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PRIMARY RESEARCH PAPER

Hydrologic gradient and vegetation controls on CH_4 and CO_2 fluxes in a spring-fed forested wetland

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Abstract Four different habitats in a spring-fed forested wetland (Clear Springs Wetland, Panola County, Mississippi, USA) varying in hydrologic regime were examined for methane and carbon dioxide fluxes from soils over 15 and 9 months, respectively. There was an increasing gradient of CH_4 flux rates from an unflooded upper-elevation forest site to an occasionally flooded bottomland forest site to a shallow permanently flooded site, and then to a deeper-water permanently flooded site. Depending on the time of year, all sites were sources of methane but only at the upper-elevation forest site, when gravimetric soil moisture content fell below 54%, was atmospheric methane consumed. On average, summer CH_4 emission rates were higher than those in other seasons. A multiple regression model with soil temperature and soil redox potential as independent variables could explain 65% of the variation in CH_4 flux rates. In the flooded zone, variation in CH_4 flux rates was correlated with aboveground plant biomass and stem density of emergent vascular plants, and plant-mediated CH_4 transport depended on plant type. The efflux of CH_4 to plant biomass (Eff:B) ratio was generally lower in *Hydrocotyle umbellata* compared to *Festuca obtusa*. Compared to several other freshwater forested wetlands in the southeastern USA, this spring-fed forested wetland ecosystem was a strong source of atmospheric CH_4, likely due to a long hydroperiod and high soil organic matter content. Carbon dioxide fluxes show a reverse spatial pattern than CH_4 fluxes with highest CO_2 emissions in the non-flooded zone at all times of the year, indicating the dominance of aerobic soil respiration. A multiple regression model also revealed a strong dependency of CO_2 fluxes ($r^2 = 0.73$) on soil temperature and soil redox potential.

Keywords Methane · Carbon dioxide · Redox potential · Temperature · Spring-fed forested wetland · Emergent vascular plants

Introduction

Wetland soils play a critical role in global carbon cycling (Matthews & Fung, 1987; Aselmann & Crutzen, 1989; Cao et al., 1996). Wetlands sequester carbon from the atmosphere through photosynthesis

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by wetland plants. Sequestered wetland carbon may accumulate due to slow decomposition of organic matter, especially in soils experiencing extended periods of water saturation (Fenchel et al., 1998). However, this sequestration of carbon can be lost by efflux of methane (CH_4) and carbon dioxide (CO_2) gases produced during biological degradation of organic matter.

Carbon dioxide emission is the primary mechanism of gaseous carbon loss from wetlands (Bridgham & Richardson, 1992). CO_2 is produced by prokaryotic and eukaryotic organisms in aerobic respiration, and by some fungi and many different groups of prokaryotes in anaerobic respiration and fermentation.

Methane, in contrast, is produced only in anoxic environments by methanogenic prokaryotes (Domain Archaea). In anoxic environments, complete mineralization of complex molecules requires a series of biochemical processes mediated by a community of organisms (Fenchel et al., 1998). Methanogenic bacteria utilize a variety of simple substrates at the terminal steps of the mineralization process. Disproportionation of acetate and CO_2 reduction by hydrogen are the most common mechanisms of CH_4 production (Conrad et al., 1989; Fenchel & Finlay, 1995). Gaseous CH_4 may diffuse directly through the soil–water and air–water interface. Alternatively, it may be transported from soils into the atmosphere through the aerenchymal tissues of vascular plants (Schütz et al., 1991; Frenzel & Karofeld, 2000).

Methanotrophic bacteria (Domain: Bacteria) utilize methane as an energy source, oxidizing it to CO_2. These methane-oxidizing bacteria function at the interface of oxic and anoxic environments in a wide variety of terrestrial ecosystems, including forests, grasslands, and wetlands. About 30–50% of the global CH_4 soil sink is thought to be due to methanotrophy in the temperate zone (Ojima et al., 1993).

Although wetlands occupy a small proportion (2–3%) of earth's terrestrial surface, they accumulate a significant proportion (18–30%) of the terrestrial carbon pool and account for 20% of the total global source of atmospheric CH_4 (Matthews & Fung, 1987; Bartlett & Harriss, 1993). Atmospheric CH_4, after CO_2, is the most important greenhouse gas and contributes about 15% of the elevated global greenhouse effect (IPCC, 2007).

Multiple environmental factors affect CH_4 and CO_2 emission in wetland ecosystems. First, temperature has a strong impact on CH_4 and CO_2 emission. Higher temperatures increase CH_4 and CO_2 production by increasing microbial and plant metabolic activities (Davidson et al., 1998; LeMer & Roger 2001). The degree of soil moisture content also regulates CH_4 and CO_2 production (Moore & Dalva, 1993). Flooded soils are characterized by anoxic conditions allowing for active growth of methanogen populations, and inhibiting methanotrophic activity by reducing the oxidized zones (Czepiel et al., 1995; Otter & Scholes, 2000; Yu et al., 2007). In contrast, extremely dry or wet conditions can hamper aerobic microbial activity and reduce CO_2 emission (Keith et al., 1997). CH_4 and CO_2 emissions are also controlled by the amount of organic matter, which serves as the substrate for fermentation, heterotrophic respiration, and methanogenesis (Moore & Knowles, 1989).

Much carbon trace gas research has been conducted in river floodplain forested wetlands, or freshwater swamps. However, few studies have quantified soil carbon gas fluxes (CH_4 and CO_2) from spring-fed forested wetlands, a highly productive ecosystem type common to temperate regions. Spring-fed wetlands in temperate forests may be extensive in size, or limited in area, but they potentially are important "hot spots" for methanogenesis, especially where the hydroperiod is long and organic matter accumulates (McClain et al., 2003).

The overall objective of this study was to quantify the magnitude, spatial and temporal patterns, and regulating factors for CH_4 and CO_2 fluxes from a spring-fed forested wetland in the southeastern USA. Two research hypotheses were addressed. First, we hypothesized that spatial variation across the wetland in CH_4 and CO_2 fluxes is directly but oppositely related to hydrologic regime, as modified by soil organic matter and temperature. We addressed this hypothesis by a series of measurements for up to 15 months of CH_4 and CO_2 fluxes across a spatial gradient of soil moisture, redox potential, and organic matter content. Second, we hypothesized that emergent vascular plants can increase methane transport from the soils to the atmosphere. We addressed this hypothesis by a series of measurements over 10 months of CH_4 transport from chambers enclosing and excluding the wetland vascular plants: *Hydrocotyle umbellata* and *Festuca obtusa*. Our results are compared with the studies of CH_4 and CO_2 fluxes obtained from other forested freshwater wetlands in the southeastern United States.

