<sub>2</sub>O flux ( $P = 0.07$ ). The lack of correlation with nitrification, and the correlation with denitrification potential suggest (weakly) that denitrification is the dominant source of N<sub>2</sub>O in these soils, but that nitrification and/or factors influencing N<sub>2</sub>O reduction during denitrification are important regulators of net emissions from these sites.

Our N<sub>2</sub>O flux rates ( $-0.27$  to  $0.65$  ng N cm<sup>-2</sup> h<sup>-1</sup>) were similar to those reported from other northern hardwood forests (Keller et al., 1983; Bowden et al., 1991; Groffman et al., 2000; Venterea et al., 2003a), including a spruce-fir forest in the Adirondacks ( $0.211$  ng N cm<sup>-2</sup> h<sup>-1</sup>; Castro et al., 1993). Interestingly, our average net mineralization ( $0.13$  mg N kg<sup>-1</sup> d<sup>-1</sup>) and nitrification rates ( $0.05$  mg NO<sub>3</sub><sup>-</sup> kg<sup>-1</sup> d<sup>-1</sup>) were substantially lower than those from other northern hardwood forests (Venterea et al., 2003a; Ross et al., 2004, 2009). Venterea et al. (2003b) found much higher nitrate concentrations and nitrification rates from forests at HBEF ( $2.8$ – $5.0$  mg NO<sub>3</sub><sup>-</sup> kg<sup>-1</sup> and  $1.2$ – $3.2$  mg NO<sub>3</sub><sup>-</sup> kg<sup>-1</sup> d<sup>-1</sup>) than we found in our forested riparian sites ( $0.06$  mg NO<sub>3</sub><sup>-</sup> kg<sup>-1</sup>). However, Ross et al. (2004) reported one site in the Adirondacks to have negative nitrification rates in the spring ( $-0.17$  mg N kg<sup>-1</sup> d<sup>-1</sup>), which fits within our reported range. The N<sub>2</sub>O flux rates that we observed are much lower than those observed in highly N enriched forested riparian sites in the Netherlands ( $41.7$  ng N cm<sup>-2</sup> h<sup>-1</sup>; Hefting et al., 2003).

The N<sub>2</sub>O flux rates that we observed do not appear to be significant to landscape and regional scale N balances. Our average N<sub>2</sub>O emission rate ( $0.09$  ng N cm<sup>-2</sup> h<sup>-1</sup>) is equivalent to an annual flux of  $0.079$  kg N ha<sup>-1</sup>, which is equal to approximately 3% of average summer ammonium ( $0.66$  kg N ha<sup>-1</sup> year<sup>-1</sup>) and nitrate ( $1.90$  kg N ha<sup>-1</sup> year<sup>-1</sup>) atmospheric deposition in the immediate area (NADP, 2009).

Control of net CH<sub>4</sub> flux in riparian areas is likely to be complex because of the varying balance of factors affecting anaerobic production and aerobic consumption (Brumme and Borken, 1999; Le Mer and Roger, 2001; Conrad, 2007). We expected that CH<sub>4</sub> production rate would be positively correlated with percent clay because clayey soils hold more water, which creates the anaerobic conditions necessary for CH<sub>4</sub> production. High clay, and high soil moisture, also inhibits diffusion of atmospheric CH<sub>4</sub> to the microbes responsible for CH<sub>4</sub> oxidation. While we found correlations between percent clay and soil moisture ( $r = -0.54$ ,  $P = 0.03$ ) and average CH<sub>4</sub> flux ( $r = -0.56$ ,  $P = 0.03$ ; Fig. 3C), we did not find a correlation between soil moisture and average CH<sub>4</sub> flux. Similar to soil moisture, depth to the water table can be an important influence on greenhouse gas emissions. While we did not measure this variable, others have found significant relationships between depth to water table with soil redox potential (Yu et al., 2008) and with CO<sub>2</sub> and CH<sub>4</sub> flux (Hendriks et al., 2007) in wetland ecosystems. Clearly, the balance between production and consumption is too complex and/or dynamic in these forested riparian sites to see strong relationships between CH<sub>4</sub> flux and process-level controllers such as soil moisture. It is possible that measuring

**Table 3**  
A comparison of carbon dioxide emissions from a variety of riparian areas.

CO <sub>2</sub> (g C m <sup>-2</sup> h <sup>-1</sup> )	Ecosystem	Location	Citation
0.01–0.10	Riparian	Adirondacks, NY	Presented data
0.008–0.073	Riparian	Adirondacks, NY	Yavitt et al., 1995
0.036	Beaver impoundment	Adirondacks, NY	Yavitt and Fahey, 1994
0.06	Riparian	Europe	Teiter and Mander, 2005
0.53	Riparian	Tennessee, USA	Jones and Mulholland, 1998

soil properties below 10 cm depth would provide us more insight into what is driving CH<sub>4</sub> flux at these sites.

Our CH<sub>4</sub> flux rates ranged from  $-1.44$  to  $3.64$  mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> with Pancake being the only site to emit CH<sub>4</sub>. Our CH<sub>4</sub> consumption rates were similar to rates from other studies in the Adirondacks (Castro et al., 1993; Yavitt et al., 1993, 1995). However, our emission rates from Pancake were much lower than those from an Adirondack peatland ( $12.1$  mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup>; Yavitt et al., 1993). In addition, the CH<sub>4</sub> consumption rates we measured were similar to rates from some forests in the northeast (Lessard et al., 1994; Tyler et al., 1994; Groffman et al., 2006a), but less than many other northeastern forests (Steudler et al., 1989; Crill, 1991; Goldman et al., 1995) that were likely drier than our riparian sites. However, none of these other northern hardwood forests emitted CH<sub>4</sub>.

The most marked spatial pattern that we observed was the difference between the Pancake site and the other sites. Pancake had the lowest soil C:N, percent plant cover, percent clay and the highest pH, CH<sub>4</sub> flux and N<sub>2</sub>O flux. Pancake was the only site that was a net source of CH<sub>4</sub> while the other sites were net sinks for this gas. A large emergent marsh formed by beaver dams is located several hundred meters upstream of the measured riparian area at Pancake and organic matter may be swept downstream of this wetland during high flow in early spring. Indeed, this could explain the high soil organic matter we found in this area with a low percent cover of understory vegetation.

It is interesting that ecosystem-scale variables such as percent understory plant cover and percent clay in the soil were stronger predictors of trace gas fluxes than more specific process-level variables such as soil moisture, mineralization and nitrification rate. This suggests that there may be prospects for scaling information on trace gas fluxes up to landscape and regional scales using the distribution of ecosystem types or soil types found in remote sensing or GIS-based data (Groffman et al., 2006b). Developing these prospects will require more intensive spatial and temporal sampling regimes to determine if the complex controls over trace gas production and consumption are expressed at landscape and regional scales in a coherent way. While these approaches have been applied successfully in several different ecosystem types (Wessman et al., 1988; Martin and Asner, 2005) they may be particularly challenging to develop in riparian zones, with their variable and dynamic conditions. Still, given the functional importance of these ecosystems, further efforts to quantify riparian trace gas fluxes and to develop tools for scaling to landscape and regional scales are warranted.

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