Methods

Study site description

Clear Springs Wetland is located in a temperate forest eight miles southeast of the town of Sardis, Panola County, Mississippi, U.S.A. (34°24′ N, 89°50′ W). It is approximately 9 hectares in size. Water sources for the wetland are groundwater and rainfall, and there is no surface connection by flooding of the Tallahatchie River, which flows 0.6 km to the south. A major spring flows out of the upland hillside and spreads into the wetland. There are many other smaller springs that provide water to the wetland. The pH of standing water in the wetland is approximately 6.3.

The vegetation community consists of blackjack oak (*Quercus marilandica*), white oak (*Quercus alba*), loblolly pine (*Pinus taeda*), sweet gum (*Liquidambar styraciflua*), water tupelo (*Nyssa sylvatica*), and bald cypress (*Taxodium distichum*). Sweetspire (*Itea virginica*) and alder (*Alnus serrulata*) are the most abundant shrub species. Common herbaceous species include sedges (e.g., *Carex hyalinolepis*), water penny (*Hydrocotyle umbellata*), fescue (*Festuca obtusa)*, and duckweed (*Lemna minor*).

The standing water table of the wetland fluctuates, as it is influenced by the amount of rainfall that percolates into the aquifer and eventually determines spring flow. This results in the wetland consisting of a permanently flooded zone, an occasionally flooded zone, and a permanently non-flooded forested zone. For this study, the permanently flooded zone was subdivided into two areas for sampling: an open floating vegetation (OFV) site and an emergent vegetation (EV) site. These two sites had different standing water tables (ca. 13–25 cm, 4–6 cm, respectively). The occasionally flooded zone (standing water table <2 cm when flooded) located in the bottomland forest (BF) site was non-flooded between June and November. At a slightly higher elevation adjacent to the wetland, there was an upper forest (UF) site which never flooded, but did exhibit large variations in soil moisture content depending on the amount of rainfall. The elevation gradient between the OFV and UF sites was from 240 to approximately 245 m above sea level. These four habitats (OFV, EV, BF, and UF) were chosen to represent a range across the study area in soil water saturation, vegetation biomass, and plant community composition for examination of spatial and temporal variation in CH_4 and CO_2 flux rates (Table 1). The most distant sites, the OFV and UF sites, were separated by approximately 150 m.

Some authors distinguish between wetland “soils” and “sediments” according to the water content and associated chemical properties. For example, Fenchel et al. (1998) describe soils as having a water content of less than 50% and sediments as having a water content of 50–90% by volume. According to this definition, the OFV and EV sites could be described as wetland sediments, and the BF and UF sites as wetland soils. However, for the sake of convenience in comparison, we use the word “soils” for all four study sites.

CH_4 and CO_2 flux measurements from soil chambers

On a monthly basis from May 2005 to July 2006, soil CH_4 flux rates were measured using a static closed chamber method (Mosier, 1989). Chambers for collecting CH_4 gas were made of circular, open-bottom PVC pipes (base area 0.0182 m^2, height 0.5 m). In order to quantify CH_4 flux, three replicate chambers were inserted into the soil at each site. At each site, replicate chambers were situated across a transect with chambers located 4–5 m apart. For placement, the chambers were pushed approximately 5 cm into the soil surface. These chambers, referred to as “permanent” chambers, were kept in place throughout the study period. In order to determine whether long-term placement of chambers affected CH_4 flux

Table 1 General site characteristics of the four habitats in Clear Springs Wetland

Site name	Flooding type	Dominant vegetation
Open floating vegetation (OFV)	Permanently flooded	*Lemna minor, Brasenia shreberi*
Emergent vegetation (EV)	Permanently flooded	*Festuca obtusa, Hydrocotyle umbellata*
Bottomland forest (BF)	Occasionally flooded	*Nyssa sylvatica, Taxodium distichum*
Upper forest (UF)	Not flooded	*Quercus marilandica, Quercus alba, Pinus taeda,*

rates, we compared flux rates from the permanent chambers with chambers installed at the same four site locations on 16 dates, but on a temporary (24 h) basis.

All the gas samplings were conducted during daylight, after 11:00 A.M.. For gas collection, each chamber was sealed at the top by an airtight PVC cover into which a 1-cm diameter rubber septum was inserted for sampling. A 10-ml air-tight B-D® plastic syringe, fitted with a three-way stopcock, was inserted through the septum, and pumped several times to gently mix the headspace air prior to sampling. Gases were subsequently collected using the syringe. The collected gases were immediately transferred from the syringe through a septum into a 10-ml He-flushed glass vial. From each chamber, three gas samples were collected over a 30–40-min period at 15- or 20-min intervals (e.g., time 0, 15, and 30: time 0, 20, and 40 min).

Within 2 h after sampling, the vials were transported to the laboratory for gas analysis. Gas samples were loaded by an airtight glass syringe (0.5 ml) onto a 0.1-ml injection loop for gas chromatography (HP-6850). Methane was separated using a HP capillary molecular sieve column (50 m × 0.53 mm) at 60°C with nitrogen as a carrier gas at a flow rate of 10 ml/min. A flame-ionization detector (FID) at 200°C was used to measure CH_4. Methane concentrations were calibrated with commercial (Scott Specialty Gases, Matheson Tri-Gas) gas standards of known concentration. Emission rate was quantified based on linear changes in chamber CH_4 concentrations over time. Methane flux was defined as the net result of the anaerobic production and aerobic consumption of CH_4. Gas emission is presented by a positive flux and consumption by a negative flux.

Carbon dioxide measurements were conducted by taking gas samples from the chambers (PVC pipes), but only between November 2005 through July 2006. Carbon dioxide was separated using a HP capillary molecular sieve column (15 m × 0.53 mm) at 40°C. A thermal conductivity detector (TCD) at 200°C was used to analyze CO_2. Helium was used as the carrier gas at a flow rate of 5.5 ml/min. Gas concentrations were calibrated by comparing samples with commercial gas standards of known CO_2 concentration (Scott Specialty Gases).

In order to determine flux rates of CH_4 and CO_2, a linear regression of gas concentration with time was obtained for the three samples collected from each chamber during the period for which the chamber was closed. To be accepted as a reliable measurement of gas flux rates, the regression coefficient of determination (r^2) must exceed 0.90 (Shannon et al., 1996; Hyvönen et al., 1998). Emission rates (f) of both gases were determined as $f = (\mathrm{d}\,C/\mathrm{d}t)\ V/A$, where V is the chamber headspace volume (m^3), A is its basal area (m^2), and $\mathrm{d}C/\mathrm{d}t$ is the rate of concentration change (Livingston & Hutchinson, 1995).

Methane flux from plant chambers

Between September 2005 and July 2006, we examined the importance of the presence of emergent aquatic plants on flux rates of CH_4. The two plants tested were *Hydrocotyle umbellata and Festuca obtuse*. *Hydrocotyle umbellata* is a small umbelliferous perennial C_3 plant indigenous to the southern United States; *Festuca obtusa* is an annual C_3 grass. Both species are common in the flooded portion of the wetland.

Chambers used for these measurements were rectangular plastic boxes (area: 0.0792 m^2, height: 0.22 m). These chambers were inverted over the water surface, and either contained emergent plants or did not (control chambers). The bottom edge of each chamber was placed below the water surface, but without disturbing the soil surface. In chambers enclosing plants, only one species or the other was enclosed. In each experiment, there were three replicate chambers for each level of treatment. Chambers were installed 60 min prior to gas sampling to minimize soil disturbance and to allow for equilibrium with ambient air. Chambers were removed following the completion of sampling (e.g., St. Louis et al., 2000; Kankaala et al., 2003). Three measurements of CH_4 concentration were conducted from these chambers over a period of 30–40 min at 15- or 20-min intervals (e.g., time 0, 15, and 30: time 0, 20, and 40 min). The rate of flux was determined as described above for soil chambers.

Plant biomass and stem density of *H. umbellata* and *F. obtusa* in chambers were measured for comparison with CH_4 fluxes. Stem density (number of stem/m^2) within a chamber was measured in the field by counting plant stems above the water surface. In order to measure aboveground plant biomass, the plants were clipped at approximately 3 cm above the soil surface, placed in plastic bags, and transported to the laboratory in an ice cooler. In the laboratory, plants were washed free of sediments and detritus by rinsing with tap water, and dried at 70°C to a constant weight. In order to separate the effect of plants from other variables and to directly compare wetland plant species for their role in CH_4 emission, we calculated the ratio of CH_4 emission to aboveground plant biomass for each plant species at each sampling time (Kankaala et al., 2005). For this calculation, we subtracted the rate of CH_4 flux from control chambers (chambers without plants) from the rate of CH_4 flux in chambers containing plants. This control-adjusted flux rate was then divided by plant biomass to give the Efflux:Biomass, or Eff:B, ratio (mg CH_4/gram/h). The Eff:B ratio is a measure of CH_4 emission from a plant species relative to aboveground biomass of the species (Kankaala et al., 2005).

Soil properties

The upland soil type at Clear Springs Wetland is classified as Waverly Silt Loam (USDA, 1963). Soil properties were measured concurrently with gas sampling. Temperatures (°C) and redox potential at a depth of 5 cm were measured with a digital thermometer (Digi-thermo®, Fisher Sci.) and a portable redox meter (Orion 280®, Orion platinum electrode, Thermo Electron Corp.), respectively. Surface samples collected to a depth of 5 cm were brought to the laboratory in an ice cooler for analysis of moisture content and organic matter content. Soil moisture content was measured with soils collected only from the BF (occasionally flooded) and UF (non-flooded) sites. Soil moisture content is expressed as percent of water by dry weight, or gravimetric moisture content. It was calculated as $(W - D/D) \times 100$, where W is the wet mass of the soil, and D is the dry mass after the removal of evaporable water content (Weight & Sonderegger, 2001). Evaporable water content was determined by the weight difference after drying at 70°C to a constant weight. Organic matter content of soils was determined by loss of dry soil mass on ignition in a muffle furnace at 500°C for 24 h (percentage loss on ignition).

Statistical analyses

Relationships between CH_4 and CO_2 flux rates and soil properties were tested with univariate and multivariate regression analyses. Univariate tests were conducted to analyze the relationships of gas flux and individual soil properties. A multiple regression model was used for analysis of gas flux and the combined effect of the five selected soil properties. Akaike's Information Criterion (AIC) was used to determine the best multiple regression model for prediction of CH_4 and CO_2 fluxes. A t-test was conducted to examine whether adjusted Eff:B ratios were different between the two plant species. Results are considered significant at $P \leq 0.05$.

Results

Meteorological conditions and soil properties

In May 2005–July 2006, the study area had an annual mean air temperature of 17.8°C, and annual precipitation of 1360 mm. Monthly mean air temperatures varied between 5.6°C (December 2005) and 28.7°C (July 2005). Monthly mean precipitation was 119 mm, ranging between 74 mm (August 2005) and 155 mm (March 2005) [US Army Corps of Engineers (Vicksburg, Mississippi), unpublished data].

Soil temperature exhibited a distinctive seasonal pattern, ranging from a wetland mean of 4.6°C (December 2005) to 26.6°C (July 2005), with little difference between habitats throughout the year. There was a gradient of soil redox potential from the OFV site to the UF site. The UF site always had the highest monthly mean redox potential among the four habitats, whereas the OFV site always had the lowest potential, reflecting the anoxic environment. There were distinct differences in the gravimetric soil moisture content between the BF and UF sites at all times when both sites were not flooded. The BF site was flooded between December 2005 and May 2006. Organic matter content exhibited the opposite spatial pattern of redox potential, generally decreasing from the OFV to the UF site (Table 2).

Methane flux from soils

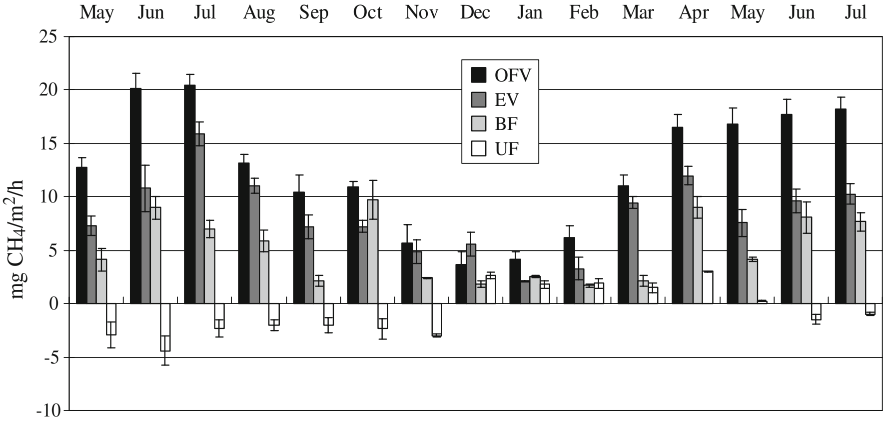
Monthly mean CH_4 flux rates, including consumption rates, ranged from −4.39 mg $CH_4/m^2/h$ at the UF site in June 2005 to 20.43 mg $CH_4/m^2/h$ at the OFV site in July 2005 (Fig. 1). There were clear spatial and seasonal patterns in CH_4 flux rates across the wetland during the 15-month sampling period. On almost

Table 2 Mean values and range for soil characteristics during study period (May 2005–July 2006)

	Temperature (°C)	Soil redox (mV)	Gravimetric soil moisture content (%)	Soil organic matter content (%)
Open floating vegetation (OFV)	16.7 [4.9 to 24.1]	−179.8 [−230.0 to −99.5]	Flooding	49.0 [27.7 to 85.0]
Emergent vegetation (EV)	18.4 [6.2 to 26.6]	−25.0 [−51.0 to −3.0]	Flooding	39.4 [19.8 to 57.9]
Bottomland forest (BF)	16.8 [4.6 to 24.0]	133.6 [68.4 to 187.5]	316.5 [212.1 to 446.6]	29.6 [24.0 to 47.0]
Upper forest (UF)	17.0 [7.8 to 23.5]	309.8 [272.6 to 342.7]	48.8 [18.2 to 93.4]	12.1 [4.8 to 19.0]

[] Indicates the range

Fig. 1 CH_4 emission rates (mg $CH_4/m^2/h$) from the four habitats in Clear Springs wetland (May 2005–July 2006) (Mean and Standard Error, $n = 3$)



every sampling date, the highest emission rates occurred at the permanently flooded OFV site, followed in decreasing order from the EV site, the BF site, and the UF site. Except for the UF site, CH_4 emission rates followed the pattern of change in soil temperature.

Methane consumption (mean: −2.38 mg $CH_4/m^2/h$) due to oxidation at the soil surface occurred only at the UF site in dry months (May–November 2005, June–July 2006). CH_4 was consumed at rates between 0.6 and 3.13 mg $CH_4/m^2/h$. The difference in CH_4 flux rates between permanently placed chambers and temporarily placed chambers ($n = 16$) was not significant (mean = ±0.80 (SE = 0.11) mg $CH_4/m^2/h$, $t = -0.07$, $P = 0.94$), indicating that long-term placement of the chambers had little or no effect on soil methane flux rates.

Relationships between CH_4 flux and soil properties were best described by regression analysis when the gas fluxes were divided into the three zones: the permanently flooded zone (OFV and EV sites), the occasionally flooded zone (BF), and the non-flooded zone (UF). In general, warmer and wetter soil conditions led to higher flux rates of CH_4. In the permanently flooded zone, there was a strong exponential relationship between CH_4 flux rate and soil temperature (Fig. 2A). However, in the occasionally flooded site, the relationship between emission rate and soil temperature was weak (Fig. 2B), because in non-flooding months, soil temperature was not correlated with CH_4 flux rates. There was no significant correlation between CH_4 emission or consumption rates and soil temperatures in the non-flooded UF site.

Soil moisture content was positively related to CH_4 flux rate in the two regions of the non-flooded area (i.e., the drained bottomland forest and upper-elevation forest sites) (Fig. 2C). Results were clearly separated into two groups. Below 54% gravimetric soil moisture, CH_4 was consumed (mean: −3.32 mg $CH_4/m^2/h$) at the UF site. High soil moisture content in the flooded months (December to April) (mean gravimetric soil moisture content: 74%), however, converted the site from a sink to a source of CH_4 to the atmosphere. A negative correlation between soil redox potential and CH_4 flux rate indirectly indicates the importance of water content on CH_4 flux, since water content influences the redox potential by

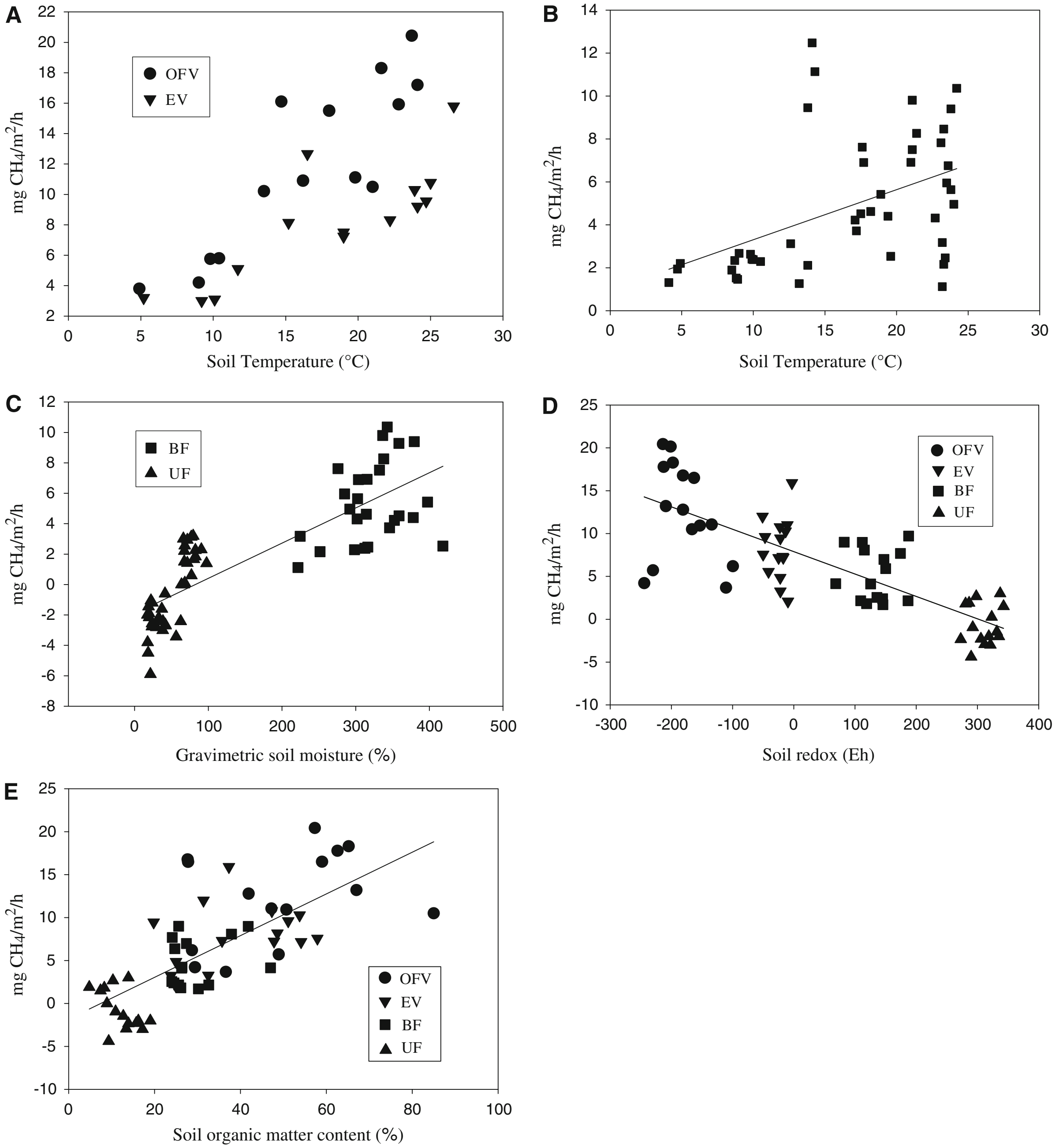


Fig. 2 Relationships between CH_4 emission and habitat variables. **A** Relationship with soil temperature in the two regions of the permanently flooded zone ($y = 2.65\ e^{0.07x}$, $r^2 = 0.62$, $P < 0.001$). **B** Relationship with soil temperature in the occasionally flooded zone (i.e., bottomland forest site) ($y = 0.19x + 1.39$, $r^2 = 0.16$, $P < 0.001$). **C** Relationship with gravimetric soil moisture content in the non-flooded zone ($y = 0.02x - 1.93$, $r^2 = 0.71$, $P < 0.0001$): BF and UF sites. **D** Relationship with soil redox potential (mV) from the four habitats ($y = -0.03x + 7.88$, $r^2 = 0.62$, $P < 0.0001$). **E** Relationship with soil organic matter content (percent loss on ignition) from the four habitats ($y = 0.24x - 1.83$, $r^2 = 0.51$, $P < 0.0001$)

reducing oxygen diffusion (Fig. 2D). Above a redox potential of about 300 mV, the soils consumed methane from the atmosphere.

CH_4 flux rates were positively correlated with soil organic matter content (Fig. 2E). The highest rates of flux occurred in the permanently flooded zone (i.e., OFV and EV sites) where soil organic matter content was highest, and the lowest flux rates occurred in the UF site where organic matter content, as well as gravimetric soil moisture, was the least.

Methane efflux from plants

Variation in CH_4 flux rates was affected by the presence of plants. The control-adjusted Eff:B ratios were positive for all sampling months of the growing season (March–September) for both plant species, indicating that the plants contributed to enhanced methane fluxes (Fig. 3). Only in late fall and winter (October–January) did the plant-free chambers exhibit higher CH_4 fluxes, resulting in negative Eff:B ratios. However, Eff:B ratios were significantly different ($P < 0.001$) between the two species (*H. umbellata*: mean = 0.67, range: −2.0 to 3.7; *F. obtusa*: mean = 1.71, range = −4.2 to 5.6), indicating that the two different species might have different capabilities to transport gaseous CH_4 through their vascular tissues, or different effects on soil methanogenic activity, or both. There were positive correlations between CH_4 emission rates and aboveground plant biomass and stem density of both species, except during the fall and winter months (Figs. 4A, B and 5A, B). In order to isolate the effect of temperature versus plant biomass or stem density on CH_4 emission, the relationships for both plant types were examined by multiple regression. For neither multiple regression was the temperature effect significant ($P > 0.1$).

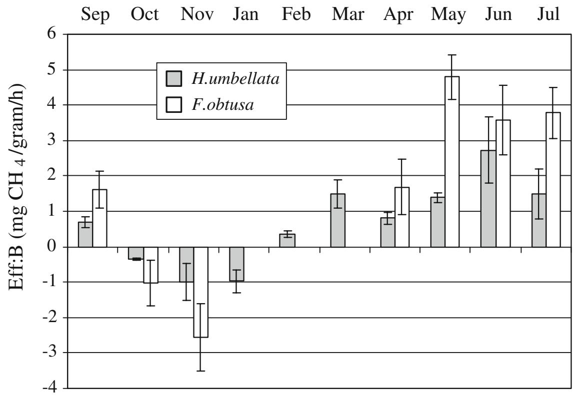


Fig. 3 Control-adjusted Eff:B ratios (mg CH_4/gram/h) from chambers enclosing plants (*Hydrocotyle umbellata* and *Festuca obtusa*) (September 2005–July 2006) (Mean and Standard Error, $n = 3$)

Carbon dioxide flux from soils

Carbon dioxide emission rates ranged from 67 to 933 mg $CO_2/m^2/h$ (Fig. 6) across the wetland, and followed a reverse pattern by location from the CH_4 flux. The highest emission rates were observed in the UF site in June and July, and the lowest rates in the OFV site in mid-winter. Carbon dioxide emission rates ranged between 180 and 908 mg $CO_2/m^2/h$ in the non-flooded zone (BF and UF sites). Following 6 months of flooding, there were high emission rates of CO_2 in the BF site in June and July 2006, which were correlated with relatively low gravimetric soil moisture content. In the permanently flooded zone, CO_2 emission rates were much lower than those in the BF and UF sites, ranging from 67 to 472 mg $CO_2/m^2/h$. On average, the aerobic forest soils had three- to fourfold higher CO_2 emission rates than those of the flooded soils.

In the non-flooded soils, there was a strong seasonal pattern in CO_2 emission. From November through February, when soil temperatures were at a minimum, rates of CO_2 emission were also at a minimum. The correlation of soil temperature and CO_2 emission was strong in the non-flooded zone (Fig. 7), but weak in the flooded sites (OFV and EV sites and flooded BF site). There was no correlation between CO_2 emission and soil organic matter content.

Predictive models of CH_4 and CO_2 fluxes

Using Akaike's information criterion (AIC) we determined that the best multiple regression models for CH_4 and CO_2 fluxes from the wetland soils include temperature, redox potential, and the interaction of temperature and soil redox potential. Gravimetric soil moisture content, redox potential, and organic matter content are closely related to each other as each of them are influenced by hydrologic regime. Inclusion of organic matter content did not improve the model, and soil moisture content was not measured for the

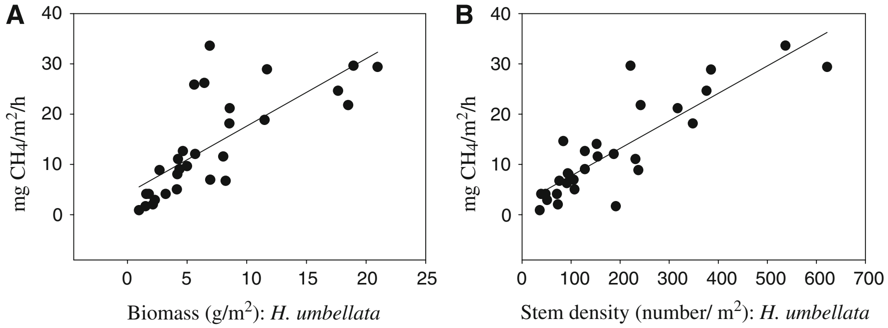


Fig. 4 Relationships between CH_4 emission rates and (**A**) aboveground biomass ($y = 1.34x + 4.21$, $r^2 = 0.56$, $P < 0.01$) and (**B**) stem density ($y = 0.05x + 3.73$, $r^2 = 0.78$, $P < 0.01$) (September 2005, February–July 2006): *Hydrocotyle umbellata*

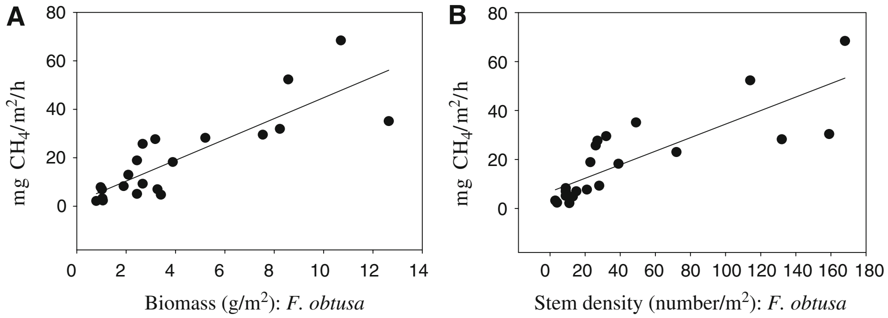


Fig. 5 Relationships between CH_4 emission rates and (**A**) aboveground biomass ($y = 4.30x + 1.77$, $r^2 = 0.71$, $P < 0.01$)) and (**B**) stem density ($y = 0.28x + 6.79$, $r^2 = 0.67$, $P < 0.01$) (September 2005, April–July 2006): *Festuca obtusa*

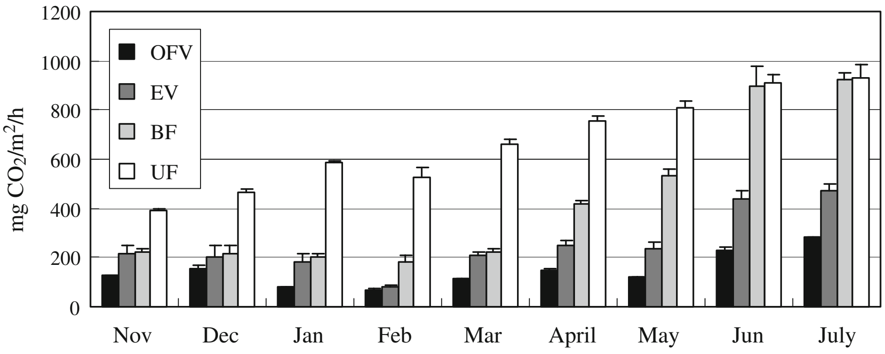


Fig. 6 CO_2 emission rates (mg $CO_2/m^2/h$) from the four habitats (November 2005–July 2006) (Mean and Standard Error, $n = 3$)

flooded sites. The models were able to explain 65% and 73% of the variation in CH_4 and CO_2 flux rates, respectively.

CH_4 flux rate (mg/m^2/h) = 1.234 + 0.393(temp) + 0.006(Eh) − 0.002 (temp * Eh) ($r^2 = 0.65$, $F_{(3,\ 179)} = 107$, $P < 0.001$) (Table 3A).

CO_2 flux rate (mg/m^2/h) = −1.743 + 21.65 (temp) + 0.282(Eh) − 0.049 (temp * Eh) ($r^2 = 0.73$, $F_{(3,\ 99)} = 89$, $P < 0.001$) (Table 3B).

The relative importance of CO_2 and CH_4 in wetland carbon gas flux at the four sample sites was examined from the molar ratios of emission rates (Table 4). The molar ratios (CO_2:CH_4) of emission rates were highest at the UF site, whereas the OFV site had the lowest ratios. These results reflect differences in aerobic versus anaerobic respiration across the four sites. Where the soils were aerobic, much more CO_2 was produced and little or no CH_4 was produced compared with flooded anoxic soils.

Discussion

Methane flux from soils

Forested wetlands are a substantial source of methane, although when the water level drops during dry summer periods and the soils become dry and oxic,

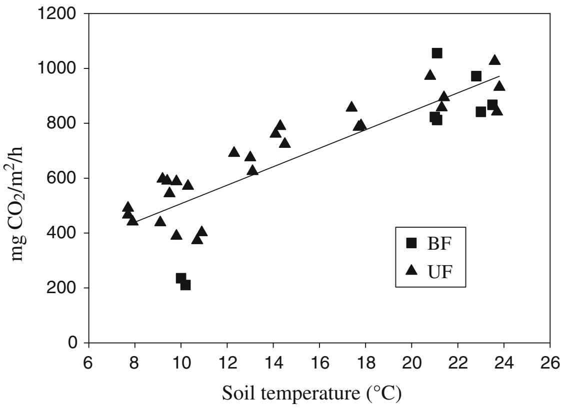


Fig. 7 Relationship between CO_2 emission rates (mg CO_2/m^2/h) and soil temperature in the non-flooded zone (BF and UF sites) ($r^2 = 0.75$, $P < 0.001$). Line shows simple linear regression of emission rate versus soil temperature

Table 3 Stepwise multiple regression models for (A) CH_4 and (B) CO_2 fluxes from Clear Springs Wetland

Term	*F*	*P*-value	Beta coefficient
(A)			
Temperature	61.8	<0.0001	0.372
Eh	1.59	0.21	0.181
Temp * Eh (mV)	41.1	<0.0001	−0.92
(B)			
Temperature	68	<0.0001	0.45
Eh	1.63	0.2	0.19
Temp * Eh (mV)	11.85	<0.0001	0.51

these wetlands may become a sink, rather than a source of atmospheric CH_4 (Bartlett & Harriss, 1993). The mean CH_4 flux rate of this spring-fed forested wetland was higher than that reported for forested freshwater wetlands in other studies conducted in the southeastern United States, although the range in flux rates was broader than that at these other locations (Table 5). The lower mean flux rates reported in other southeastern U.S. forested wetlands may be attributable to low organic matter content, low water levels and less soil inundation, and/or the influence of river flow. Soils at the Four Holes Swamp (S. Carolina) are sandy with a thin layer of organic matter (Harriss & Sebacher, 1981). In the Dismal Swamp, water levels were well below the soil surface over the summer intensive sampling period (Harriss et al., 1982). A third possible explanation for lower flux rates is that Four Holes Swamp and the Ogeechee Floodplain Wetlands are river floodplain wetlands. Well-mixed and oxygen-saturated river water flooding the wetlands may impact CH_4 emission by increasing levels of oxygen in over-lying water (Pulliam, 1993). This could hamper methanogenesis and/or cause CH_4 oxidation in the wetland soil surface.

Methane flux rate was significantly correlated to soil temperature. High soil temperature in summer might facilitate CH_4 production by increasing not only the activity of methanogens but also that of other bacteria that produce substrates for methanogens (syntrophic H_2-producing bacteria, or acetogenic bacteria). The relationship between emission rates and soil temperature fit better with an exponential regression than a linear regression, especially in the flooded zone. Otter & Scholes (2000) also observed an exponential relationship of temperature with CH_4 emission rate in a floodplain wetland of South Africa. However, an exponential relationship of CH_4 emission and soil temperature does not appear to be an inherent characteristic of methanogenesis. For instance, in laboratory studies where other factors were controlled, there was a linear response of methane production to soil temperature (Kelly & Chynoweth, 1981; Moore & Dalva, 1993). Hence, the exponential response observed in field studies may

Table 4 Molar ratios (CO_2:CH_4) of emission from the four habitats in Clear Springs Wetland (November 2005–July 2006)

	N	D	J	F	M	A	M	J	J
Open floating vegetation (OFV)	10 [2]	16 [3]	10 [2]	4 [0]	4 [1]	3 [0]	3 [0]	5 [1]	6 [0]
Emergent vegetation (EV)	16 [0]	22 [5]	34 [9]	10 [1]	8 [1]	7 [1]	13 [4]	17 [3]	17 [1]
Bottomland forest (BF)	32 [0]	38 [9]	29 [3]	42 [10]	45 [14]	14 [1]	77 [4]	44 [3]	44 [4]
Upper forest (UF)	[a]	65 [8]	136 [10]	140 [25]	214 [85]	92 [1]	597 [26]	[a]	[a]

Mean [Standard Error], $n = 3$

[a] Methane consumption

Table 5 Soil CH_4 flux rates (mg $CH_4/m^2/h$) from southeastern U.S. forested freshwater wetlands

Wetland	Mean	Range	Time period	Reference
Four Holes Swamp (S. Carolina)	0.41	0.34 to 0.90	ND	Harriss & Sebacher (1981)
Great Dismal Swamp (Virginia)	ND	−0.02 to 6.30	Sep. 1978–Feb. 1981	Harriss et al. (1982)
Ogeechee Floodplain Wetland (Georgia)	1.20	−0.77 to 14.23	Jul. 1987–Sep. 1989	Pulliam (1993)
Clear Springs Wetland (Mississippi)	5.85	−4.39 to 20.43	May 2005–Jun. 2006	This study

ND: No data

arise from the interaction effects of soil temperature, flooding, or other factors that influence methanogenesis and methanotrophy. In addition, seasonal changes in microbial community structure and/or supply, and composition of organic matter from growing plants, may contribute to a non-linear response of CH_4 flux and temperature (Wilson et al., 1989; Joabsson & Christensen, 2001).

In the non-flooded months (June–November), the upper forest site consumed atmospheric CH_4 at the mean rate of 2.71 mg $CH_4/m^2/h$. Similarly, Wickland et al. (1999) found that unsaturated areas at the boundary of a riparian wetland emitted much less CH_4 than in the flooded area, or consumed atmospheric CH_4. Methane consumption due to oxidation in aerated soils has been reported to be significant in the global budget of methane (Reeburgh et al., 1994). Forty percent of the global CH_4 consumption occurs in dry and warm soils in wetlands, forests, grasslands, and agricultural lands (Flessa et al., 1995; Potter et al., 1996; Dong et al., 1998; Nakano et al., 2004). The degree of soil moisture can affect CH_4 emission by altering oxygen diffusion and availability, shifting the balance from oxidation toward CH_4 production, as microsites become saturated and anoxic (Adamsen & King, 1993; Czepiel et al., 1995). In this study, the switch between CH_4 consumption and production in the UF site occurred where gravimetric soil moisture was between 54% and 67%.

There were no significant relationships between CH_4 consumption rates and soil temperature and organic matter content. The reason for this may be that CH_4 consumption occurred only in summer dry months when variations in soil temperature and organic matter content were very little. In addition, methanotrophy seems to be less sensitive to soil temperature than methanogenesis. King & Adamsen (1992) have reported that methanotrophy by soil cores from a temperate forest did not vary much between −1 and 30°C. Castro et al. (1995) found in Massachusetts forests that methane consumption rates varied between −5 and 10°C, but were not affected between 10 and 20°C. Sitaula et al. (1995) observed that significant CH_4 consumption was still found in a Norway forest even at temperatures lower than 1°C.

Influence of aquatic vascular plants on methane flux

In order to properly assess total CH_4 emission from a wetland, the role of aquatic vascular plants must be considered. Aquatic vascular plants contribute to CH_4 emission by supply of substrates from plants to methanogens in the soil, and by providing a transport route for CH_4 from the anoxic soils to the atmosphere via aerenchymal tissues (e.g., Chimel, 1995; Kelker & Chanton, 1997; Yu et al., 1997; King et al., 1998; Van der Nat & Middelburg, 1998). However, the effects of aquatic vascular plants on methane emission rates could be variable depending on the season. We hypothesize that seasonal variation in CH_4 emission rates from the plants used in this study was affected by the seasonal difference in physiological activities of soil microorganisms and plants. Most aquatic plants undergo optimum growth under conditions of warm temperature. Similarly, the decomposition rate of organic matter by microorganisms increases with temperature. In fall and winter (October, November, and January) when the temperature dropped, plant-free chambers had slightly higher rates of CH_4 emission than chambers containing either aquatic plant (*Hydrocotyle umbellata* and *Festuca obtusa*), suggesting that these plants may not serve as a conduit of CH_4 transport from sediment to atmosphere throughout the year. Alternatively, winter temperatures may limit the production of root exudates as substrates for methanogenic bacteria, as well as microbial activities that contribute to the production of substrates used for methanogenesis. Another explanation is that during winter, when water levels increase, more of the vascular tissues of emergent plants become submerged and die, reducing gas release (Chanton et al., 1993).

In this study, we found empirical strong positive correlations at the EV site of plant biomass and stem density with CH_4 flux, at least during the growing season. Positive relationships between aboveground plant biomass and CH_4 emission have been reported for wetlands across a wide latitudinal range (Whiting & Chanton, 1993; Bellisario et al., 1999; Joabsson & Christensen, 2001). With more plant biomass, there would be more pathways for CH_4 emission and substrates for methanogenesis.

The magnitude of the contribution of aquatic vascular biomass to CH_4 emission is also influenced by plant species (Van der Nat & Middelburg, 1998). Since the two species compared in this study were under similar environmental condition in the wetland, Eff:B ratios were hypothesized to vary primarily due to morphological and/or physiological properties of the plants. The ratio of CH_4 emission rate to plant biomass (Eff:B) was, on average, 2.6 times as high in *Festuca obtusa* as *in Hydrocotyle umbellata in* the growing months. This suggests that *F. obtusa* is higher in its efficiency as a gas conduit compared with *H. umbellata*. Roots of *H. umbellata* are coarse, short, and shallow rooted. In addition, many fibrous roots of *H. umbellata* emerge from the stems at the nodes, which hang free in the water column, possibly reducing the effectiveness of these roots in transporting gaseous CH_4 from anoxic sediments to the atmosphere. Although the packed cells of the grass species (*F. obtusa*) is thought to restrict the transfer of gases due to smaller intercellular spaces, this plant has a much deeper root system than *H. umbellata* (Sebacher et al., 1985), possibly reducing rhizosphere oxidation and enhancing methane transport through the vascular system. Also, vascular plant species with shallow, coarse root systems generally do not have well-developed aerenchyma in rhizomes, roots, and leaves compared to species with roots penetrating deeper into anoxic horizons (Malmer et al., 1994).

Soil differences also will affect the Eff:B ratio. For example, Kankaala et al. (2004) found lower Eff:B ratios in *Phragmites australis* stands compared to *Equisetum fluviatle* stands in a sub-arctic bog, which they attributed to spatial variation in soil types. *P. australis* stands were found mostly in a sandy bottom, whereas *E. fluviatle*-dominated areas had higher soil organic matter concentrations derived from deposition of detritus by river flooding.

Future studies could focus on estimating oxidation rates of CH_4 in the vegetation rhizosphere. Oxygen transported by aerenchymal tissue from the air to rhizomes supports CH_4 oxidation in wetland soils. Methane-oxidizing bacteria have been found to exist in the rhizosphere of various emergent vascular plants, and the oxidation rates differ among species (King, 1996; Lombardi et al., 1997; Kankaala et al., 2004). Quantifying oxidation rates would help us improve our ability to explain the mechanisms of a given vascular species in transporting CH_4 gas, and to accurately determine to what extent plant-mediated CH_4 emission is due to variation in soil properties, meteorological conditions, and plant physiology.

Carbon dioxide flux from soils

Few in situ CO_2 flux data exist for southeastern U.S. forested freshwater wetlands (Table 6). The amount of CO_2 released to the atmosphere hourly in this study was in good agreement with the range reported in a gum swamp in North Carolina (Bridgham & Richardson, 1992), but somewhat higher than that in an Ogeechee river floodplain forested wetland in Georgia (Pulliam, 1993). As mentioned above, the sediments of the river floodplain wetland are sandy with a low organic matter content, conditions which probably reduced soil respiration compared to this study. Although microbial respiration increases with temperature up to a point, effects of soil temperature on soil respiration are not always straightforward as shown in this and some previous studies (Nadelhoffer et al., 1991; Binkley et al., 1994; Davidson et al., 1998). For example, Kutsch & Kappen (1997) and Malhi et al. (1998) found a poor relationship between soil CO_2 emission and soil temperature in dry seasons in an Amazon rain forest and in a temperate agricultural land, respectively. In both locations, both plant and soil microbes were water-stressed due to very low soil water content.

Soil microbial activity is reduced when water content is too low or too high (Fenchel et al., 1998). If water content is too low, then microbial activity may

Table 6 Soil CO_2 flux rates (mg $CO_2/m^2/h$) from southeastern U.S. forested freshwater wetlands

Wetland	Mean	Range	Time period	Reference
Gum Swamp (N.Carolina)	455	100 to 917	Mar.–Dec. 1990	Bridgham and Richardson (1992)
Ogeechee Floodplain Wetland (Georgia)	192	30 to 253	Jul. 1987–Sep. 1989	Pulliam (1993)
Clear Springs Wetland (Mississippi)	350	67 to 908	Nov. 2005–Jun. 2006	This study

become limited by diffusion rate of dissolved nutrients and organic substrates. If water content is too high, then microbial respiratory activity may become limited by the rate of oxygen diffusion. In this study, soil moisture at the continuously non-flooded upper-elevation forest site, where CO_2 emission was highest, varied between 21% and 97% (mean 57% of dry soil mass). The linear response of CO_2 emission to soil temperature at this site suggests that microbial activity at this site was not limited by either substrate availability, oxygen availability, or water stress (Oechel et al., 1998). In contrast, in neither of the flooded sites, nor in the bottomland forest site when flooded (mean gravimetric soil moisture content = 325% of dry soil mass), was the correlation between soil temperature and CO_2 emission rate significant.

The range in the ratio of CO_2 production in non-flooded compared to flooded sites was 3–4. Although CO_2 is also produced by anaerobic metabolism, it is produced at a greater rate where oxygen is available (Kristensen et al., 1995). Bridgham and Richardson (1992) found in peat soil samples collected in a pocosin and gum swamp that aerobic microbial CO_2 respiration was 2.5–2.9 times the rate of anaerobic CO_2 respiration. Glatzel et al. (2004) found ratios between aerobic and anaerobic CO_2 production of Quebec bog soil samples ranging from 1.8 to 9.3, with a mean of 4.3.

The molar ratios of CO_2 to CH_4 emission rates are not only a function of hydrologic condition (i.e., flooding regime), but also are influenced by inherent physicochemical properties of the wetland soils. For example, Moore & Knowles (1989) found that in flooded sites of a sub-arctic region, molar ratios of CO_2 to CH_4 were low, averaging 173 for bog soil samples, but more than 20,000 in non-flooded soil samples. In this study, in contrast, the mean molar ratio for the entire study period was 19 in the flooded zone, and the highest value found was 597 in the non-flooded upland forest site. A bog is a still-water wetland with no underground spring of fresh water to feed it. Although bog soils are very low in oxygen, which might favor methanogens, the habitat is extremely acidic. Methane production is optimal around a pH of neutrality or under slightly acidic conditions (Garcia et al., 2000). A higher CO_2:CH_4 ratio in the flooded part of the bog is attributable to low emission of CH_4 from acidic soils. In the non-flooded part of the bog, CO_2 emission rates ranged from 275 to 392 mg $CO_2/m^2/h$, which is lower than those in this study, but CH_4 emission rates were negligible (Moore & Knowles, 1989).

Some of the CO_2 or CH_4 measured in the submerged portions of Clear Springs Wetland may derive from allochthonous (e.g., groundwater), rather than autochthonous sources (in situ chemotrophy and methanogenesis). The direct assessment of the importance of allochthonous sources would require a detailed analysis of the hydrological budget of the wetland, and of spring-water chemistry. To our knowledge, however, none of our sample sites were located in proximity to seeps, and given the clear relationships of wetland soil properties to gas fluxes, it can be inferred that CO_2 and CH_4 fluxes from these sites are primarily, and possible entirely from biological metabolism internal to the wetland. In multiple regression analysis, soil temperature and soil redox potential were the most important factors explaining microbial gas emission. Some of the unaccounted variance in the multiple regressions may be a consequence of soil properties being measured outside the chambers, rather than within the chambers where the gases were collected. In addition, unmeasured properties of the soil environment, such as soil fertility (N and P content), soil structure, and macro-biological activity, could affect the rate at which these gases were produced (MacDonald et al., 1999; Gulledge & Schimel, 2000).

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